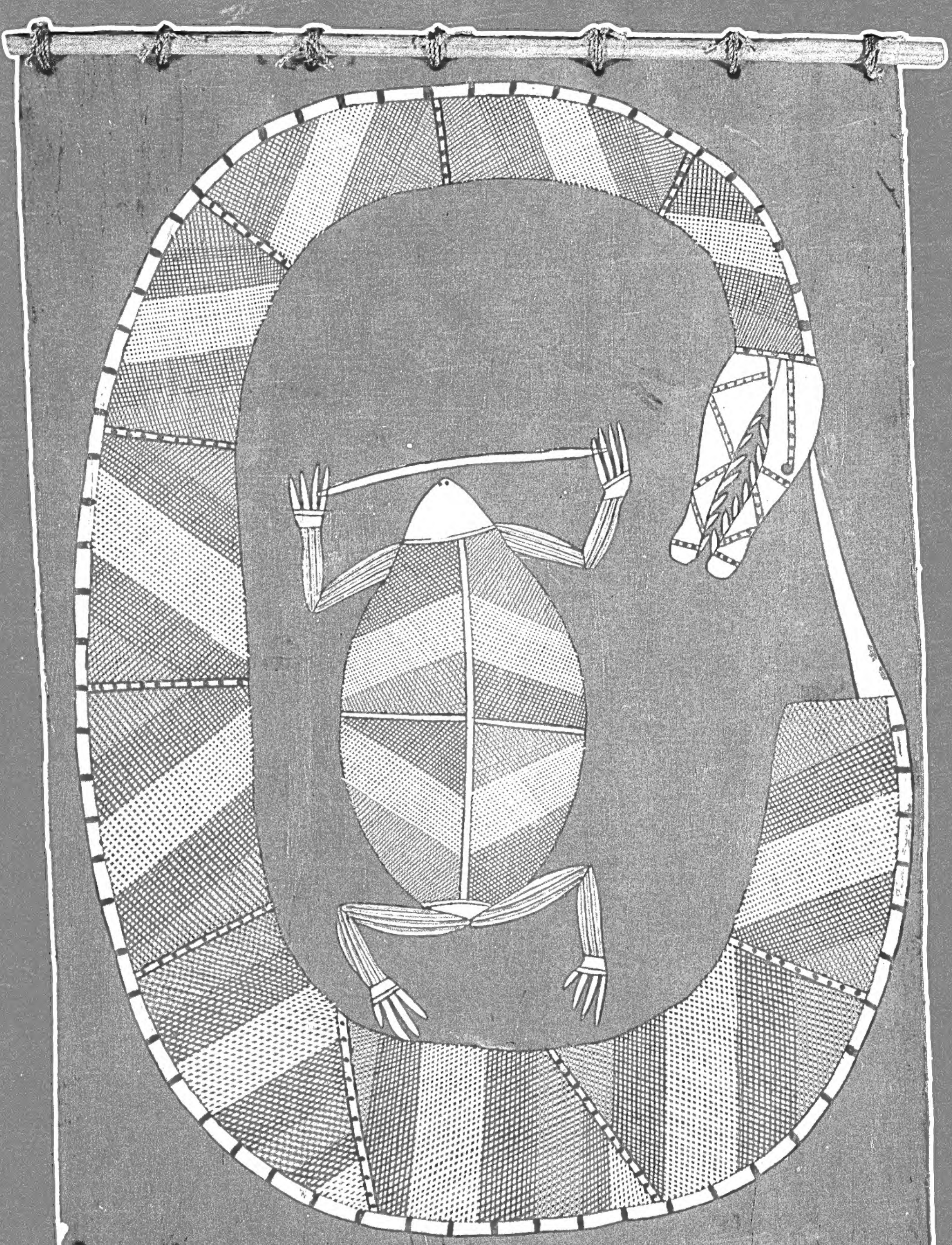
AUSTRALIA

FAUNA of AUSTRALIA

VOLUME 2A AMPHIBIA & REPTILIA



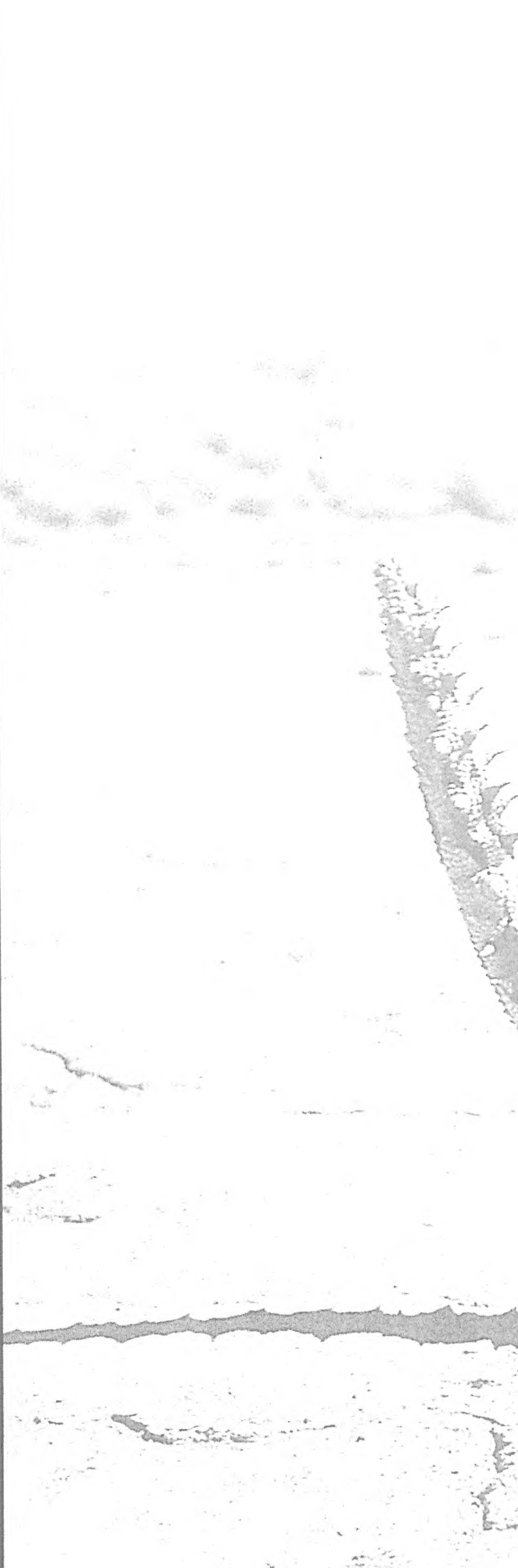
David Milaybuma (ca. 1935 –)
Kuninjku (Eastern Kunwinjku)
Barrihdjowkkeng and Marrkolidjban, Man and Liverpool
Rivers District, Arnhem Land
Djaddi and Ngalyod
(Frog and Rainbow Serpent)
Ochres on *Eucalyptus tetradonta* bark June 1993, 74.5 × 52 cm
Collection: Australian Nature Conservation Agency

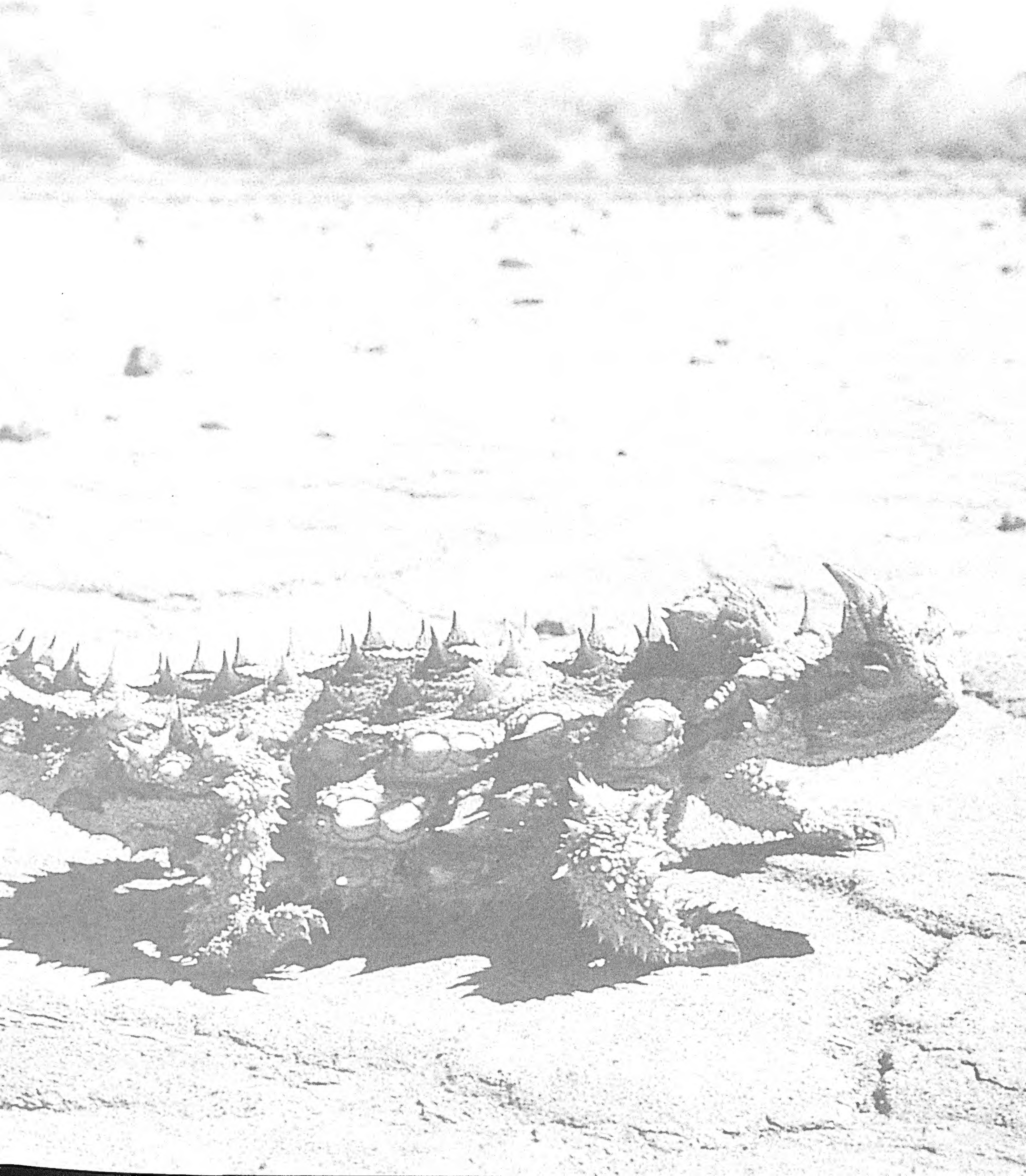
The artist has painted Djaddi (frog) and Ngalyod (rainbow serpent) from a sacred site called *Bolkdjamo* in *Marrin* clan estate near the Liverpool River south of Maningrida. The frog creation ancestor carried a ceremonial stick upon which a number of frogs would sit in a line as they do today. The frog and rainbow serpent are linked through their association with water. The serpent is attributed with the creation of fresh water springs, soaks and billabongs which frogs inhabit.

The frog ancestor, which travelled the country in the form of a human, became entangled by the rainbow serpent and was submerged by the snake at the site *Bolkdjamo* where he took the form of a frog. Numerous rock paintings of frogs and rainbow serpents also appear in this area. This image by the artist is in keeping with the style of these rock paintings except for the addition on bark of cross hatching.

The frog is the artist's personal 'dreaming' and is celebrated as a yirridjdja moiety totem in the great regional cult ceremony *Yabbadurruwa*, which is performed still over several months almost every year.

Frogs have a special religious significance for Aboriginal people in northern Australia. Frogs are never used as food, and they are regarded as special because of the ability of some species to 'die' and lie buried in the ground until they 'come back to life' suddenly with the arrival of the wet season. This apparent ability to defy death is also a feature of the snake which sheds its skin and is 'reborn' with a new body. For this reason, too, Milaybuma often paints the two reptiles together. Frogs are also associated with the rainbow serpent because of their loud calls during the wet season. The fall of rain and the arrival of the wet season is attributed to the rainbow serpent and frogs are believed to herald this activity of the great snake.





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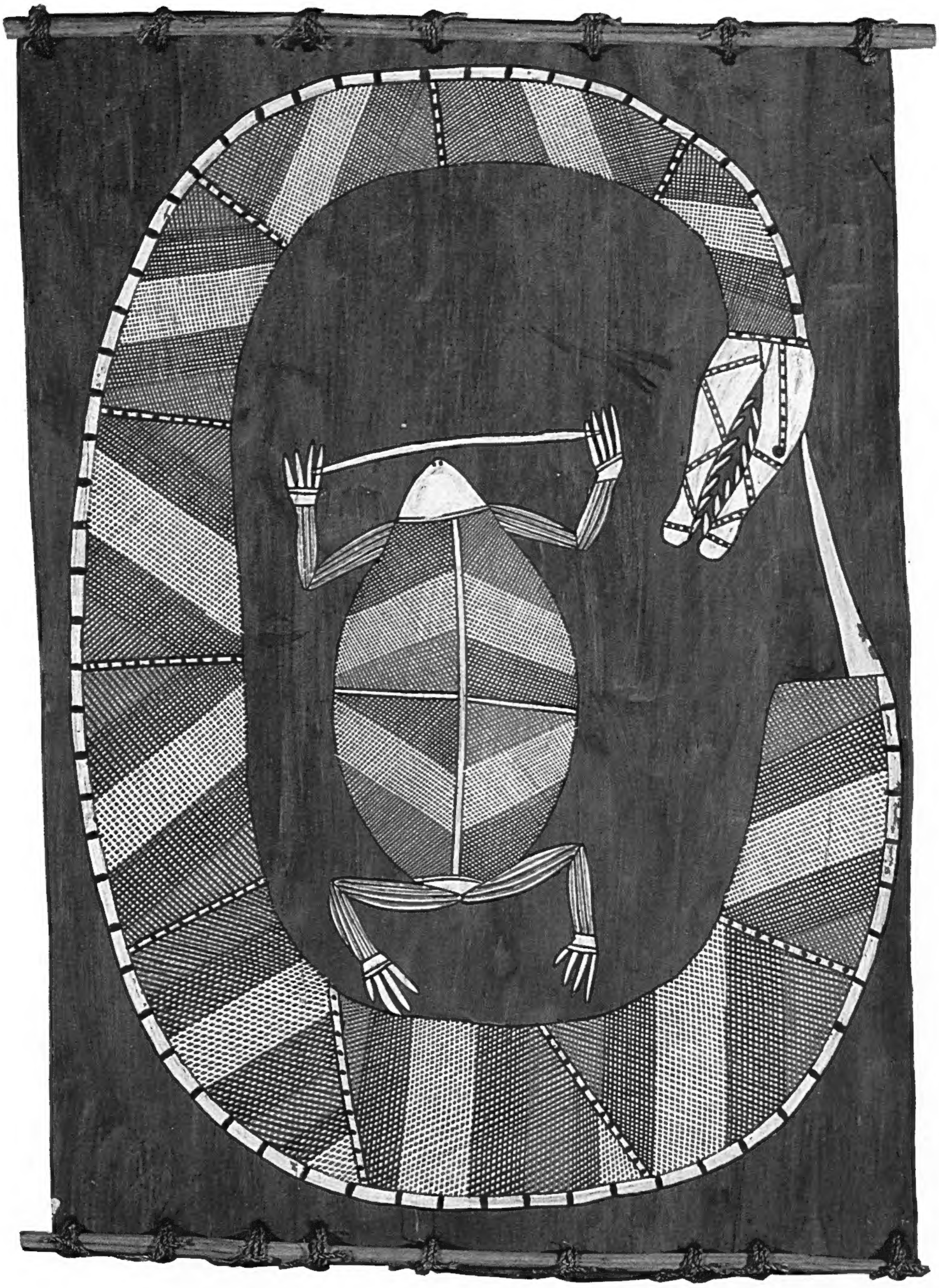

David Milaybuma (ca. 1935 –); Kuninjku (Eastern Kunwinjku); Barrihdjowkkeng and Marrkolidjban, Man and Liverpool Rivers District, Arnhem Land; **Djaddi and Ngalyod** (Frog and Rainbow Serpent); Ochres on *Eucalyptus tetradonta* bark June 1993, 74.5 × 52 cm; Collection: Australian Nature Conservation Agency

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Australian Biological Resources Study, Canberra

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VOLUME 2A
AMPHIBIA & REPTILIA

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Endpapers: the agamid *Moloch horridus* is endemic to arid regions of western and central Australia. [Photo by Paul Scott/Auscape International]

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PREFACE

The amphibians and reptilians of Australia together comprise some 940 species, or nearly half of all Australian vertebrate species excluding fishes. By world standards, the Australian herpetofauna is not diverse, at least not at the family level. Of the 24 anuran families recognised, only five occur in Australia, and one of these is introduced. Similarly, only two of ten non-marine families of turtles, five of some fifteen lizard families, and seven of twelve snake families are present in Australia. Of these families, only the Myobatrachidae is endemic to Australia; the Pygopodidae and Carettochelyidae occur only in the Australasian region. The distinctive nature of the Australian herpetofauna becomes more apparent at the subfamilial level, as for example in pelodryadine frogs and diplodactyline gekkonids. Several groups, such as scincids, varanids, typhlopids and hydrophiine elapids, reach their greatest diversity, taxonomically and morphologically, in Australia.

Australian-based herpetology has grown exponentially since the 1950s, taking a firm grasp of the taxonomic, biological and bigeographical challenges presented by the herpetofauna of the whole continent. Throughout these studies, themes relating to the physiological and morphological adaptations to the aridity of the continent persist. Equally, new biogeographical insights, arising from modern approaches to systematics and advances in our understanding of regional plate tectonics, are challenging more traditional views on the origins of the Australian herpetofauna. While the presence of ancient Gondwanan elements and more recent elements, with affinities to South-East Asian faunas, have been recognised generally, the predominance of the former group within Australia is becoming increasingly apparent.

Within the Australian herpetological community, diverse views are held on a wide range of topics. Expression of such differences, indicative of healthy science, has been encouraged in this volume, to ensure an adequate coverage of the field. The success of this approach is particularly evident in Biogeography and Phylogeny of the Anura. Less successful, at least from an editorial standpoint, has been the adoption of a common taxonomy for the volume. In general, the names of Cogger (1992) have been used as a standard for all text and the colour plates. In some chapters, however, use of different generic names reflects personal preference. Some of these differences arise from changes in taxonomy during the preparation of this volume, which have yet to gain general acceptance. Others reflect continuing differences of opinion on the acceptability of taxon names bestowed by Wells & Wellington (1984, 1985).

The Literature Cited has been assembled into one section each for the Amphibia and the Reptilia, to eliminate duplicate references and to provide a useful bibliographical resource in a single unit. The block of colour plates marks the end of the amphibian references. The colour plates have been selected to illustrate the range of morphologies across Australian representatives of each family, and, to a lesser extent, as an adjunct to the text and keys, as appropriate.

The editorial team of the Australian Biological Resources Study express their appreciation to the authors, as indicated in the list of contributors. We thank especially the illustrators, whose work has enhanced this volume greatly: M. Cilento, J. Courtenay, K. Couper, M. Davies, C. Eadie, K. Hollis, B. Jantulik, D. Kirschner, W. Mumford, R. Plant, M. Thompson, J. Thurmer, D. Wahl and T. Wright. Original illustrations for which we have obtained permission to use are indicated by the use of 'from' in a figure caption credit; 'after' infers that the figure has been redrawn. The production team of the *Fauna of Australia* series is advised by an Editorial Committee, membership of which changes according to publication priorities. Members at the time of publication are listed on the adjacent page. During the planning and production phase, we were advised by Professor W.D. Williams, then Chairman of the Committee, and greatly assisted by committee members Professor H. Heatwole and Dr M. Littlejohn on matters relating to Reptilia and Amphibia, respectively. Professor Heatwole and Dr Littlejohn also undertook a full review of text for their respective sections, and R. Alford, D.G. Broadley, A.A. Burbidge, B.T. Clarke, W.E. Duellman, A. Greer, M.S. Hoogmoed, G.R. Hughes, J.D. Lynch, A.R. Main, S.B. McDowell, E.R. Pianka, L.E. Taplin and G. Underwood reviewed text for particular taxa. We thank them all for their careful evaluation of the text and numerous additional contributions given so freely, in particular those of Dr Greer. The editors extend special thanks to Catherine Jordan, librarian at the Australian National Botanic Gardens, and to library staff of the Australian Nature Conservation Agency, CSIRO at Black Mountain, Canberra and Division of Wildlife and Ecology, Gunghalin, the National Library and the Australian Museum, Sydney, for their invaluable assistance in innumerable ways. Thanks are due to the curators of Museum herpetological collections in Australian museums, for providing material for illustrative purposes, in particular J. Coventry, Museum of Victoria. Last, though by no means least, we thank L. Randall and W. Murray for their input and willing computer support at all times.

We are especially grateful to photographers who have provided transparencies for use in this volume, and to photolibraries who have provided every assistance in meeting our needs. Photographic credits for the colour plates, by number, are: Aitken, K./ANT, 3.1; Beste, H. & J./Auscape International, 6.3, 6.7, 7.6; Beste, H. & J./NPIAW 1.3, 4.7, 4.8; Blagden, D. & V./NPIAW, 9.4; Bush, B./NPIAW, 8.9; Cann, J., 3.9, 3.10, 3.11, 3.12, 3.14, 3.15; Cann, J./NPIAW, 6.13; Cermak, M./NPIAW 1.1; Cogger, H.G. 1.4, 2.5, 3.3, 7.13; Cook, P./Auscape International, 5.12; Cook, R./NPIAW, 8.1; de Couet, H.H./Auscape International, 7.11; Ehmann, H. 2.7, 5.4; Ehmann, H./NPIAW 2.1, 2.2, 2.3, 2.4, 2.9, 2.11, 4.6, 4.11, 5.9; Ferrero, J.-P./Auscape International 1.2, 3.4, 5.7; Frithphoto/ANT, 7.12; German, P./ANT, 6.11; Gillam, M.W./Auscape International, 8.8; Griffiths, K./ANT, 6.5; Grigg, G., 9.1, 9.2, 9.3, 9.7; Hanlon, M./NPIAW, 5.5; Hearden, M., 4.4; Hertog, A.L./NPIAW, 2.6; Horner, P./NPIAW, 5.11; Hoye, G.A. & M.M./NPIAW, 6.6; Hoye, G.A./NPIAW, 2.10, 6.1, 8.11; Jenkins, R.W.G./ANT, 3.13, 6.9, 7.4; Jenkins, R.W.G./NPIAW 1.6, 8.3; Keller, R. & D./ANT, 7.1; Kuiter, R., 7.8, 7.10; Limpus, C./NPIAW, 3.6; Miller, B./NPIAW, 6.5; Newton, M./Auscape International, 4.11; Park, F./ANT, 6.2; Peterson, M./NPIAW, 8.12; Pollitt, C. & S./ANT, 7.3; Sauvanet, J./Auscape International, 3.7; Schmida, G.E./ANT, 4.12; Schmida, G.E./NPIAW, 4.5,; Shea, G., 4.1, 4.9, 6.8, 6.10. 6.12, 7.2, 8.2, 8.5; Swanson, S./NPIAW, 5.3, 5.6, 7.9; Taylor, R. & V./ANT, 3.2, 3.5, 3.8, 7.7; Trenerry/NPIAW, 2.13; Webb, G., 9.5, 9.6; Weigel, J./ANT, 5.10; Whitford, R./NPIAW, 4.2; Wilson, S./ANT, 5.13; Wilson, S./NPIAW, 5.1; Wombey, J. 1.5, 1.7, 2.8, 2.12, 4.3, 5.2, 5.8, 7.5, 8.4, 8.7; Wombey, J.C./Auscape International, 8.6; Wombey, NPIAW, 8.10.

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CONTENTS VOLUME 2A

AMPHIBIA & REPTILIA

1. GENERAL DESCRIPTION AND DEFINITION OF THE CLASS AMPHIBIA

Michael J. Tyler, Margaret Davies & Graeme F. Watson

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 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.

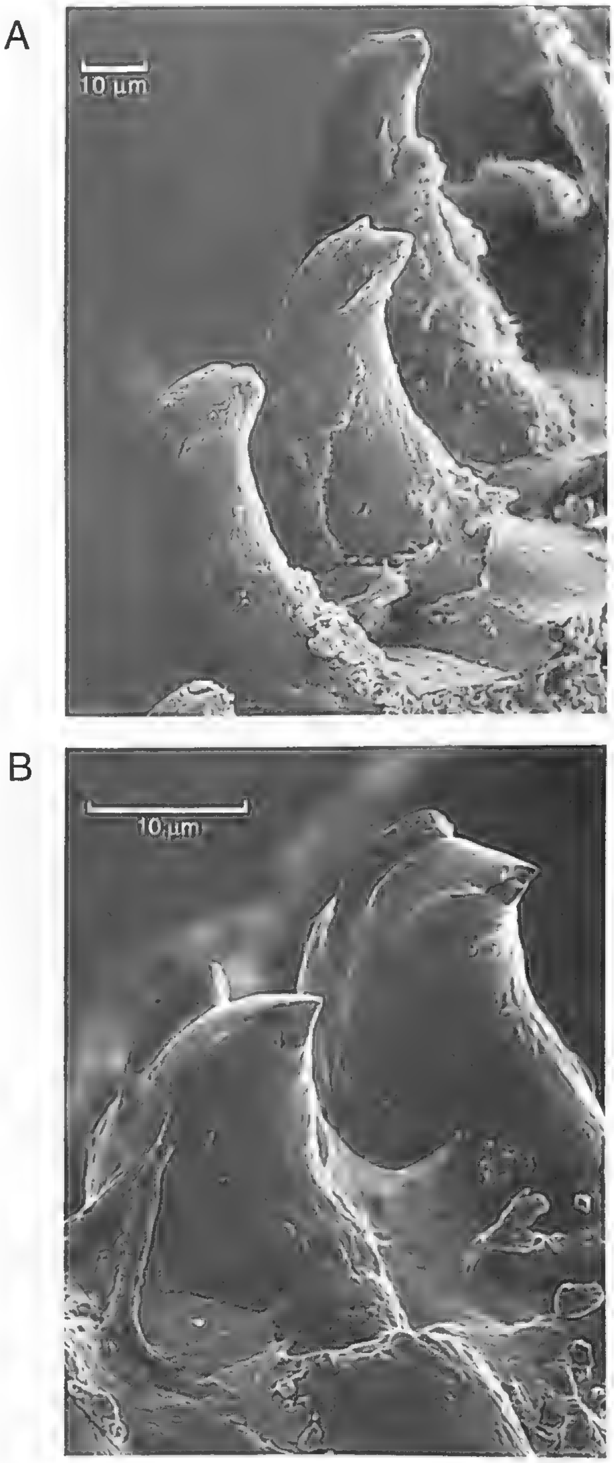

Figure 1.1 Scanning electron micrograph of maxillary teeth. A, *Cyclorana australis*; B, *Rheobatrachus vitellinus*. (From Tyler 1989a)
[Photo by M.J. Tyler]

Contributors. **M.J. Tyler:** Definition, General Description and Classification of the Amphibia; Definition, General Description and Classification of the Lissamphibia; Definition, General Description and Classification of the Anura; Key to the adults of Australian anurans – in part. **M. Davies:** Key to the adults of Australian anurans – in part. **G.F. Watson:** Key to the larvae of Australian anurans.

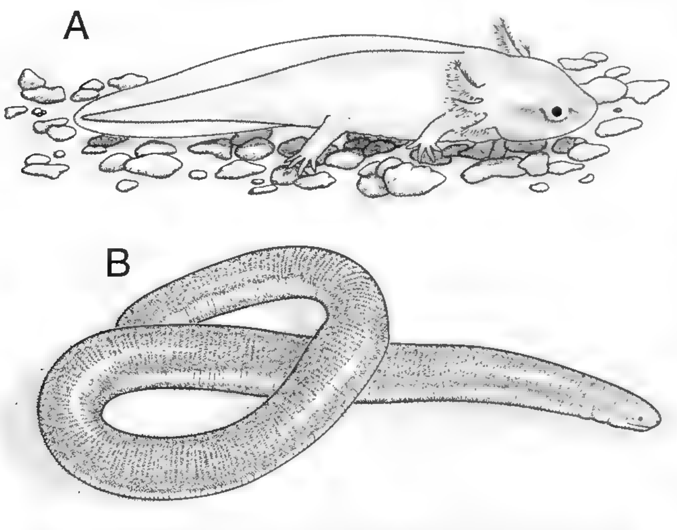

Figure 1.2 Orders Caudata and Gymnophiona. **A**, the Mexican axolotl, *Ambystoma mexicanum*; **B**, the caecilian, *Ichthyophis kohtaoensis*. (After Nussbaum 1992) [C. Eadie]

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.

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*, (Fig. 1.2A) 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 (Fig. 1.2B) 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.

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 1987).

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 1971d). 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; Wardell-Johnson & Roberts 1989), 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).

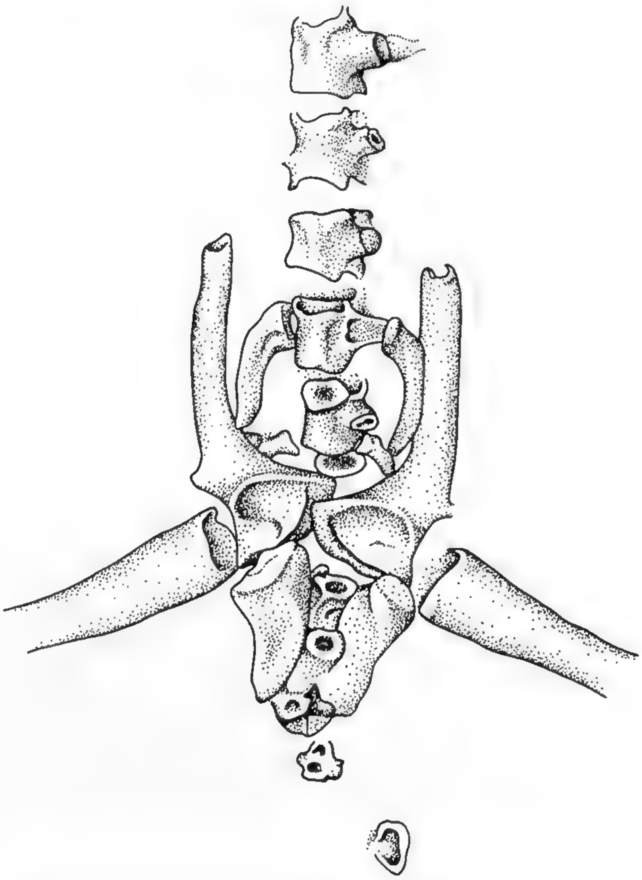

Figure 1.3 The fossil of *Triadobatrachus massinoti* from Betsieka in northern Madagascar. Specimen is complete but for the extreme anterior end of the skull, the loss of an unknown number of distal caudal vertebrae, and the distal portions of the hands and feet. (After Rage & Rocek 1989)
[D. Wahl]

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 (Fig. 1.4A); transverse prepharyngeal folds absent .... Hylidae
(b) The *m. intermandibularis* with lateral element (Fig. 1.4B); transverse prepharyngeal folds present .... Microhylidae

3 (a) Pectoral girdle arciferal (Fig. 1.4C); *m. cutaneous pectoris* absent 4
(b) Pectoral girdle firmisternal (Fig. 1.4D); *m. cutaneous pectoris* present .... Ranidae

4 (a) Elevated, bony, post-ocular bar present (Fig. 1.4E); Bidder's organ present (Fig. 11.1) .... Bufonidae
(b) Elevated, bony, post-ocular bar absent; Bidder's organ absent .... Myobatrachidae

Key to the subfamilies of the Myobatrachidae

1 (a) The *m. intermandibularis* underlies at least a portion of *m. submentalis* (Fig. 1.4F) 2
(b) The *m. intermandibularis* does not underlie *m. submentalis* (Fig. 1.4G) .... 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 aquatic .... Limnodynastinae

Key to the genera of the subfamily Limnodynastinae

1 (a) Constricted pupil a horizontal slit (Fig. 1.4H) 5
(b) Constricted pupil a vertical slit (Fig. 1.4I) 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 (Fig. 1.4J) .... *Mixophyes*
(b) Toe webbing rudimentary (Fig. 1.4K) .... *Lechriodus*

5 (a) Vomerine teeth in long rows posterior to the choanae (Fig. 1.4L) 6
(b) Vomerine teeth in short rows, variously located with respect to the choanae (Fig. 1.4M) 7

6 (a) Tympanum large and prominent (Fig. 1.4N) .... *Megistolotis*
(b) Tympanum small, hidden or indistinct (Fig. 1.4O) .... *Limnodynastes*

7 (a) Upper jaw toothed 8
(b) Upper jaw lacking teeth .... *Notaden*

8 (a) Odontoids on Mentomeckelian bones present (Fig. 1.4P) .... *Adelotus*
(b) Odontoids on Mentomeckelian bones absent 9

9 (a) Sub-dermal glands hypertrophied; dorsal prominence and dorsal protuberance of ilial shaft poorly developed (Fig. 1.4Q) .... *Philoria*
(b) Sub-dermal glands not evident; dorsal prominence and dorsal protuberance of ilial shaft prominent and hook-like (Fig. 1.4R) .... *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 (Fig. 1.4S); male lacking inguinal brood pouches 3
(b) First toe with one phalanx (Fig. 1.4T); male possessing inguinal brood pouches .... *Assa*

3 (a) Terminal phalanges T-shaped (Fig. 1.4U) .... *Taudactylus*
(b) Terminal phalanges knobbed (Fig. 1.4V) 4

4 (a) Parotoid and inguinal glands poorly developed or absent 5
(b) Parotoid and inguinal glands well developed (Fig. 1.4W) .... *Uperoleia* (in part)

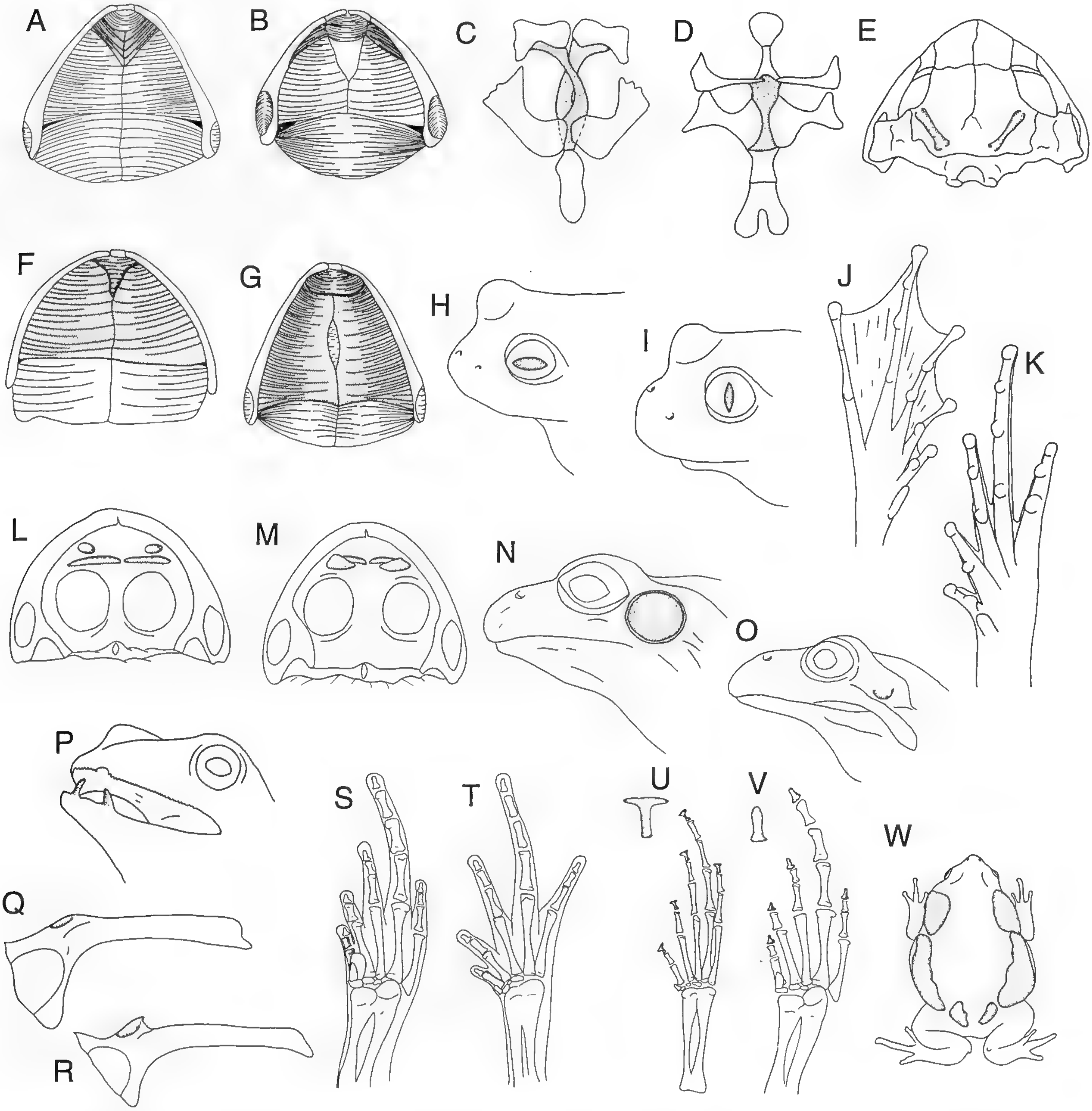

Figure 1.4 Key characters for adult anurans. Pertinent features of elements A–W are noted in the adjacent Keys to the anuran families, and myobatrachid subfamilies and genera. (A, B, F, G, after Tyler 1971; C, after Davies 1984; L, M, after Burton 1984; P, after Barker & Grigg 1977) [M. Davies]

5 (a) Ventral surface smooth to slightly granular .... *Geocrinia*
(b) Ventral surface moderately to coarsely granular 6

6 (a) Vomerine teeth present (Fig. 1.5A) .... *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 (Fig. 1.5B) .... *Metacrinia*
(b) Columella absent; tympanum absent .... *Pseudophryne*

9 (a) Fourth finger with three phalanges; metatarsal tubercles compressed (Fig. 1.5C) .... *Uperoleia* (in part)
(b) Fourth finger with two phalanges; metatarsal tubercles not compressed (Fig. 1.5D) 10

10 (a) First toe with one phalanx (Fig. 1.5E); eyes conspicuous; body robust .... *Arenophryne*
(b) First toe with two phalanges (Fig. 1.5F); 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 (Fig. 1.5G) .... *Nyctimystes*
(b) Palpebral venation absent; constricted pupil a horizontal slit or a rhomboid (Fig. 1.5H) 2

2 (a) Inner metatarsal tubercle large and compressed (Fig. 1.5I); intercalary structures absent .... *Cyclorana*
(b) Inner metatarsal tubercle small and rounded (Fig. 1.5J) or absent, rarely compressed; intercalary structures present (Fig. 1.5K) .... *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 (Fig. 1.5L) .... *Cophixalus*
(b) Supplementary slip of *m. intermandibularis* broad, arising from ventral fascia of angulosplenial and oriented medially and only slightly anteriorly (Fig. 1.5M) .... *Sphenophryne*

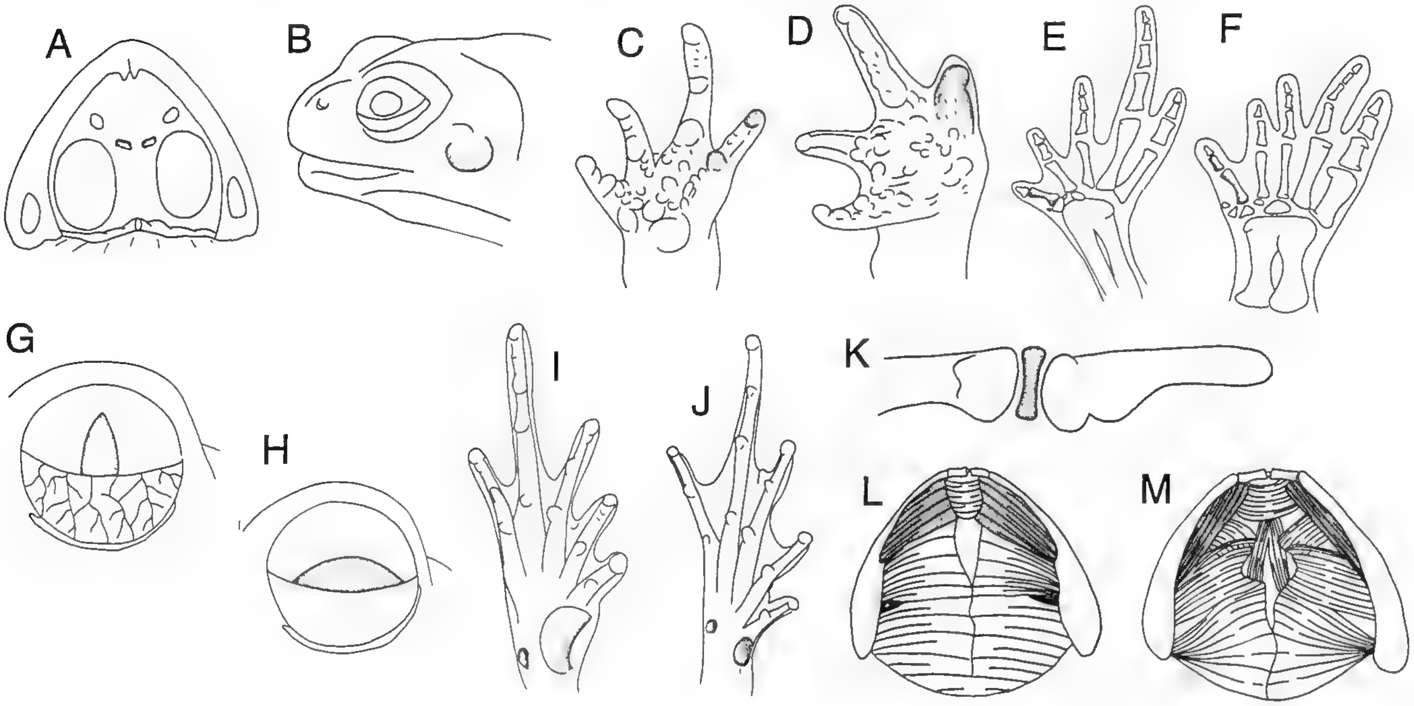

Figure 1.5 Key characters for adult anurans. Pertinent features of elements A–M are noted in the Keys to the genera of the Myobatrachinae (in part), Hylidae and Microhylidae. (C–F, after Davies 1984) [M. Davies]

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).

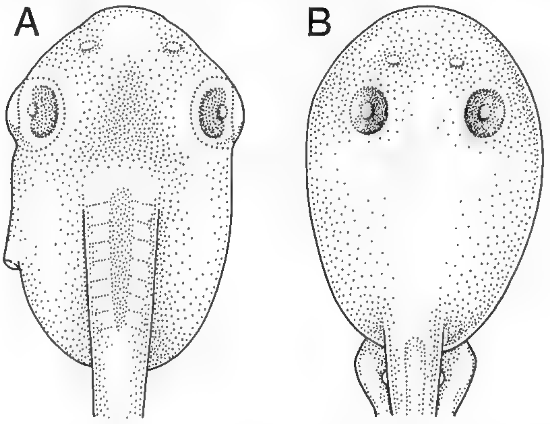

Figure 1.6 Generalised dorsal views of tadpoles that may help in quick familial identification. A, hylid tadpole; B, myobatrachid tadpole. (After Altig 1970) [R. Plant]

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).

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 (Fig. 1.7A)	8
(b)	Labial teeth present (Fig. 1.7B)	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 (Fig. 1.7C)	*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*

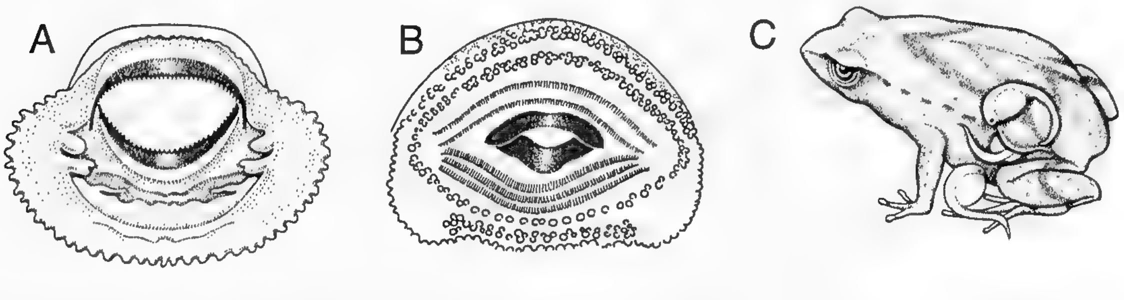

Figure 1.7 Key characters for larval anurans. A, mouth disc of *Kyarranus sphagnicolus* tadpole without labial teeth; **B**, mouth disc of *Litoria nannotis* tadpole with labial teeth; C, adult male *Assa* with tadpoles. (A, B, after Watson & Martin 1973; C, after photo by H. Ehmann/NPIAW) [A, B, R.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

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 (Fig. 1.8B) .... *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* (Fig. 7.7C)
Taudactylus diurnus

11 (a) Deep-bodied larvae having two upper and two lower rows of labial teeth .... *Crinia haswelli*
(b) Shallow-bodied larvae (Fig. 1.8D) having three lower rows of labial teeth (Fig. 1.8C) 12

12 (a) Larvae with two upper rows of labial teeth (Fig. 1.8C) 13
(b) Larvae with more than two upper rows of labial teeth (Fig. 1.8E) 15

13 (a) Papillary border complete; usually found in streams .... *Litoria* (in part) (Fig. 1.8C)
Nyctimystes (Fig. 1.8H)
(b) Papillary border incomplete 14

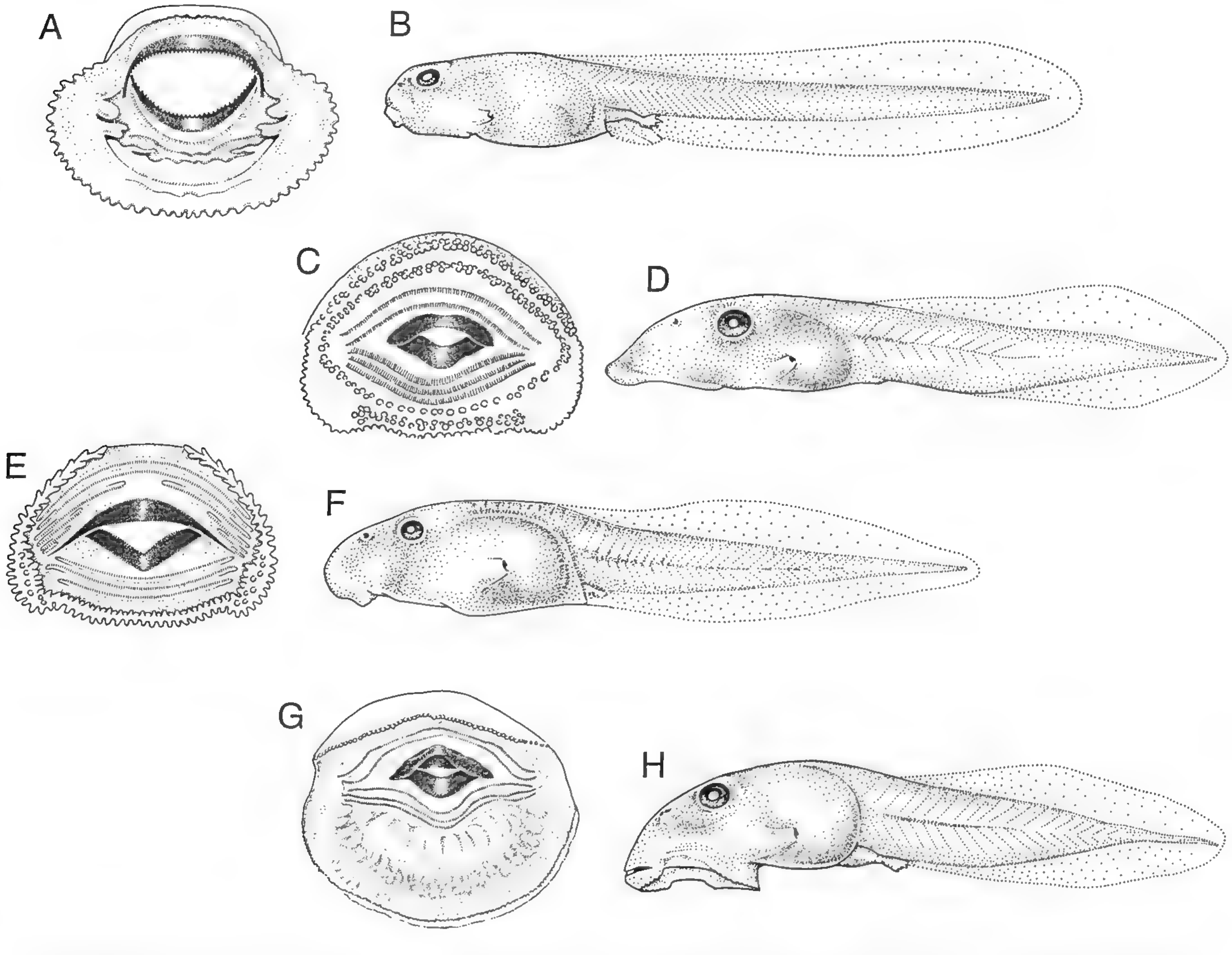

Figure 1.8 Tadpoles and mouth discs of anurans. **A**, *Kyarranus sphagnicolus* mouth disc; **B**, *Kyarranus sphagnicolus* tadpole; **C**, *Litoria nannotis* mouth disc; **D**, stream-adapted tadpole of *Litoria nannotis*; **E**, *Megistolotis lignarius* mouth disc; **F**, stream-adapted tadpole of *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]

14 (a) Papillary border with an anterior gap .... *Litoria* (most species) (Fig. 1.9C)
Cyclorana (Fig. 1.9A)
Limnodynastes spenceri
Taudactylus acutirostris

(b) Papillary border with both anterior and posterior gaps .... *Geocrinia* non-*rosea* group (Fig. 1.9G)
Notaden melanoscaphus
Crinia (most species)
Bufo (Fig. 1.9E)
Uperoleia

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

(b) Papillary border incomplete 16

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 (Fig. 1.8E)
Heleioporus
Lechriodus

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

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

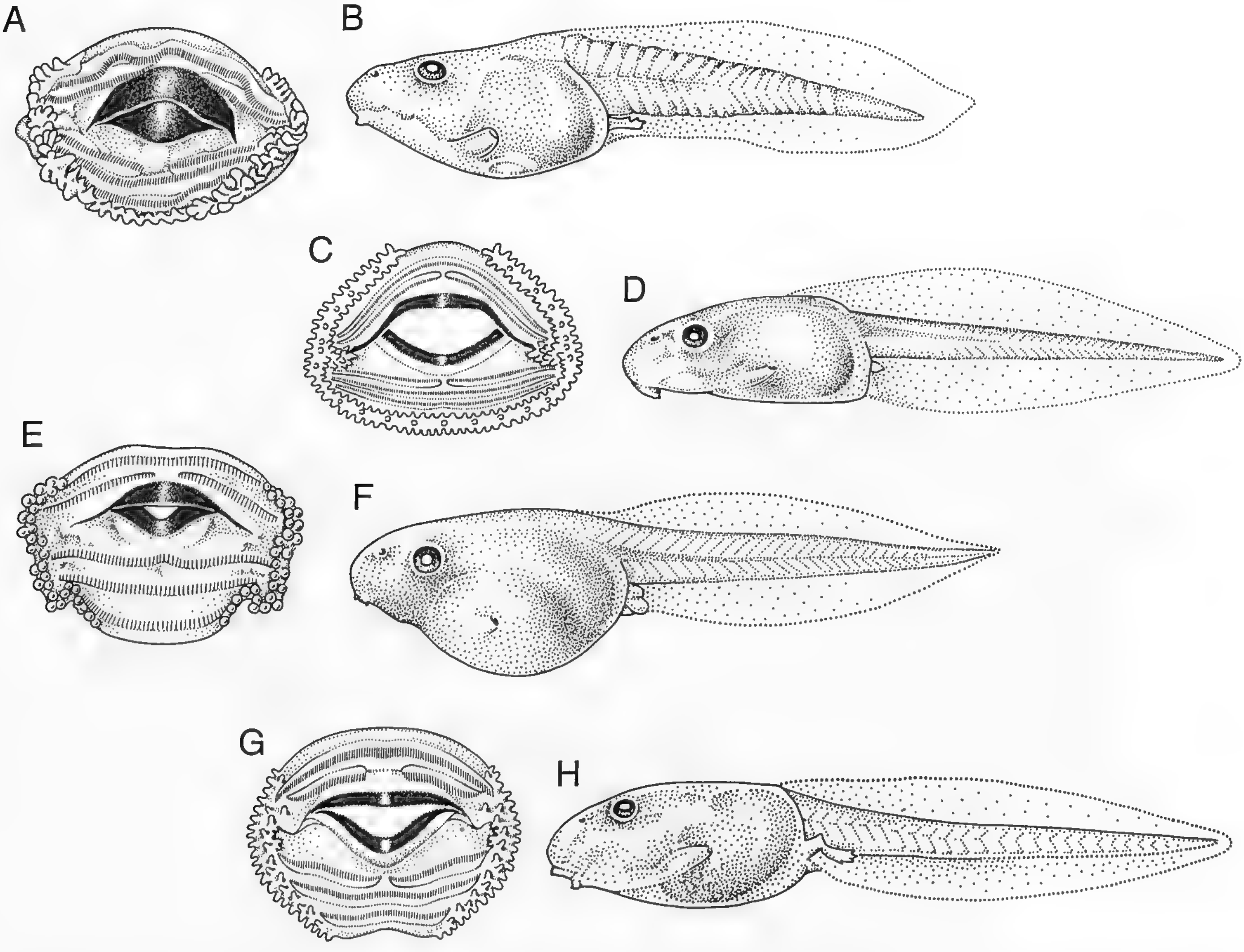

Figure 1.9 Tadpoles and mouth discs of anurans. A, *Cyclorana longipes* mouth disc; B, *Cyclorana longipes* tadpole; C, *Litoria gracilenta* mouth disc; D, *Litoria gracilenta* tadpole; E, *Bufo marinus* mouth disc; F, *Bufo marinus* tadpole; G, *Geocrinia laevis* mouth disc; H, *Geocrinia laevis* tadpole.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

2. HISTORY OF DISCOVERY OF THE ANURA

Bert Main

The earliest descriptions of Australian frogs were based on material collected opportunistically, or on illustrations, by early travellers. The first species to be described was *Rana caerulea* (White, 1790), now *Litoria caerulea*, the type of which is presumed lost (Tyler 1976b). The original figure is reproduced in Fig. 2.1. Shaw & Nodder described *Rana australiaca* (= *Helioporus australiacus*) in 1795, based on a drawing by Nodder (Fig. 2.2).

Subsequently, more intensive collections were made. Surprisingly, those of Péron and Lesueur, naturalists on the Baudin Expedition, received little more than a mention by Péron (1807). Indeed, the illustrations held in the Lesueur collection at the Muséum d'Histoire Naturelle in Le Havre, France have been published only recently. Bonnemains, Forsyth & Smith (1988) reproduced three vellums (77 001 to 77 003) of Lesueur, which are cross-referenced to Péron's notebooks 77 010 to 77 012, with identifications by M.J. Tyler, and are accompanied by Péron's name.

Seven of these were hylid species, referred to on the illustrations and by Péron (1907) as *Hyla citripoda*, *Hyla cyanea quadrimaculata viridi aurea*, *Hyla erythropoda*, *Hyla xanthogaster*, *Hyla bufonoïdes*, *Hyla nebulosa* and *Hyla violaceapoda*. They represent *Litoria lesueuri*, *L. aurea*, *L. phyllochroa*, *L. chloris*, *L. verreauxi*, *L. peronii* and *L. citropa* respectively. Three myobatrachid species were illustrated also: *Limnodynastes tasmaniensis*, as *Rana pustulosa*; *Limnodynastes peronii* as *Rana patersonia*; *Ranidella* species (now *Crinia*) as *Bufo leucogaster*. The above were all from Port Jackson with the exception of *Litoria peronii* which was from Parramatta. Also figured was the Western Australian *Litoria adelaidensis*, as *Hyla viridi aurea* from Terre de Nuitts.

Gould's collector, Gilbert, made two visits to Western Australia, in 1839 and in 1842–1843. In the latter period, Gilbert visited Houtman Abrolhos (Gilbert 1843). Boulenger (1882) listed Gilbert as the collector of the type of *Myobatrachus gouldii* (Fig. 2.3), *Heleioporus eyrei*, and as having collected *M. gouldii* and *Limnodynastes dorsalis* on the Abrolhos. Specimens of *Crinia* from these islands presented to the British Museum (Natural History) by Günther are likely to have been collected by Gilbert. Frogs have not been collected recently on the Abrolhos, but the eucalypt copse noted by Gilbert in East Wallabi still persists and may be the site to look for *M. gouldii*. On West Wallabi the later guano workings may have so affected the water table that the samphire flat which 'very evidently displays a large body of water in the rainy season' no longer supports *Limnodynastes* or *Crinia*. Gilbert also collected the type of *Litoria adelaidensis* (Fig. 2.4).

TAXONOMIC DEVELOPMENTS

The difficulties of early taxonomists with poorly preserved specimens is shown by the following placement of species presently well known. Examples are *Rana aurea* Lesson, 1829 (*Litoria aurea*), *Bombinator australis* Gray, 1835 (*Pseudophryne australis*), *Breviceps gouldii* Gray, 1841 (*Myobatrachus gouldii* (Fig. 2.3A)), *Alytes australis* Gray, 1842 (*Cyclorana australis*) and *Hylorana daemeli* Steindachner 1868 (*Rana daemeli*).

At the generic level, recognition of the distinctive nature of the Australian frog fauna began with the descriptions by Tschudi (1838) of *Crinia* and *Litoria*, two of 19 endemic genera presently recognised (Cogger, Cameron & Cogger 1983). When Boulenger described *Lechriodus* in 1882, 13 genera had been described, primarily between 1841 and 1867, including *Cyclorana*,

Figure 2.1 Two specimens of *Rana caerulea* (= *Litoria caerulea*) appear in White's (1790) illustration. The small frogs in the centre are probably *Crinia* species. The blue colour of White's specimens, embodied in the specific name, resulted from the alcoholic preservation medium, probably rum. [Photo by Australian Museum]

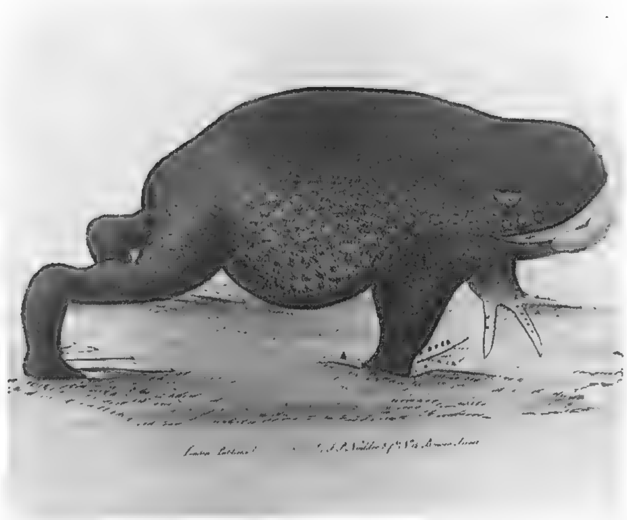

Figure 2.2 Nodder's illustration of *Rana australiaca*, on which the type of *Heleioporus australiacus* is based. (From Shaw & Nodder 1795) [Photo B. Main]

Heleioporus (Fig. 2.3B), *Limnodynastes*, *Mixophyes*, *Myobatrachus*, *Neobatrachus*, *Notaden*, *Pseudophryne*, *Ranidella* and *Uperoleia*. The deposition in European museums of all known holotypes of type species for these genera reflects the domination of this phase of description by European taxonomists.

In the ensuing 70 years, only three new genera were added to the list (*Philoria*, *Adelotus* (Pl. 2.4) and *Metacrinia*). Fry (1912) added the family Microhylidae to the Australian fauna when he described species of *Austrochaperina*, which have been transferred subsequently to the Papuan genera *Cophixalus* and *Sphenophryne*.

A revival of scientific interest in Australian amphibians from 1950 onwards resulted in extensive new collections of material. These led to the description of the four new genera *Arenophryne*, *Megistolotis*, *Rheobatrachus* and *Taudactylus*, and the presence of the Papuan hylid genus *Nyctimystes* (Pl. 1.7) in Australia was shown by Tyler (1964).

Taxonomic revisions based on these collections also resulted in the recognition of the new genera *Assa*, *Geocrinia* and *Paracrinia*, in which overall similarity in body shape had masked morphological differences between these and related taxa. This second phase of description was conducted primarily by Australian taxonomists, as reflected in the large proportion of type material deposited in Australian collections.

The genus *Bufo* was added to the Australian frog fauna with the introduction to Queensland of *Bufo marinus* (Pl. 1.2) in 1935 (Easteal 1981).

EARLY OBSERVATIONS

The atypical calls and behaviour of many Australian frogs often misled or confused travellers. Thus Heirissons's party were transfixed with terror by a horrible cry 'like the bellowing of an ox' that appeared to come from the reeds close by, when they were attempting to camp overnight in June 1803 (Péron 1807). This has been interpreted by D.L. Serventy as undoubtedly the cry of the brown bittern (Marchant 1982). An alternative interpretation is offered by Landor (1847), who described the caution displayed by Stirling in his first passage up the Swan in March 1827, because they had the records of the French fully in mind and were kept 'in constant vigilance by the same fearful sounds'. Landor then related how the colonists had changed from believing the incessant noises to be made by wild bulls, the howling of wolves or cries of savages to being 'convinced that the dreadful sounds which assailed their ears at night proceeded from myriads of frogs'. The calling season of *Heleioporus eyrei* extends from March into June. As males characteristically chorus in unison, the sound alternates between a low moan or hum and a loud resonant sound not unlike the lowing of cattle, and possibly alarmed the French, Stirling, and the early settlers.

Landor also told of how he was startled by a loud 'bomb' when hunting ducks in tall bulrushes, and was ready to retreat 'when I espied a little frog perched on top of a reed ... which every now and then inflated his cheeks and uttered the fearful sound I had heard'. A single loud 'bonk' is often made by *Limnodynastes dorsalis* during daylight and *Litoria adelaidensis* perches on reeds and calls in daylight.

Grey (1841) described how Aboriginal women collected frogs in all seasons, but especially when the swamps were nearly dry by using long sticks or 'their arms which they plunge up to the shoulder in the slime', and how he had often seen them with 'ten or twelve pounds weight of frogs in their bags'. Moore (1884) recorded that the eggs of frogs most prized by natives were dug from the ground; these would have been eggs of *H. eyrei*. Moore also noted that frogs of a green colour were not eaten, and that the good ones lived in the ground.

Aitken (1870) described the finding of a water-holding frog in dried up water holes in central Australia, later identified as *Cyclorana platycephalus* by Spencer & Gillen (1912). Dakin (1920) described the larval life of *Heleioporus eyrei* (as *H. albopunctatus*).

RECENT INCREASES IN KNOWLEDGE OF BIOLOGY

In the 1940s and 1950s, the status of named species as biological entities was unresolved and there was strong antipathy to any biological species concept or to considering frog species as populations as proposed by Dobzhansky (1950). At this time I was interested in using frogs in comparative studies on how Australian animals adapted to aridity and so needed to identify species as biological entities. Confidence in the status of nominal species was not encouraged by the differences of opinion between Parker (1940) and Loveridge (1935) on species limits for *Crinia signifera* and *C. georgiana*. While the absence of red indicated *C. georgiana* to Loveridge, Parker held that the colours of

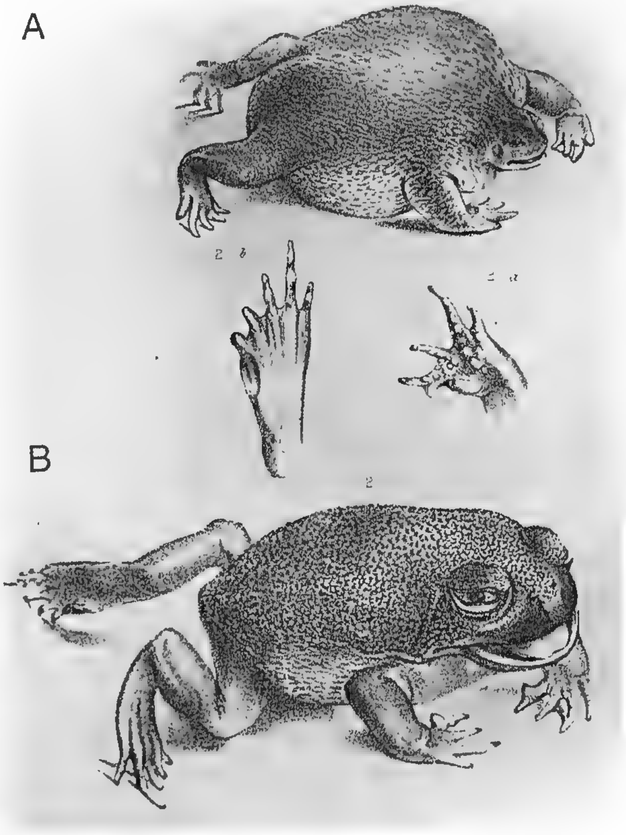

Figure 2.3 Illustrations from Gray's (1941) descriptions of A, *Myobatrachus gouldii*, and B, *Heleioporus albopunctatus*. [Photo B. Main]

Figure 2.4 *Hyla adelaidensis* (= *Litoria adelaidensis*), as illustrated by Gray (1841). [Photo B. Main]

C. georgiana were 'fast' in alcohol but 'fugitive' in formalin. Clearly an objective measure was needed to identify living specimens. One such measure with potential was the comparison of male calls. This would be possible if male calls could be recorded on magnetic tape and subsequently analysed by means of an oscilloscope.

Staff of the Australian Broadcasting Commission cooperated in demonstrating that single calls could be recorded (Anon. 1953). Analysis of these calls showed that they were distinctive in duration, frequency of repetition and pulse rate. This discovery was exploited by M.J. Littlejohn, who constructed a portable tape recorder in 1954, and soon demonstrated the presence of many distinctive calls indicative of cryptic or sibling species in *Crinia*, *Heleioporus* and *Neobatrachus*. The species status was confirmed by genetic crosses, using the *in vitro* technique of Moore (1946).

These studies showed a great range of calls within genera and rapidly clarified the taxonomy and so established comparative physiology on a sound basis. Littlejohn & Lee (1955) published illustrations of the oscillographs of *Heleioporus*, and species specific calls of this genus and of *Neobatrachus* were analysed by Littlejohn & Main (1959). A comparative analysis of the calls of *Crinia* species by Littlejohn (1959) demonstrated the great differences between the calls of species within a genus. Taken in association with the results of crosses using the *in vitro* techniques, these call differences enabled Main (1957) and Lee (1967) to resolve the taxonomy of *Crinia* and *Heleioporus*, respectively.

Over the period of the foregoing studies in Western Australia, W.F. Blair had used tape recordings and a sound spectrograph in the United States to analyse frog calls (Blair 1958). Littlejohn was able to continue the analysis of calls previously recorded in Australia in Blair's laboratory (Littlejohn & Main 1959). John Moore, a Fulbright Scholar at Sydney, showed by crossing eastern and western *Crinia* that the western form, hitherto believed to be conspecific with eastern *C. signifera*, was a genetically separate entity which he named *C. insignifera*. He demonstrated also that eastern and western *Litoria* attributed to *L. aurea* were also genetically distinct (Moore 1954). These studies were later placed in a broader context of the frog fauna of eastern Australia by Moore (1961).

The comparative physiology of *Heleioporus* and *Neobatrachus* (Bentley *et al.* 1958) showed that the species recognised on biological criteria were also unique with respect to their ability to tolerate dehydration. Similarly, Main & Bentley (1964) showed that burrowing frogs and tree frogs were distinctive.

Earlier workers, such as Loveridge (1935), interpreted the different dorsal patterns in *Crinia* as morphological species, while Parker (1940) interpreted the differences as morphological variation. Main (1965b) showed by breeding experiments that variations in dorsal patterns in *C. insignifera*, *C. pseudinsignifera*, *C. glauerti* and *C. georgiana* could be interpreted as a polymorphism controlled by a simple genetic system.

A review of the studies of calls, *in vitro* crosses, biology, physiology and ecology initiated in the 1950s (Main 1968), together with Moore's (1961) review, demonstrated the richness of the frog fauna, and its suitability for studies on speciation, evolution and isolating mechanisms. The fauna also provides a wide range of life histories and physiological abilities appropriate for comparative studies. This early work thus kindled interest, and provided the basis for the subsequent wide-ranging studies on frogs which are reviewed in the following chapters.

3. COLLECTION AND PRESERVATION OF THE ANURA

Margaret Davies

INTRODUCTION

The collection and preservation of frogs is an important component of several research disciplines. Specimens are required for taxonomic research and phylogenetic studies. Increasingly, pharmacological studies show that animals, as well as plants, are storehouses of potentially beneficial substances. Frogs are sensitive environmental indicators and records of their occurrence, abundance and disappearance are of prime importance for environmental monitoring purposes. Voucher specimens may be vital in surveys, maintaining some of the information lost through habitat destruction.

Only the minimum numbers necessary to achieve scientific objectives should be collected. In particular, species with restricted distributions, small population sizes and low recruitment should be collected sparingly to minimise impact.

CAPTURE

Frog collecting is often fortuitous because it is heavily weather dependent, especially for fossorial species which only emerge after heavy rain. Although aestivation sites of cool temperate species may sometimes be located (McDonald & Davies 1990), the breeding season is the most effective time to collect frogs. A powerful torch is essential for this predominantly nocturnal activity. A head torch frees both hands and permits recognition of eye shine in many species, while a hand-held torch generally is more powerful.

Calling by male frogs to advertise their presence during the mating season tends to bias collections towards males. As direction but not distance from which calls emanate can be judged quite readily, triangulation is the most effective way of finding calling frogs, despite the ventriloquism of many species. Two or three persons stand 2 to 3 m apart in the general vicinity of the calling frog, identify the direction of the call, and aim their torches at its source. The frog will be located close to where the beams intersect. During this process, the frog may stop calling, but usually it will resume if the observers stand quietly.

Foraging frogs and females homing toward calling males can be located by torchlight near free water or choruses of frogs. It is important to establish landmarks prior to such searches, as they can be extremely disorientating.

Roads, especially sealed ones, can be fruitful collecting areas, particularly after rain. With some experience, species can be recognised in the headlights of a vehicle travelling up to 40 km/hr by traits of posture and gait. This 'road running' technique is a valuable form of survey, especially combined with stationary periods to identify species by call.

By day, inactive frogs can be collected in damp places such as vegetation around pools, under rocks and logs, in crevices of tree trunks and in caves. Frog spawn and tadpoles are usually collected by day using a dip net or a soup strainer; terrestrial spawn are collected by hand.

Collectors must ensure that their specimens are not unduly stressed, and consider the sensitivity of frogs to heat and their need for constant moisture at all times. For short periods only, adult frogs, spawn and tadpoles should be placed in inflated and moistened polythene bags (305 mm x 445 mm x 50 µm). The number of frogs in a single bag should be limited, according to their size. Often it is inadvisable to mix frogs of different sizes within a bag because some species are cannibalistic or will eat smaller species held with them. Under the stress of captivity and confinement, some species also release skin secretions which are toxic to other frogs.

Moist calico bags are excellent repositories for frogs, particularly if they are to be kept alive for long periods. Loose cotton threads should be removed from the inside of the bag to avoid entanglement of limbs or digits.

Polythene or calico bags should be kept in a cool place; a polystyrene cooler is ideal (Fig. 3.1A). Calico bags should be suspended within the container to enable plenty of air flow if they are to be transported over long distances (Fig. 3.1B). Over long periods, frogs survive less successfully in inflated polythene bags. Dry polythene bags are best, as evaporation from the frogs maintains the required humidity; additional water becomes contaminated very easily and putrefies. Bags must be checked regularly if kept in the field for any length of time, to ensure that they remain moist, inflated and cool, and to remove fatalities before they decompose and cause further deaths.

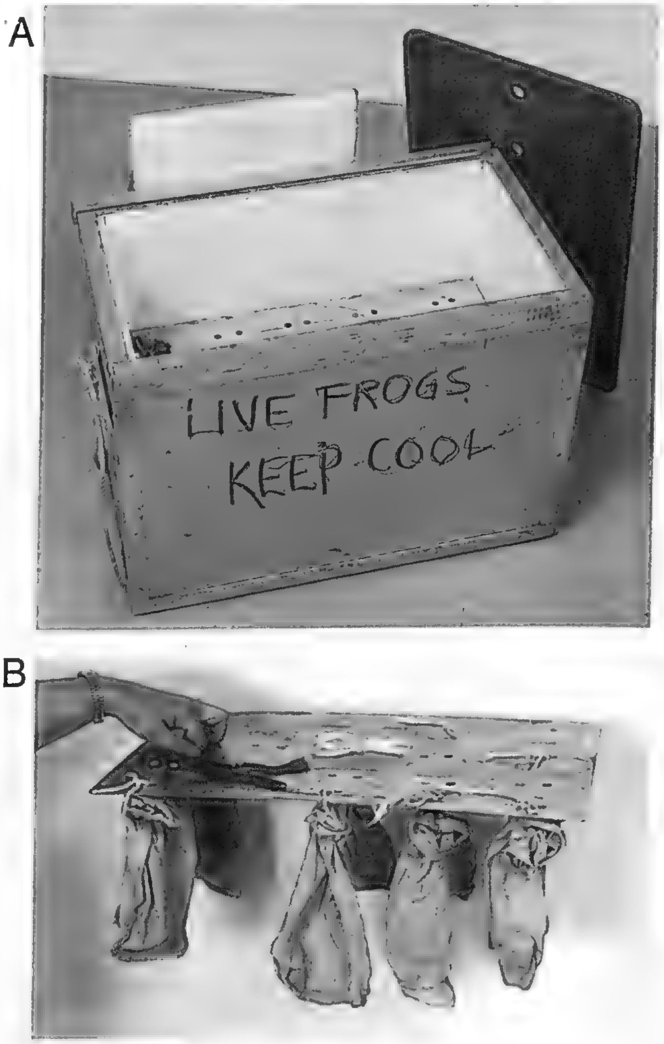

Figure 3.1 Collecting box for frogs. A, aluminium container lined with polystyrene. B, a narrow lip at mid-depth supports a perforated aluminium shelf from which calico bags are suspended in the lower section. Tadpoles, or frogs in calico or inflated bags can be transported in the upper section.
[Photos by P. Kempster]

Separation of sexes will prevent spawning. If spawning is required, males and females (amplectant or not) should be placed together in inflated polythene bags with enough water for spawning to occur. For foam nesting species, the water depth should be sufficient for the female to paddle her forelimbs during foam formation (Tyler & Davies 1979c). Water required by terrestrial ovipositors for deposition of eggs should be replaced with damp vegetation after laying. Bags should be kept upright during oviposition because eggs laid out of water are generally infertile or are hard to retrieve.

As a minimum requirement, all specimens must be identified by a name, and the date and locality of collection. Behavioural and ecological data should be recorded whenever possible. These include whether the frogs called, their calling location, whether other species called in synchrony, and the nature of the aquatic habitat (permanent, ephemeral, static or moving).

Frogs are totally protected in most States, in all National Parks and State Forests and partially protected in other areas, so permits to collect and, in some cases, to export between States are required. As regulations vary from State to State, it is essential to find out from the appropriate State or Federal authorities the nature of the restrictions applicable in any area and the types of permits required before collecting. Export of live or preserved frogs from Australia is subject to Federal control, irrespective of the origin of the fauna. Some species, including the gastric brooding frogs *Rheobatrachus silus* and *R. vitellinus*, are prohibited exports. Comments on pertinent State and Federal legislation and other sources of information for collectors are provided in Chapter 14.

PRESERVATION AND STORAGE

Frogs die in a relaxed position, following gentle anaesthesia, when placed in enough 3% chloral hydrate (1% for small frogs) solution to allow absorption through the ventral skin. The dead specimens should be placed in a tray or baking dish on paper towelling moistened with 3% formalin (to facilitate subsequent histology). The fingers and toes should be arranged to enable maximal information to be obtained (Fig. 3.2). The specimens should be covered with another layer of moistened paper towelling and the tray sealed in a polythene bag to prevent desiccation. After about an hour *rigor mortis* should have set in and identification labels can be attached at the knee. Labels must be waterproof and written in pencil or waterproof ink.

Specimens should be stored in 3% formalin or 65% ethanol. Formalin is convenient in the field as it can be transported in concentrated form for dilution with water as required. Before transport, it can be drained and replaced with formalin-soaked cotton wool to reduce weight and prevent possible spillage. In the laboratory, specimens should be transferred to 65% ethanol. Specimens should be stored in glass jars that are large enough not to distort the spread limbs.

Tadpoles should be killed in 3% chloral hydrate and preserved in Tyler's (1962) fixative (10 ml concentrated formalin, 4 ml 10% aqueous calcium chloride, 0.2 g cobalt nitrate, 90 ml water). This fixative prevents degradation of the outer epithelium and thus maintains specimens suitable for histology. Alternative preservation techniques are discussed by Pisani (1973).

Snap freezing in liquid nitrogen or dry ice and long term storage at -80°C is the most effective method for preserving the widest variety of tissue constituents for biochemical and karyological analyses. Dessauer, Cole & Hafner (1990) provide information on collection and preservation of material for various biochemical analyses. If snap freezing is not possible under field conditions, and material cannot be transported live back to the laboratory, an aqueous solution of 2% 2–phenoxyethanol preserves many enzymes for at least three weeks (Nakanishi, Wilson, Nolan, Gorman & Bailey 1969). Plasma albumins for microcomplement fixation studies can be preserved in this solution at room temperature for up to a year.

Figure 3.2 Frogs laid out on formalin dampened paper. The limbs are positioned for maximal information. [Photo by P. Kempster]

LABORATORY CULTURE

Amphibians can be reared and housed successfully in a laboratory, in conditions similar to their natural habitat requirements. Tropical species should be kept at 25 to 30°C while temperate species can be housed satisfactorily at 20°C. Daylight fluorescent tubes should be installed to ensure adequate synthesis of keratin if natural light is unavailable.

Tadpoles can be reared in glass or plastic containers, in aerated pond water or tap water which has been suitably 'aged' by thorough aeration for 24 hr before use. Hylid tadpoles can be reared successfully on a diet of lightly boiled or frozen lettuce or spinach leaves, whilst many myobatrachids require a high protein supplement such as breakfast cereal or fish food. It is important not to overfeed tadpoles as this fouls the water, which should be changed before it becomes tainted; usually this means a daily change of water for older tadpoles. As metamorphosis approaches, an accessible surface extending above the water should be provided for froglets to leave the water.

Newly metamorphosed frogs require large amounts of small food items. Vinegar flies *Drosophila melanogaster*, especially flightless forms, are particularly suitable. Slightly larger froglets can eat small mealworms, *Tenebrio molitor*, or cockroach nymphs. Rearing froglets from metamorphosis to a size at which a varied diet of larger prey items can be provided is difficult, and mortality at this stage is high.

Adult frogs keep well in an aquarium with a pond at one end and land at the other. Moss, rocks, leaf litter and other vegetation provide ideal shelter, and should allow ground dwelling species to enter or leave the pond easily. A light wooden frame to support fine cloth or wire mesh, with foam glued along two inside edges, will deter the escape of large, actively-climbing frogs and prey items alike.

Frogs generally require moving prey. Most species thrive on a diet of mealworms varied with other insects. Dusting mealworms with powdered vitamins will improve an unvaried diet. Frogs of different sizes should not be mixed in an aquarium, to prevent some frogs eating others and starvation of smaller ones through competition for food. However, ground dwelling and tree frogs of similar sizes can be housed together.

Redleg is a contagious bacterial disease of captive amphibians that is difficult to eradicate (Banks 1980). Tyler (1987b) noted an oedema of unknown origin which appears to be incurable.

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 (Fig. 4.1C). The eyes are prominent, vary slightly in size and tend to be lateral rather than dorsal. When constricted, the pupil is usually horizontal (Fig. 4.1C), 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* (Fig. 4.6B) 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 species have

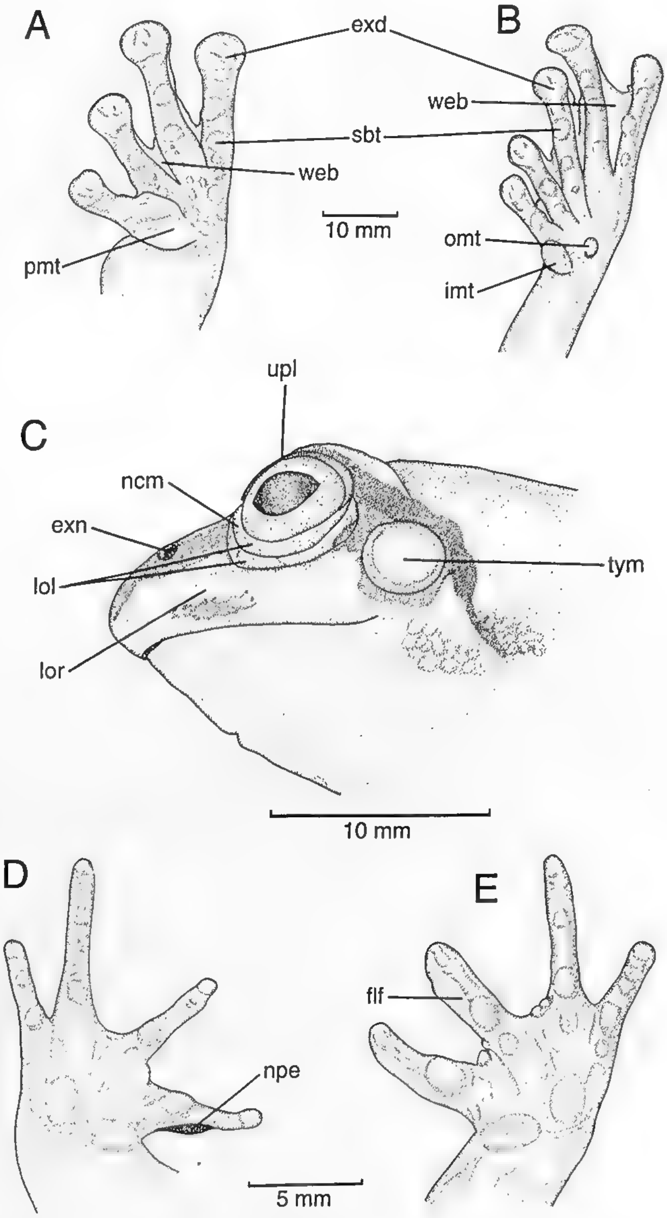

Figure 4.1 External features of frogs. **A**, palmar view of the hand, and **B**, plantar view of the foot of *Litoria splendida*; **C**, lateral view of the head of *Cyclorana longipes*; **D**, palmar view of the hand of a male *Limnodynastes convexiusculus*, **E**, palmar view of the hand of a female *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]

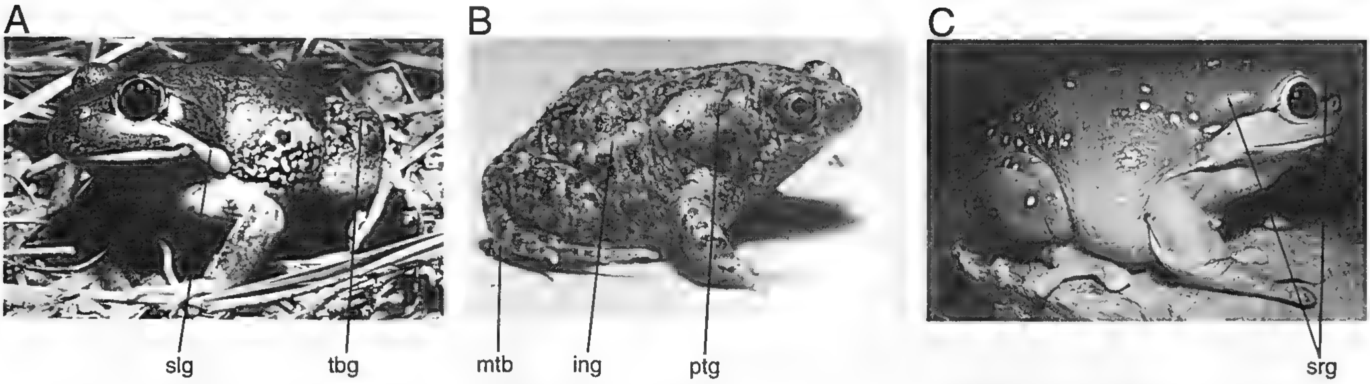

Figure 4.2 Skin glands of frogs. **A**, *Limnodynastes terraereginae*; **B**, *Uperoleia littlejohni*; **C**, *Litoria splendida*. **ing**, inguinal gland; **mtb**, metatarsal tubercle; **ptg**, parotoid gland; **slg**, supralabial gland; **srg**, suprarostral gland; **tbg**, tibial gland. [Photos by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

non-webbed fingers, but toe webbing varies from the extensive webbing of the aquatic *Rheobatrachus*, *Litoria dahlii* 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 (Fig. 4.2B). A second pair, the outer metatarsal tubercles also are sometimes compressed (Fig. 4.1B). 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* (Fig. 4.1D), 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*).

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 (Fig. 4.1E), 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, suprarostral, 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 (Fig. 4.1C). 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).

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 (Fig. 4.3) 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).

Figure 4.3 Water-conserving posture of *Neobatrachus sutor*. [Photo by P.C. Withers]

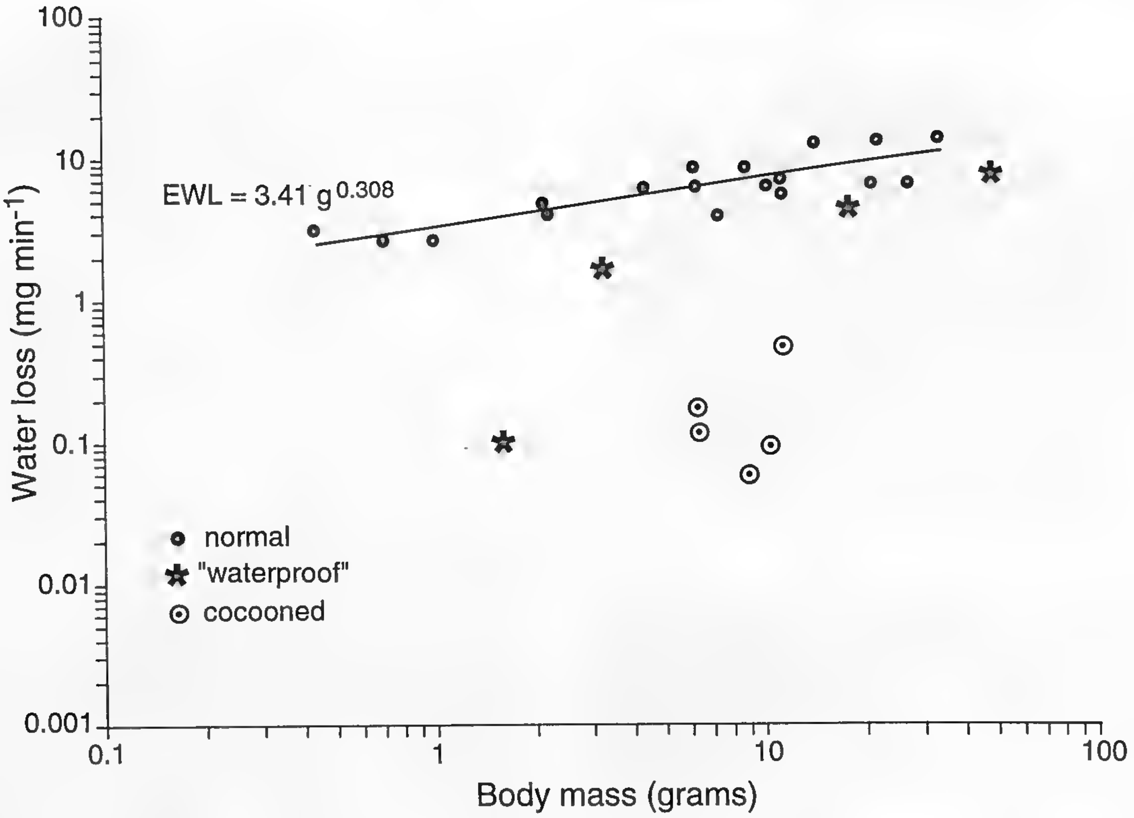

Figure 4.4 Relationship between rate of evaporative water loss, EWL, and body mass for a variety of Western Australian frogs, for cocooned *Cyclorana* and *Neobatrachus*, and for water-proof *Litoria*. (From Withers unpub. data; van Beurden 1984; Buttemer 1990) [P.C. Withers]

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 (Fig. 4.4), 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.

Some 'water-proof' Australian tree frogs have an EWL that is much lower than that of a free water surface. For example, *Litoria gracilenta* 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. pelobatoides, 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 (Fig. 4.5B); 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.

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/cm^2/h to over 140 mg/cm^2/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. wilsmorei*; 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).

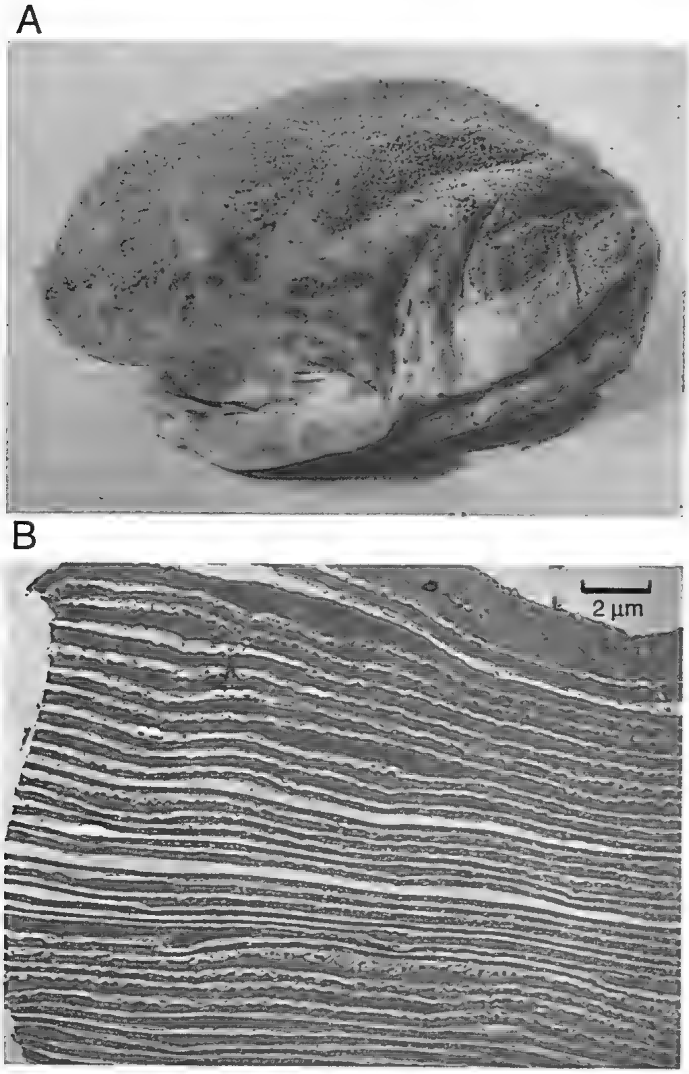

Figure 4.5 Structure of the cocoon of fossorial frogs. A, *Neobatrachus sutor* in a cocoon; B, transmission electron micrograph of a section of a cocoon from *Neobatrachus sutor*, showing the multiple layers of single-cell thick stratum corneum. [Photos by P.C. Withers]

SKELETAL SYSTEM

The bones and their arrangement in adult Australian frogs follow the basic anuran pattern (Fig. 4.6C). 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 (Fig. 4.6A).

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 (Fig. 4.6A). 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 (Fig. 4.6B).

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.

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 (Fig. 4.6A). 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 (Fig. 4.6B). 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

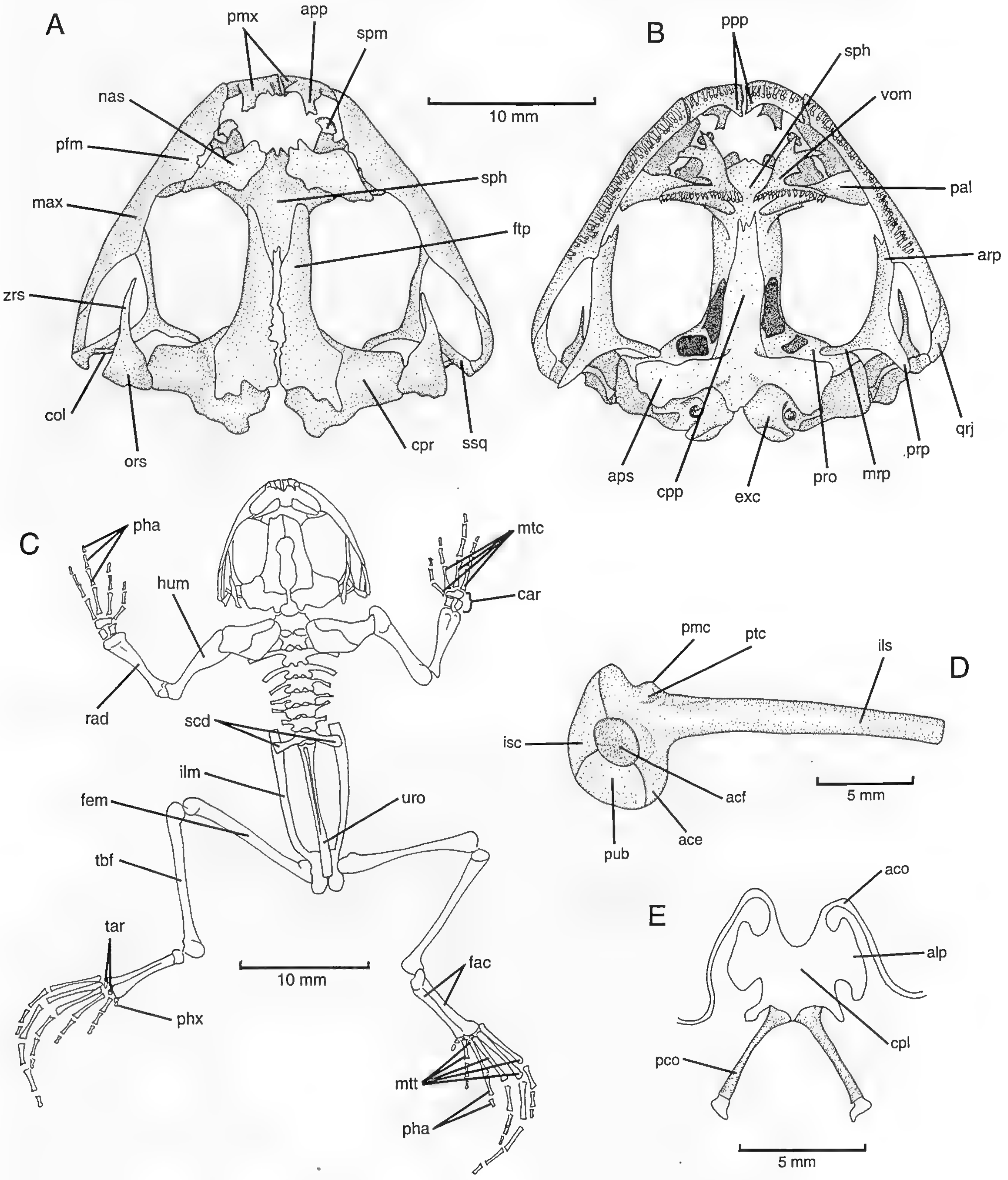

Figure 4.6 Skeletal components of frogs. A, dorsal, and B, ventral views of the skull of *Limnodynastes peronii*; C, skeleton of *Crinia haswelli* in dorsal view; D, lateral view of the ilium of *Heleioporus inornatus*; E, ventral view of the hyoid of *C. haswelli*. **ace**, acetabular expansion; **acf**, 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 diapohyses; **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]

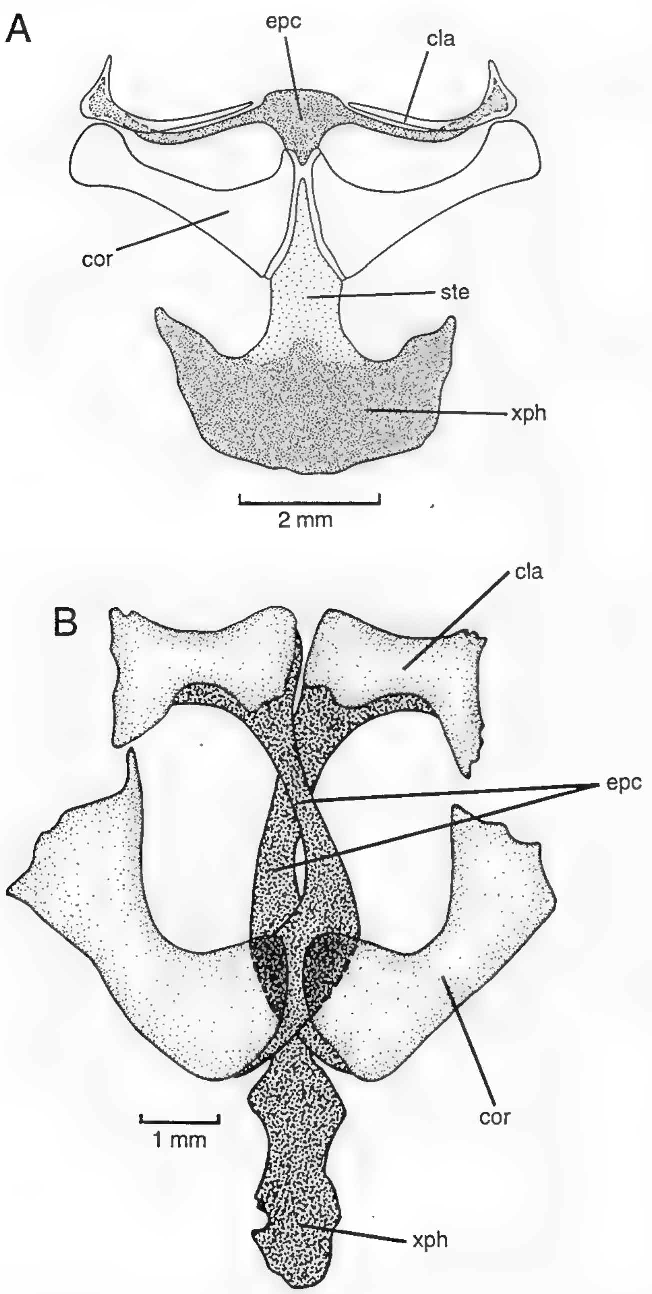

Figure 4.7 Pectoral girdles of frogs. **A**, firmisternal girdle of the microhylid *Sphrenophyne fryi*; **B**, arciferal girdle of the myobatrachid *Myobatrachus gouldii*. **cla**, clavicle; **cor**, coracoid; **epc**, epicoracoid cartilage; **ste**, sternum; **xph**; xiphisternum. [A, C. Eadie; B, M.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

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 (Fig. 4.6A). 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 angulosplenial, the dentary and the mentomeckelian bones and cartilages. Dorsal processes are present posteriorly on the angulosplenial in many species, such as the *Litoria citropa* species group (McDonald & Davies 1990).

The hyolaryngeal skeleton (Fig. 4.6E) 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 (Fig. 4.6C). 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 (Fig. 4.7A). 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 (Fig. 4.7B).

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 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 (Fig. 4.6D). 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 (Fig. 4.6D). 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.

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 (Kestevan 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 (Fig. 4.8).

In the Pelodryadinae, *m. submentalis* is moderate in size and lacks a raphe, and *m. intermandibularis* has a supplementary apical element (Tyler 1971a; Tyler & Davies 1978) (Fig. 4.8A). In the Limnodynastinae, but not in the Myobatrachinae, the most anterior fibres of *m. intermandibularis* attach upon the ventral surface of *m. submentalis* (Fig. 4.8B). In all Myobatrachidae, *m. intermandibularis* is not differentiated into separate elements (Tyler 1972b; Davies & Burton 1982; Burton 1983) (Fig. 4.8C). 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).

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).

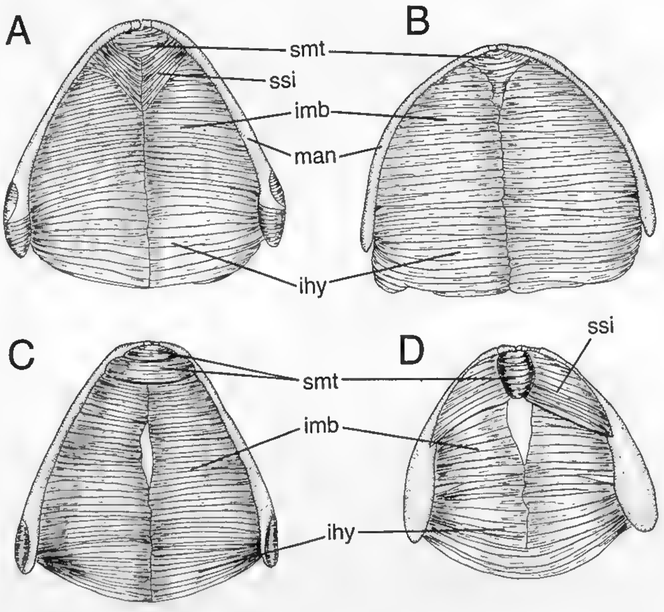

Figure 4.8 Superficial mandibular musculature of frogs. **A,** *Litoria aurea* (Hylidae: Pelodryadinae); **B,** *Limnodynastes tasmaniensis* (Myobatrachidae: Limnodynastinae); **C,** *Taudactylus acutirostris* (Myobatrachidae: Myobatrachinae); **D,** *Sphenophryne* species (Microhylidae: Microhylinae). **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]

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 prodigous 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 O_2 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 actived 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 E_2 (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 O_2 transport. They tend to be large, as in *Neobatrachus sutor* (a diploid species), in which the red blood cells are about 17 μm × 11 μm, and *N. kunapalari* (a tetraploid) with even bigger red blood cells about 21 μm × 13.5 μm. There are generally about 5×10^5 to 10^6 red blood cells/mm^3 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 exernal 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).

Cardiovascular physiology has been extensively studied for *Bufo marinus*. Oxygen delivery to the tissues by the circulation depends on the O_2 content of arterial and venous blood, and the blood flow rate. The O_2 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 O_2/gram (Hillman 1976). The oxygen dissociation curve is generally sigmoidal, but the P_{50} value (the partial pressure of O_2 for 50% saturation) varies dramatically depending on the partial pressure of CO_2, pH and temperature. For *Bufo marinus*, the P_{50} is about 5.9 kPa (pH 7.4, 25°C; Hall 1966). The P_{50} varies for tadpoles and adults, and also for different species. The Bohr shift increases the O_2-unloading capacity of the blood to the tissues.

Dramatic adjustments of cardiovascular and respiratory function during activity increase O_2 delivery to tissues to match their increased O_2 requirements. Blood flow increases because of elevated arterial blood pressure and decreased peripheral resistance. The arterial blood O_2 level increases during activity, facilitating O_2 delivery. Most of the increased O_2 demand of activity is met by increased O_2 extraction from the blood (A–V O_2 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 CO_2. 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 O_2 exchange. For resting *Bufo marinus*, the resting VO_2 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 O_2 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 (Fig. 4.9). 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 (Fig. 4.9). MRR 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 MRR 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 (Fig. 4.9). For example, the metabolic rate of *Neobatrachus pelobatoides* declines by about 80% from

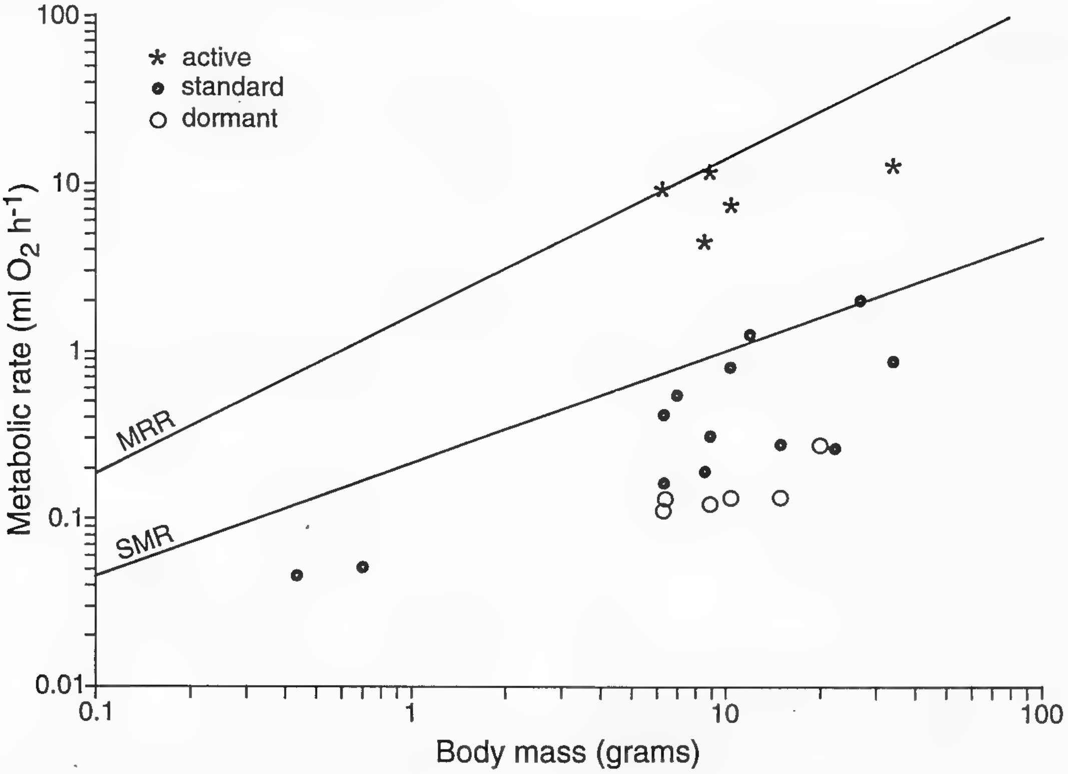

Figure 4.9 Relationship between metabolic rate and body mass for resting Western Australian frogs, and for dormant, cocooned frogs. **MRR**, maximal metabolic rate; **SMR**, standard metabolic rate. (From Withers unpub. data) [P.C. Withers]

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 ammoniotely to terrestrial ureotely has been documented for the Australian tree frogs *Litoria raniformis* and *L. ewingii* (Cree 1985). There is a similar shift for *Pseudophryne corroborree* from ammoniotely as aquatic tadpoles to ureotely 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/cm^2/h, and for *Bufo marinus* from 28 to 85 ml/cm^2/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 infrafrenata*, 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.

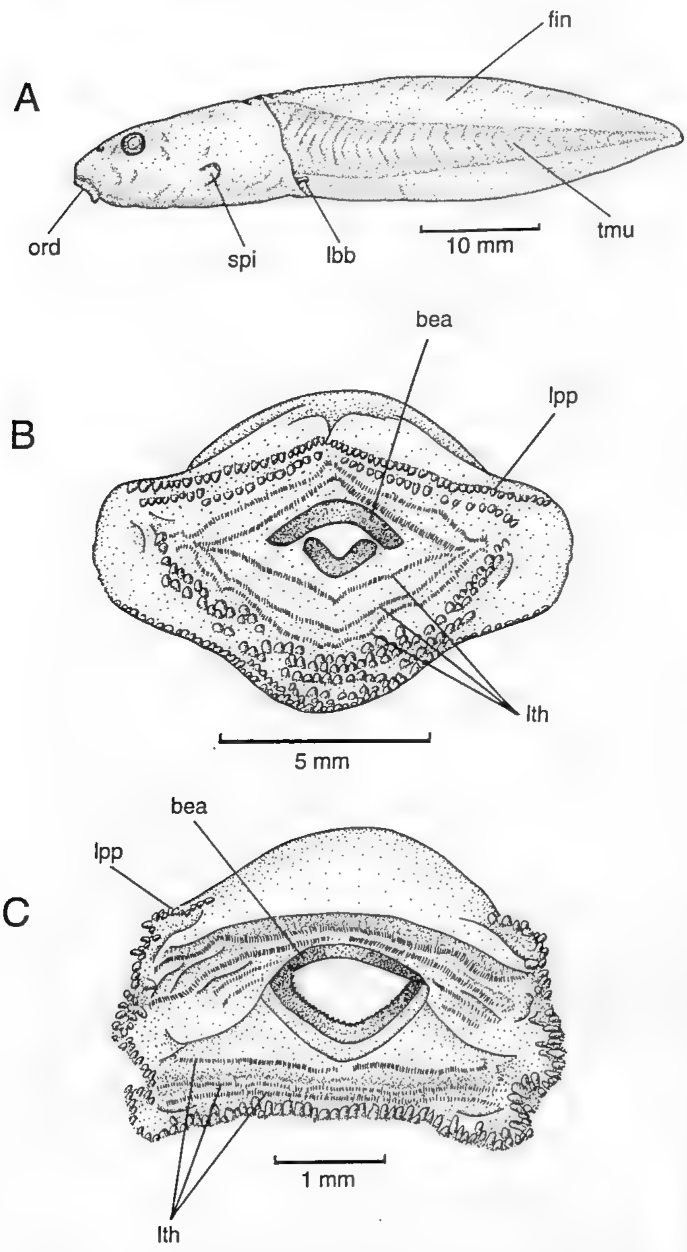

Figure 4.10 Tadpoles of Australian frogs. **A**, lateral view of *Limnodynastes salmini* (stage 33 of Gosner 1960); **B**, mouth disc of *Litoria nyakalensis*, a lotic species; **C**, mouth disc of *Limnodynastes salmini*, a lentic species. **bea**, horny beak; **fin**, fin; **lbb**, limb bud; **lpp**, labial papillae; **lth**, labial teeth; **ord**, oral disc; **spi**, spiracle; **tmu**, tail musculature. [M. Davies]

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 (Fig. 4.10A), 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) (Fig. 4.11A).

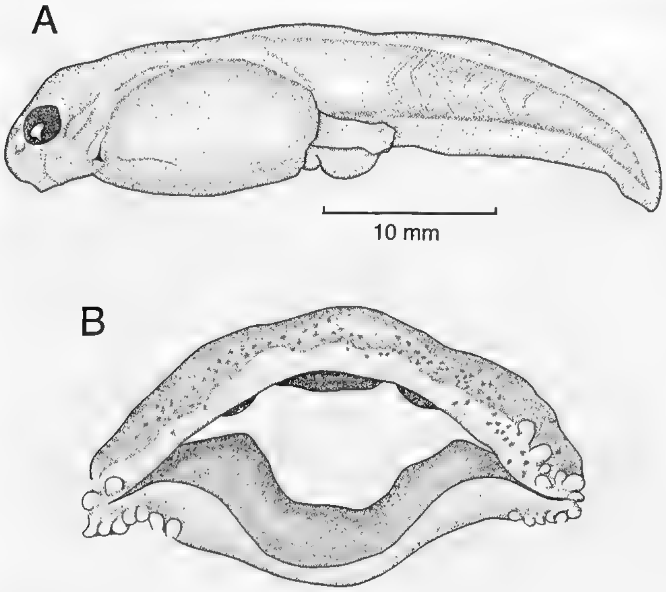

Figure 4.11 Tadpole of *Rheobatrachus silus*, a direct developing species. **A**, lateral view of stage 34 of Gosner (1960); **B**, mouth disc. (From Tyler & Davies 1983a) [M. Davies]

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) (Fig. 4.10C) whilst lotic species have elaborations of the discs that enable larvae to attach to the substrate in fast flowing waters (Fig. 4.10B). 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) (Fig. 4.11B).

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 (Fig. 4.10A), 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 by the water potential of the substrate, 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).

5. NATURAL HISTORY OF THE ANURA

J. Dale Roberts

INTRODUCTION

The Australian frog fauna is diverse and widespread, although regional species richness may vary. Frogs are found in all parts of Australia, from the tops of the coldest, highest mountain ranges in the Australian Capital Territory and New South Wales to the most remote desert areas in inland Australia. For example, *Pseudophryne corroboree* (Pl. 2.5) occurs at elevations of greater than 1800 m in the Brindabella Range near Canberra (Osborne 1989), whereas the type locality for *Neobatrachus centralis* is on the arid Birdsville Track, 112 km east of Lake Eyre (Ledo & Tyler 1973). Areas of highest species diversity are in the tropics and around the wet continental margins, particularly on the east coast near the New South Wales—Queensland border and in far north Queensland, but even desert regions may support up to six species (Fig. 5.1; Pianka & Schall 1981).

This chapter reviews the biology and natural history of frogs with specific reference to Australian species. An excellent, detailed treatment of the biology of amphibians has been given recently by Duellman & Trueb (1986). A specific treatment of many aspects of the biology of Australian frogs is given by Tyler (1989a).

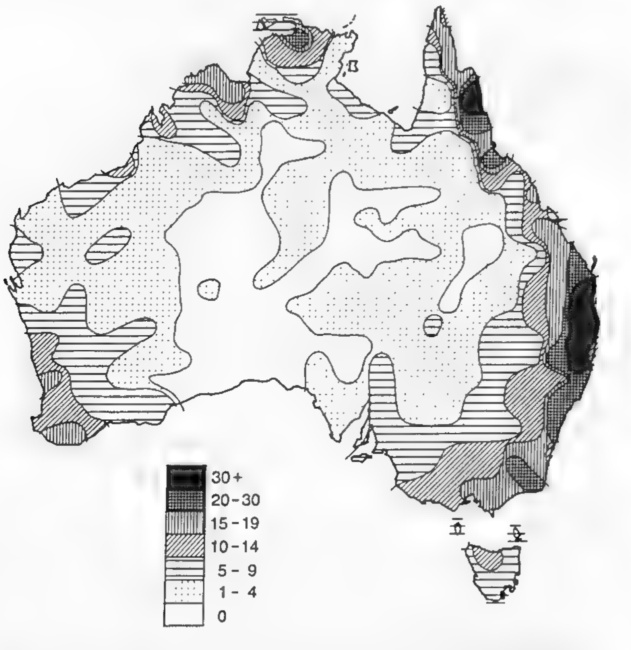

Figure 5.1 Species diversity plot for Australian frogs. The most detailed data available have been used for plotting distributions of all species. However, ranges for species that might cover half the continent, such as *Neobatrachus sutor*, may have significant gaps in remote areas. Therefore areas of zero diversity should be viewed critically, as frogs may occur there. (Updated from Brook 1983) [W. Mumford]

LIFE HISTORY

Reproductive Strategies

Breeding in frogs may be explosive, extending over one or a few nights per year, or be prolonged over weeks or months (Wells 1977). Prolonged and explosive breeding are the divergent ends of a continuum. Both extreme breeding strategies may be found in temperate and arid zone species in Australia.

In explosive breeders such as many *Neobatrachus* species, there may be up to 250 or more adults in a small pond (Roberts 1978). The operational sex ratio (OSR, defined as the number of fertilisable females to available males; Emlen and Oring 1978) is typically biased towards males. For example, in a single pond near Narembeen, Western Australia, observations on 17 amplexed pairs and 14 unpaired males of *Neobatrachus kunapalari* in a breeding chorus on one night after summer rain in January 1987 (Roberts pers. obs.), indicated an OSR of roughly 1:2. This is comparable with values for six north American and European species of *Rana* and *Bufo* (Arak 1983).

Prolonged breeders, such as *Rana*, *Hyla* and *Bufo*, have OSR values ranging from 1:5 to 1:31 (Arak 1983). In *Limnodynastes tasmaniensis* calls from up to twenty males per night in a single pond were recorded, though amplexed females or females moving through the breeding chorus were rare (Roberts pers. obs.). However, the breeding season for this species extends over several months during spring and into summer (Roberts 1993).

Prolonged breeding may be more common in the tropics. All of twenty one well-studied species in the Magela Creek system, Northern Territory, have an extended calling period but often a much more limited period for egg deposition (Tyler, Crook & Davies 1983). *Pseudophryne occidentalis*, which is widespread in the arid zone of Western Australia, may call in summer after rain or in autumn (January to late June) (Main, Littlejohn & Lee 1959), while *Neobatrachus aquilonius*, from near Port Hedland, observed in 1983 and 1993, called for only one night after heavy rain (Roberts pers. obs.).

Prolonged breeders experience severe male-male competition for access to females, which may be reflected as males fighting or as strong vocal interactions (see Calls below). Such competition may be less severe or absent in explosive breeders.

Males of many prolonged breeders spend extended periods at breeding sites and some will probably mate more than once. Where a few males dominate many matings, highly skewed breeding success can occur (for example, Ryan 1983). The same dominance by certain individuals is not apparent in explosive breeders (for example, Howard 1988). No data reflecting male mating success are available for any Australian frog species. However, it is likely that these two extreme patterns of individual male success will be found in Australian frogs. Male mating success may be correlated with body size (for example, Ryan 1983, bigger males do better), calling rate (Howard 1988, faster callers do better) or number of nights attending a breeding chorus (for example, Godwin & Roble 1983) amongst other variables.

Woodruff (1976a) noted either multiple clutching by females in *Pseudophryne* species or that females spread egg laying (with a single male parent) over several nights. Humphries (1979) established that some species, for example, *Limnodynastes tasmaniensis*, may make multiple entries to breeding ponds in one season, but this was not the norm. Females bred twice in one breeding season in five species studied by Humphries. The second clutch was generally smaller than the first, but only 2 to 10% of females in these five species actually entered the breeding pond more than once in a single season.

In non-Australian frogs, reproductive patterns of females are very variable and may vary geographically within species. Females of *Hyla rosenbergi* from central America mature at one year old, deposit up to six different egg clutches at an average interval of 24.7 days, then do not return to the chorus the next year and presumably die (Kluge 1981). Patterns of maturation and egg deposition may be environment specific as Berven (1981) reported large differences in age at first egg clutch and first entry to breeding ponds for both male and female wood frogs (*Rana sylvatica*) from lowland and montane sites in North America. This species has only a single clutch per year, but it is also an explosive breeder (Berven 1981).

Egg and Tadpole Survival

Mortality of amphibian eggs and tadpoles is often very high. Malone (1985) estimated from 0 to 95% survival from egg deposition to hatching for the direct developing *Philoria frosti* (based on 77 egg masses from seven sites). Humphries (1979, Table 5.7) estimated a survival rate of 0 to 2.7% from egg to metamorphosis for seven species over two years. These data are comparable with studies on other continents (*cf.* Table 11.3, in Duellman & Trueb 1986). No other data on egg or tadpole survival are known for Australian frogs.

Duration of the tadpole stage is known for many species and ranges from 16 to 30 days in *Notaden nichollsi*, a species found in north-west desert areas (Main 1968). In temperate species, larval life-spans may be as long as 160 days (for example, *Limnodynastes dorsalis*; Main 1968) and up to 430 days for *Litoria moorei* (Roberts pers. obs.). Overwintering by tadpoles, resulting in very long larval life-spans, is known in several North American and European species (Duellman & Trueb 1986).

Population Size and Persistence

There are few detailed studies of population size or structure in Australian frogs. Humphries (1979) showed that the size of breeding populations was variable between species. For example, over one thousand individuals of *Limnodynastes tasmaniensis* bred in one year in a single pond of 20 m diameter, compared to only one or two individuals at the same site for *Limnodynastes dumerilii* and *Neobatrachus pictus*. Although these data give some indication of population sizes at breeding sites, there are few data which actually give a reliable estimate of density.

Frogs may be very common in some environments. Roberts (1985) estimated a minimum population density for *Arenophryne rotunda* of 277.6 frogs ha^{-1} and summarised earlier data on several other Western Australian species. Ingram (1983) gave population estimates for *Rheobatrachus silus* (Pl. 2.7) of 1.11 frogs ha^{-1} with considerable variation in density between adjacent pools and stretches of stream. Morton, Masters & Hobbs (1993) estimated 34–68 frogs ha^{-1} for the burrowing species *Cyclorana maini*, *Neobatrachus* sp., *Notaden nichollsi* and *Uperoleia micromeles* in the spinifex grasslands of the Tanami Desert, Northern Territory.

There are no studies documenting long term fluctuations in population size. Some cover two to three seasons (for example, Main 1965a; Humphries 1979; Ingram 1983; Osborne 1989). These indicate apparent large fluctuations related to annual variations in rainfall (Humphries 1979), declines resulting from unknown causes (Ingram 1983; McDonald 1990), declines where severe drought may be a cause (Osborne 1989) or, for *Crinia insignifera*, apparent stability of the adult population size over three years (Main 1965a). However, it is important to distinguish attendance at a breeding site from death. In other words, if the population estimate is low because few frogs make it to the study pond because of low rainfall, is the population truly low? Will the frogs survive and breed next season or are they dead?

We do not understand the causes of fluctuations in population estimates or the ecological phenomena they reflect. Although Humphries (1979) reported low population densities for several species around a farm dam near Canberra, the same species have been reported to be extremely abundant at other sites that have different ecological attributes. For example, *Neobatrachus pictus*, rare in Humphries's study, was extremely abundant in natural ponds in south-eastern South Australia (Roberts 1978). These differences relate to the specific habitat requirements of species like *N. pictus*, which generally breeds in temporary, rather than permanent, ponds.

Age at first breeding is known for several Australian frog species. *Heleioporus eyrei* bred at age two years (Lee 1967). Some males of *Arenophryne rotunda* may breed at age one year, but most breeders were older (Roberts 1984), and Ingram (1983) reported that *Rheobatrachus silus* attained maturity at age two years. Humphries (1979) estimated that several hylid and myobatrachid species at his study site could mature as early as nine months, but that young frogs of all species studied could attend their first breeding congress at 18 to 20 months old. However, age estimates in the studies on *H. eyrei* and *A. rotunda* were based on body size and these may not correlate with chronological age (Humphries 1979; Platz & Lathrop 1993). There are no published data on Australian frogs relating known age animals to the presence of growth rings, such as have been reported for amphibians from other continents (for example, Kalb & Zug 1990). However, Lynch (1992, pers. comm.) has demonstrated the existence of growth rings in five species of West Australian frogs.

Longevity of Australian frogs is poorly known. Duellman and Trueb (1986, Table 11.2) summarised data on longevity of frogs. The range for 12 species (representing most frog families) was from 6 to 36 years. The only Australian species in their study, *Litoria caerulea*, lived for 16 years. However, most of these records were from captive animals and may not reflect longevity in the field.

Little is known of the persistence of populations at particular sites for any Australian species. In Humphries's (1979) study, the abundance of particular species varied radically from year to year, partly in relation to obvious, proximate factors like rainfall. The disappearance of several species in eastern Australia in recent years (Czechura & Ingram 1990; McDonald 1990) is cause for some concern, but it is still not clear whether this is a natural phenomenon or a consequence of human activities (Blaustein & Wake 1990). In Brazil, similar disappearances have been attributed to severe frosts (Heyer, Rand, daCruz & Peixoto 1988). Osborne (1989) has invoked drought as a cause for the decline of *Pseudophryne corroboree*. These 'disappearing species' may actually undergo radical fluctuations in population size, previously unknown simply because they have not been studied (Tyler 1991b).

ECOLOGY

Distribution and Habitat Use

Frogs occur in a vast array of habitats and make use of both natural and disturbed areas. For example, pit-trapping on rehabilitated, bauxite mine-sites near Jarrahdale, Western Australia, captured seven of nine frog species known from adjacent undisturbed, upland jarrah forest (Nichols & Bamford 1985). However, few of the species actually bred in the rehabilitated area. Breeding may occur in fast-flowing streams (for example, *Crinia riparia*, Littlejohn & Martin 1965), arid-zone ponds that may only last 10 to 14 days before they dry up (for example, species of *Cyclorana*, *Limnodynastes*, *Notaden* and *Neobatrachus*; Main 1968) or in permanent and temporary ponds and streams (for example, *Limnodynastes* and *Crinia* species in south-eastern and south-western Australia; Main 1965a, 1968). Many species use natural breeding sites, but commonly frogs also breed in farm dams and in many other man-made structures that can hold water. Tyler (1991b) reported breeding by many northern Australian species in borrow-pits resulting from road construction.

Despite their propensity to lose water through the skin, frogs also survive well in arid areas. Several species of *Neobatrachus* and *Cyclorana* are able to burrow and form waterproof cocoons which reduce water losses to levels comparable to those of lizards (Lee & Mercer 1967; Chapter 4 this volume). These species can depress their metabolic rates when underground (van Beurden 1980; Flannigan, Withers & Guppy 1991). Such adaptations

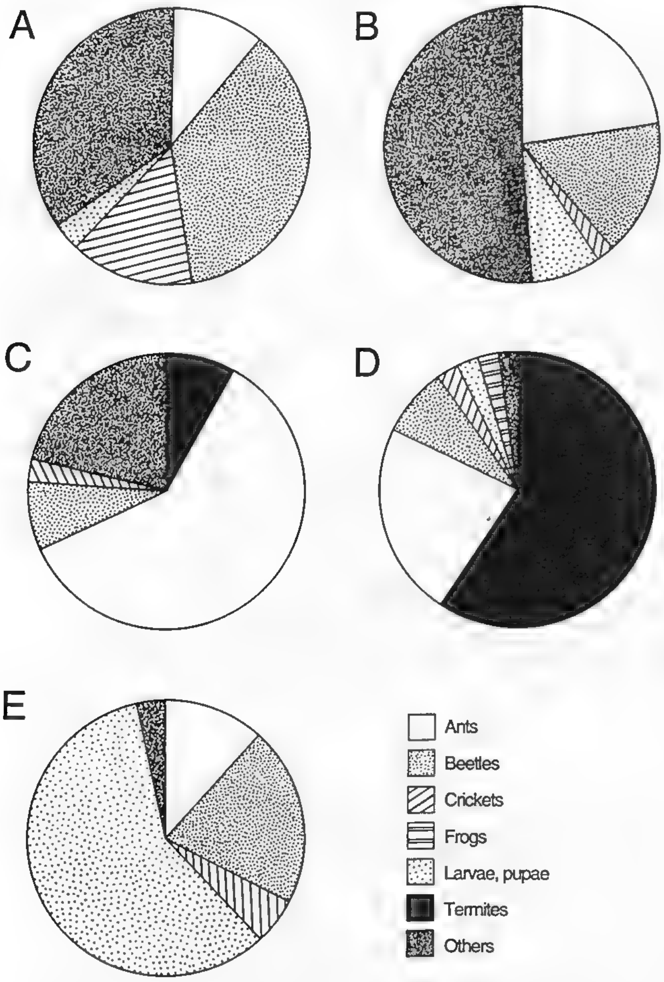

Figure 5.2 Diets of one introduced and four indigenous species from the Northern Territory. A, *Litoria pallida*; B, *L. rothii*; C, *L. rubella*; D, *Bufo marinus*; E, *Crinia* sp. (After Freeland & Kerin 1988) [D. Wahl]

facilitate long-term survival in arid habitats. Van Beurden (1980) estimated that 10% of dormant *Cyclorana platycephala* could live for at least 5 years without feeding or emerging, and some could have survived longer.

Food

Among Australian frogs, the only known feeding specialist, *Myobatrachus gouldii*, feeds almost exclusively on termites (Calaby 1956). The remainder appear to be generalists. Freeland & Kerin (1988) reported seven diet classes: termites, ants, beetles, crickets, larvae-pupae, frogs and 'other', in their analysis of the food of *Litoria pallida*, *L. rothii*, *L. rubella*, *Bufo marinus* and a *Crinia* species from the Northern Territory. Five to seven of these prey groups were found in each of the five species (Fig. 5.2). Similarly, the dietary items reported by Main (1968) for most species are very diverse, ranging from a variety of insects to land snails.

Generally, smaller frogs consume smaller prey. For example, *Crinia signifera* and *C. parinsignifera* in Victoria, eat mostly prey items weighing up to 29 µg and may actively avoid larger items, even though they are present in the habitat (MacNally 1983). However, large species also often eat surprisingly large numbers of small prey items. For example, *Heleioporus barycragus*, one of the largest Australian frogs (up to 86 mm snout-vent length), eats large numbers of ants and beetles (Lee 1967). By contrast, Lee (1967) found that the largest prey item, a centipede 9 cm long, was eaten by *H. eyrei* which has an average body length of about 55 mm.

Studies of the food of Australian frogs based on museum specimens may not necessarily represent diets at all times. For example, specimens of *Notaden nichollsi* collected after cyclonic rain are likely to have guts full of termites, as this is also a time when termites are particularly active. If this species had been collected after cool, winter rain the diet might be different (Main 1968).

Tadpoles feed either by actively foraging and scraping material off with the labial teeth and the beak or by trapping material in mucus secreted by the internal gills. The mucus traps bacteria, algae, zooplankton *etc.* from water flowing through the mouth and out over the gills. The mucus is then transferred into the oesophagus (Tyler 1989a). Most tadpoles are suspension feeders, consuming a combination of aquatic invertebrates, algae or other micro-organisms in the water column. However, tadpoles of some species are more predatory. The North American *Scaphiopus bombifrons* feeds on tadpoles of other species, and those of the Australian *Lechriodus fletcheri* (Pl. 2.10) may feed on tadpoles of its own species (Martin 1967b).

Breeding Seasons

Temperate frog species usually have a well-defined breeding season, but tropical species may reproduce throughout the year. In south-western Australia different species can be found breeding all through the year. Autumn breeders include the five species of *Heleioporus*, *Geocrinia leai*, *Pseudophryne guentheri* and *P. occidentalis*. These species deposit eggs on land where they hatch later and adopt a conventional tadpole life-style when flooded by rising water levels in winter. Winter breeders include *Crinia georgiana*, *C. insignifera*, *C. pseudinsignifera*, *C. glauerti* and *Litoria adelaidensis*. In spring, species of the *Geocrinia rosea* complex and *Litoria moorei* and *L. cyclorhyncha* breed. After heavy rains in autumn or early winter, species of *Neobatrachus* will also call and breed for short periods. In summer, *Myobatrachus gouldii* and *Metacrinia nichollsi* call after rain. In addition, some species that occur within the area of reliable winter rainfall will also breed after summer rains (*Neobatrachus kunapalari* and *Pseudophryne occidentalis*; Main 1965a, 1968).

Similar seasonal patterns are evident in other parts of the country though breeding and calling is likely to be cued in some way to local seasonal rainfall. The predictability of winter rainfall is crucial to egg survival and later tadpole survival, even in autumn breeders like *Heleioporus*.

Most species in the arid zone are explosive breeders that respond whenever significant rain falls (Main *et al.* 1959; Main 1968). However, there may be some temperature constraints on breeding activity. For example, according to Main (1965a), *Neobatrachus centralis* only breeds at temperatures above 16°C.

Egg and Tadpole Ecology

Australian frogs show a wide range of egg depositional strategies (Table 5.1). These range from the conventional frog strategy of eggs deposited in water with a free-swimming tadpole (all known hylid species and many myobatrachids), through terrestrial egg deposition with an aquatic tadpole (many myobatrachids such as *Heleioporus* and *Pseudophryne*), to total withdrawal from water with a direct developing egg (that is, no tadpole stage; microhylids and some myobatrachids such as *Geocrinia* and *Myobatrachus*). The complete withdrawal from water, combined with obligate parental care undertaken by the genera *Rheobatrachus* and *Assa* represents the ultimate depositional strategy for frogs. The diversity of egg depositional strategies is wide in myobatrachids, but only the conventional frog strategy is known certainly for hylids (Table 5.1). However, even if the eggs are deposited on land and there is a greater or lesser period of development out of water, in no case is this development independent of water. Without either free water, or water in the surrounding soil, eggs will desiccate. No known frog anywhere in the world has evolved mechanisms that allow egg survival independent of external sources of water.

Table 5.1 Reproductive modes in Australian frogs. References are given for species where unusual reproductive modes are indicated, or only certain species in a genus have a particular egg mass form. Otherwise data are taken from Table 1 of Tyler (1985).

Mode	Eggs	Larvae	Family	Genus
I	in water, non-foamy egg mass	in water	Hylidae Myobatrachidae Ranidae	*Cyclorana, Litoria, Nyctimystes* *Crinia, Limnodynastes tasmaniensis* (southern call race[1]), *Neobatrachus, Notaden, Pseudophryne douglasi*[2], *Taudactylus, Uperoleia* *Rana*
II	in water, foamy egg mass	in water	Myobatrachidae	*Adelotus, Heleioporus australiacus*[3], *Lechriodus, Limnodynastes, Megistolotis*
III	on land, in burrow, or amongst vegetation above water	in water	Hylidae (?) Myobatrachidae	possibly *Litoria longirostris*[4] *Geocrinia* (except *G. rosea* group[5]), *Mixophyes, Pseudophryne*
IV	foamy egg mass on land, in burrow.	in water	Myobatrachidae	*Heleioporus*
V	on land, in depression, hatches from capsule	direct development, no feeding stage	Myobatrachidae	*Geocrinia rosea* group[5]
VI	foamy egg mass, on land, in depression or nest	direct development, no feeding stage	Myobatrachidae	*Kyarranus, Philoria*
VII	on land, in depression or nest	direct development, no feeding stage	Microhylidae	*Cophixalus, Sphenophryne*
VIII	deep under soil surface (up to 1.2 m), intracapsular development	direct development, no feeding stage	Myobatrachidae	*Arenophryne, Myobatrachus*, possibly *Metacrinia*
IX	on land, male carries developing larvae in inguinal pouches	direct development, no feeding stage	Myobatrachidae	*Assa*
X	on land, female carries developing larvae in stomach	direct development, no feeding stage	Myobatrachidae	*Rheobatrachus*

[1] Roberts & Seymour 1989; [2] Main 1965; [3] Watson & Martin 1973; [4] Tyler & Davies 1977; [5] Roberts, Wardell-Johnson & Barendse 1990.

Ten reproductive modes are recognised here for Australian frogs (Table 5.1), compared to the eight recognised by Tyler (1985b). Modes I to X of Table 5.1 represent increasing removal of part of the development process from free-standing water. Thus I have recognised divisions based on the foamy or non-foamy form of the egg mass, and the site of egg deposition. The difference between eggs deposited in a burrow or amongst vegetation rather than buried underground represents the difference between easy and no access to free-standing water for the tadpole. Forms in which the egg hatches during development and the tadpole moves into water, or must persist in a locally moist microhabitat, are distinguished from those in which the egg is deposited in a locally moist microhabitat and all development takes place inside the egg capsule. Two categories relate to different forms of obligate parental care.

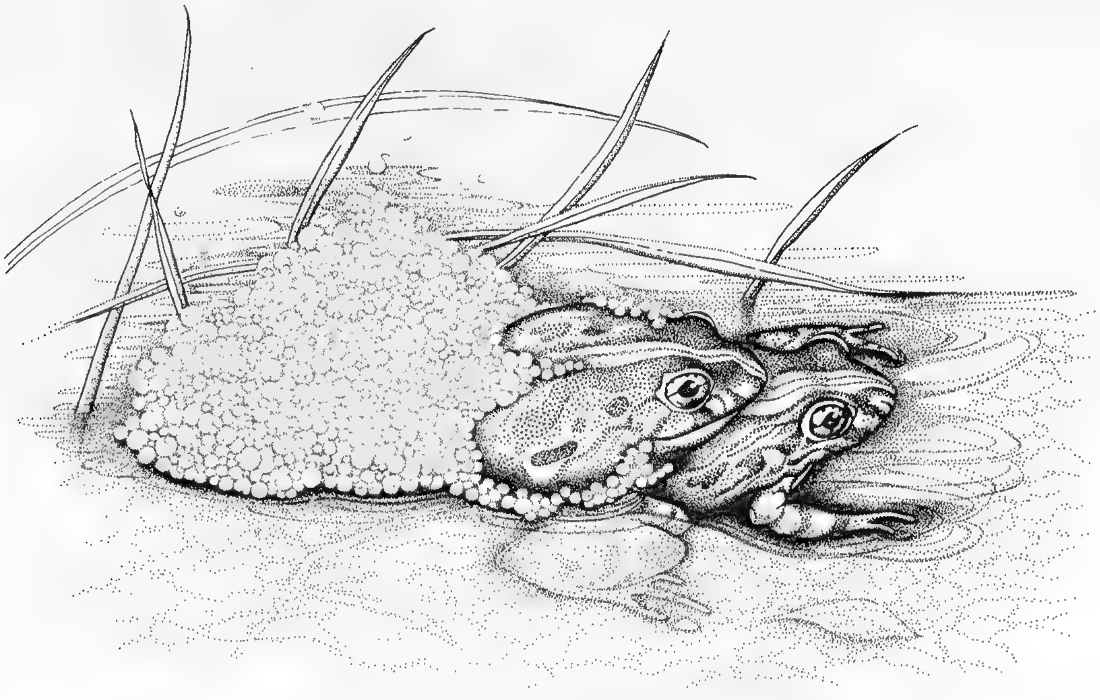

Figure 5.3 Amplexed pair of *Limnodynastes ornatus* depositing foam nest. Eggs are mixed up in the foam or are in a jelly layer at the water surface under the foam. (After photo by K. Uhlenhut/ANT) [T. Wright]

Figure 5.4 Hatched tadpoles entering the inguinal pouches of a male *Assa darlingtoni*. Eggs are deposited on land, hatch and then develop in the inguinal pouch for about 49 days. (After photo by H. Ehmann/NPIAW) [T. Wright]

However, the modes do not represent a simple phylogenetic development with mode II derived from mode I and so on. Foamy egg masses in *Heleioporus* and other members of the subfamily Limnodynastinae may not represent an homologous form as *Heleioporus* lack the flanges on the first two fingers of females of other foam nesting species (*cf.* Roberts & Seymour 1989). A foamy egg mass may protect eggs from predators and desiccation, and reduce internal temperature by reflecting heat. It may also allow development of eggs on land, giving tadpoles an advantage when they enter ponds, or hold eggs at the water surface in well-oxygenated water.

Terrestrial egg deposition has probably evolved independently in each of the genera in mode III. None of these genera are closely related (Farris, Kluge & Mickevich 1982; Maxson 1992). Mode V may have evolved from the form in mode III, but it is less certain that mode VIII evolved from mode III, despite the close relationship between *Pseudophryne* and *Myobatrachus*, *Metacrinia* and *Arenophryne* (Roberts 1984; Maxson & Roberts 1985; Roberts & Maxson 1989). Highly-derived breeding biologies have apparently evolved independently in many Australian frog genera, although in their analyses of relationships of Australian frogs both Heyer & Liem (1976) and Farris *et al.* (1982) treated direct development as an homologous character in all genera of myobatrachids.

Eggs of many Australian species which are not direct developers can survive in moist terrestrial environments. Martin (1967a) reported survival for up to 118 days for eggs of *Geocrinia victoriana*. Shorter survival periods are known for eggs of *Heleioporus* and *Pseudophryne* species held out of water (Main 1965a; Lee 1967). During this period the developing embryo grows and survives on nutrients stored in the egg yolk. Eggs of these species hatch when flooded by rising water levels.

BEHAVIOUR

Basking

Though frogs are usually active at night (for example, Tyler *et al.* 1983), several Australian species are active during the day. *Taudactylus diurnus* from south-east Queensland takes its specific name from its exclusively diurnal activity pattern (Straughan & Lee 1966). Johnson (1971) showed that body temperatures of *T. diurnus* were generally higher than ambient air temperatures (greatest differences were 5.5°C for adults and 8.0°C for juveniles), suggesting that there is active thermoregulation. However, the mechanism is not clear as eleven nocturnally active species also showed body temperatures higher than ambient (Johnson 1971).

Tyler *et al.* (1983) reported diurnal basking in *Cyclorana australis* and *Litoria dahlii* from the Northern Territory. Field body temperature in both these species was very similar to those of their local environment. Field studies on other continents have shown that many frog species may maintain body temperatures above the ambient temperature by actively moving between different thermal micro-climates. Basking forms part of this process and is particularly common in species from high mountain habitats (see summary in Hutchison and Dupré 1992).

Breeding Behaviour

The basic breeding system of frogs involves adults pairing, external fertilisation of eggs which develop in water and hatch into a tadpole, followed by metamorphosis into a small frog. However, this basic summary hides much of the complexity and diversity in breeding systems.

In most frogs, pairing of males and females is initiated by the male's call (see section on Calls below) which has a crucial function in attracting females. Once together the male and female amplex with the male on the back of the female. Eggs are released from the cloaca of the female and typically are fertilised externally by sperm released simultaneously by the male (Fig. 5.3).

A few frogs have internal fertilisation. For example, sperm is transferred by a specialised intromittent organ in *Ascaphus truei* from the north-west coast of the United States of America. Internal fertilisation may occur in *Eleutherodactylus coqui*, as sperm have been found in the female reproductive tract and fertile eggs can be deposited without male involvement (Townsend, Stewart, Pough & Brussard 1981). The American genus *Eleutherodactylus* and the West African genus *Nectophrynoides* achieve internal fertilisation by apposition of the cloaca of males and females. Though internal fertilisation may occur in Australian frogs, it has not been demonstrated.

There are several Australian species with direct development and in at least one case, *Arenophryne rotunda*, males and females stay associated for up to five months before egg deposition, suggesting that male involvement at that time is important (Roberts 1984).

Parental care by males is known in *Cophixalus parkeri* (a microhylid from New Guinea) and the presence of adults, usually males, enhances egg survival (Fig. 9.4; Simon 1983). Male parental care may be important in Australian *Cophixalus* though it has not been documented. Male parental care is well developed in *Assa*, where males carry the developing young in inguinal pouches (Fig. 5.4; Straughan & Main 1966). In the genus *Pseudophryne*, males are commonly associated with eggs but these eggs can develop without the male present (Fig. 5.5; Woodruff 1977). As Woodruff noted, the association of eggs and males may not be a form of parental care, but rather continued use of a successful calling site by males. Gastric brooding is a bizarre and unique form of parental care, where developing eggs are carried in the stomachs of females of the genus *Rheobatrachus* from Queensland (Fig. 5.6; Tyler 1989a).

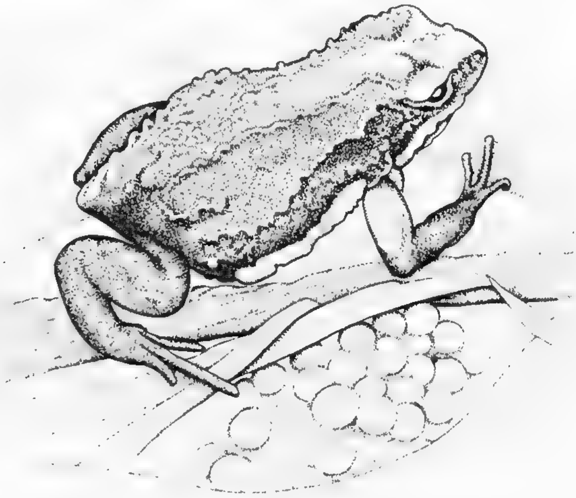

Figure 5.5 Male *Pseudophryne major* are commonly associated with eggs, but these eggs can develop without the male present. (After photo by M. Trenerry/NPIAW) [T. Wright]

Figure 5.6 Oral birth in the gastric-brooding frog *Rheobatrahcus silus*. (After photos by M. Tyler/ANT, R.W.G Jenkins/NPIAW) [T. Wright]

Calls

The functions of calls of frogs are now well known (for example, Wells 1977), with calls serving several different purposes. A detailed bibliography on calls of Australian frogs is given by Tyler (1989a, Table 4).

Advertisement calls are those that are usually heard. They are produced almost exclusively by males, and generally serve the equally important roles of attracting females and indicating the caller's location to other males. Species that call at the same site at the same time nearly always have very distinct calls. This distinction means that females are unlikely to approach males of the wrong species and there is therefore a reduced risk of hybridisation. The distinct calls of sympatric species has led to the discrimination of many Australian frog species that are morphologically similar, as discussed by Main (1968) for *Crinia*.

Advertisement call structures in myobatrachids range from simple short clicks, such as those of the southern call race of *Limnodynastes tasmaniensis*, *Geocrinia rosea* and *G. lutea* (Littlejohn & Roberts 1975; Roberts, Wardell-Johnson & Barendse 1990), through pulse trains and tones with fundamental and harmonic frequencies (for example, *Neobatrachus* and *Heleioporus* species respectively; Littlejohn & Main 1959) to rapid pulse trains with a complex harmonic structure, such as those of many *Cyclorana* species. The calls of hylid species show a similar diversity, but with more emphasis on pulse trains with high pulse repetition rates, and in some instances, complex harmonic structures. Detailed descriptions of hylid calls are not as readily available as for myobatrachid frogs, but there are data for various *Litoria* species and for a number of *Cyclorana* species (Tyler 1989a).

One notable feature of the calls of Australian frogs is the absence of significant frequency modulation, a common feature in the calls of central and South American frogs (Fig. 5.7; Duellman & Trueb 1986).

Territorial calls are used by males at close range to deter other males from a potential calling site. In many species, these calls are quite different from the advertisement call, but may be derived from it in a graded series of steps. As the level of interaction between two males increases, the form of the call alters, for example, by the addition of notes, or elongation of the call as occurs in *Crinia georgiana* (Ayre, Coster, Bailey & Roberts 1984). In *Geocrinia laevis*, for example, the territorial and female attraction functions are functionally uncoupled, with an introductory call used in male-male interactions and a repeated note used for female attraction (Littlejohn & Harrison 1985). A similar biphasic call occurs in *Eleutherodactylus coqui* from Puerto Rico. In this species behavioural studies have established that males and females respond differently to the 'co' and 'qui' components of male call (Narins & Capranica 1976, 1978). Investigations of neural anatomy confirmed that these are obligate responses by males and females: males hear and respond better to the 'co' component, and females better to the 'qui' component of coqui calls (Narins & Capranica 1980).

Release calls are well known in *Bufo* species (for example, Brown & Littlejohn 1972) and may be produced by frogs of either sex. Their function is to indicate to amplexing males that the frog amplexed is either a spent female or another male. They have not been reported in Australian native species, perhaps because they have not been looked for. Such calls may occur in explosive breeders where males persist in calling for two or more nights and spent females are active at the same calling sites (for example, *Neobatrachus* species).

Alarm calls are well known in many Australian species and may be produced by frogs of either sex. For example, *Litoria moorei*

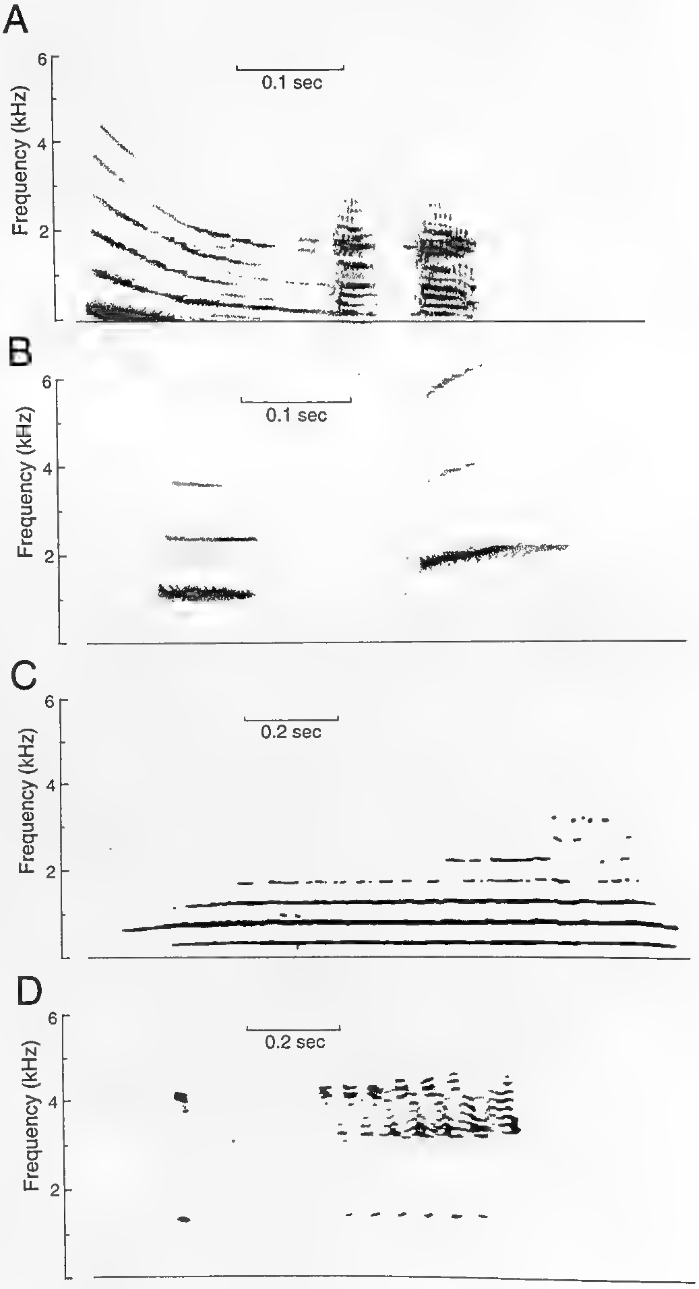

Figure 5.7 Sound spectrograms of call structure in two South American and two Australian frogs. **A**, *Physalaemus pustulosus*; **B**, *Eleutherodactylus coqui*; **C**, *Heleioporus eyrei*; **D**, *Litoria pallida*. (A, B from Duellman & Trueb 1983; C from Littlejohn & Main 1959; D from Davies, Martin & Watson 1983) [W. Mumford]

commonly scream when attacked by domestic cats. However, it is not clear how effective these calls are in deterring predators. Heel, Hugo & Watts (1985) investigated the impact of the alarm scream of *Heleioporus eyrei*, on feeding activity of the bandicoot *Isoodon obesulus*, and found that simultaneous presentation of alarm calls and food items had no impact on the feeding of this known predator of *H. eyrei*.

Calling may also occur in other contexts in which its function is unknown. Martin (1969) reported calling by male *Limnodynastes dumerilii* in underground burrows. It is also important to note that it is not easy to arbitrarily categorise a function for any particular call. For example, Roberts (1978) reported amplexus in *Neobatrachus pictus* before males called and before either frog in the pair entered the pond. Calls in this species may have a major function in male-male interactions where males are actively trying to displace other males from amplexus with females (*cf.* Davies & Halliday 1979).

Call Interactions

Variation in call structure as a result of competition with other males of the same species, or a different species, ensures that a male's signal is transmitted free of acoustic interference. Male *Crinia georgiana* vary the number of quacks per call when stimulated by an artificial stimulus similar to the call of a conspecific (Ayre *et al.* 1984). The basic call of *C. georgiana* is a single quack, like the sound of a duck (Main 1965a). Males increase the number of quacks per call to match the output of their neighbour. Adjacent males of this species, and many others, also alternate their calls. These variations in call and calling strategies are probably a response to the intense male-male competition in many species with prolonged breeding seasons.

Interspecific interactions may also occur. Littlejohn & Martin (1969) demonstrated that calling by *Pseudophryne semimarmorata* was inhibited when males of *Geocrinia victoriana* called at the same sites. In this instance, male *P. semimarmorata* called faster when the other species stopped calling.

Evolution of Calls

The evolution of call structures in frogs is not understood. Some species exhibit little change in call structure over long time periods, whilst others do not. Within the myobatrachids there are some striking examples of slow rates of call structure evolution. The call of *Arenophryne rotunda* is almost identical to the call of *Pseudophryne bibronii* (Roberts 1984), despite an estimated more than ten million years of separate evolution of these two genera (Maxson & Roberts 1985). However, this similarity might also be a result of convergence rather than stability in the form of the call.

The southern call race of *Limnodynastes tasmaniensis* has a single click call, but the closely related northern and western call races have amplitude modulated, multiple note calls (Littlejohn & Roberts 1975; Roberts 1993). These three call races have probably evolved within the last one to two million years (Roberts & Maxson 1986). In some cases interactions with related species are a likely cause of call structure variation. The calls of *Litoria ewingii* and *L. verreauxii* are almost identical where these two species are allopatric with respect to each other, but their calls diverge when the two occur together in central and eastern Victoria (Littlejohn 1965). Likely causes may be interaction between the two species and selection against hybrids, for example, by reinforcement or reproductive character displacement (Butlin 1987), or an acoustic interaction without hybridisation, as discussed above (Littlejohn & Martin 1969).

Mute males have been reported several times in Australian species, but none have been substantiated. Even species which use visual displays, foot, hand or complex body movements, to communicate in noisy environments like the splash zones of cascades and waterfalls have been found to call (Winter & McDonald 1986; Richards & James 1992). Main *et al.* (1959) reported no call for *Myobatrachus gouldii*. However, Roberts (1981) described the call of this species and showed that it called on only one or two nights per year and at times that were totally unexpected given patterns of egg development. Without the chance field observations of calling by *M. gouldii*, made by Baynes (pers. comm.) while he was catching bats, this species still might be classified as mute.

ECONOMIC SIGNIFICANCE

Conservation problems

Some Australian frog species are protected under general fauna protection legislation of the States, whilst others are protected by relevant local fauna authorities. For example, in Western Australia, *Geocrinia alba* and *G. vitellina* are listed as 'fauna that is likely to become extinct, or is rare', because *G. vitellina* has a very restricted distribution (less than 20 ha of suitable breeding habitat) and *G. alba* is threatened by land clearance (Wardell-Johnson & Roberts 1991).

Declining numbers of some species pose special conservation problems. Despite protection, both by legislation and their occurrence in National Parks, *Rheobatrachus* and *Taudactylus* species seem to have declined to the point of extinction (McDonald 1990). However, this may, or may not, be a natural phenomenon, as noted above.

The destruction of natural water courses and swamps by control of river systems and land drainage has undoubtedly affected the distribution of many species. Similarly, the widespread occurrence of land and water salination may have caused the local demise of many species (for example, Main 1990). However, there is no evidence of the loss of a significant portion of the known fauna, as has occurred with Australian birds and mammals. This may be a consequence of the poor knowledge of the Australian frog fauna until relatively recently; the loss of species with restricted ranges may well have gone unnoticed.

There is no clear evidence that interactions of native frog species with the introduced *Bufo marinus* (Pl. 1.2) have had any detrimental effects. Recent work in the Northern Territory, where *B. marinus* has arrived recently, suggested that the invader generally eats different food items and may not interact directly with native frog species (Fig. 5.2; Freeland & Kerin 1988), though these data are from a single sampling at one time of the year. Tyler (1989a) reported that *Bufo marinus* may have had an impact on other faunal components though the direct evidence is not strong.

Economic Values

No Australian frog species have been specifically exploited by European man as a food item, though many species have been used by indigenous Australians (for example, Peile 1978). The skins of many Australian species have been investigated for the presence of pharmacologically active compounds (Erspamer, Falconieri, Erspamer, Mazzanti & Endean 1984). Caerulein, in widespread use for a number of medical diagnostic procedures (Erspamer & Melchiorri 1983), was initially derived from the skin of *Litoria caerulea*, but is now manufactured artificially (Tyler 1976b). *Bufo marinus* was in widespread use as a pregnancy testing device before the advent of specific hormone analyses (Tyler 1989a).

Introduced Frogs

Only one frog species, the cane toad *Bufo marinus*, has been introduced into this country. As detailed in Chapter 11, *B. marinus* was first introduced to control insect pests in sugar cane, and is now widespread in Queensland and spreading rapidly into the Northern Territory and New South Wales. *Bufo marinus* has had a minor role in education, as items for dissection and other areas of biological research (Tyler 1989a).

Australian frogs have been introduced to several other countries. *Litoria aurea* and *L. ewingii* occur in New Zealand. *Litoria aurea* has also been introduced to Vanuatu (Tyler 1979b).

6. BIOGEOGRAPHY AND PHYLOGENY OF THE ANURA

J. Dale Roberts & Graeme F. Watson

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

Four families of frogs are native to Australia — the Microhylidae, the Myobatrachidae (or Leptodactylidae), the Hylidae (or Pelodryadidae) and the Ranidae. A fifth family, the Bufonidae, is represented by the introduced cane or marine toad, *Bufo marinus*. Two of these families (Microhylidae and Ranidae) are derived from Asian groups that colonised the area following collision of the Australian and Asian continental plates (Tyler 1989a). The remaining two families, which include most of the Australian anuran fauna (Fig. 6.1), have Gondwanan origins. Even though the general phylogenetic and biogeographical relationships of the Australian anuran fauna are established, their systematic positions are far from settled.

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

It is not our intention in this chapter to resolve the nomenclatural status of these units but rather to point out that how the groups are recognised inevitably influences perceptions of their phylogenetic and biogeographic relationships. For example, as Tyler (1989a) points out, because the families Hylidae and Leptodactylidae have extensive distributions outside Australia, application of these names to Australian families implies a close relationship to frogs of other continents. Two groups, however, deserve special mention. *Cyclorana*, a genus of primarily burrowing frogs, widespread in the arid zone and wet-dry tropics, was formerly considered a myobatrachid, and its name was used to define the subfamily Cycloraninae (Lynch 1971). Extensive evidence from studies of chromosomes and musculature led Tyler (1978) to transfer this genus to the Hylidae. This move was supported by later immunological studies based on serum albumin (Maxson, Tyler & Maxson 1982). The second controversial group is the genus *Rheobatrachus* which has been given variously familial status, subfamilial status or simply considered as a myobatrachid genus (see section on Myobatrachidae).

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

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

APPROACHES TO PHYLOGENETIC AND BIOGEOGRAPHIC RELATIONSHIPS

Traditionally, hypotheses of relationships between groups have been based on detailed morphological analyses of the included

Figure 6.1 Geographic distribution of the four indigenous families of Australian anurans. **A**, Microhylidae — 2 genera, 19 species; **B**, Ranidae — 1 genus, 1 species; **C**, Myobatrachidae — 19 genera, 112 species; Hylidae — 3 genera, 73 species. [W. Mumford]

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

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

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

One of the authors (JDR) has been a leading proponent of this technique, and has made a major contribution to the extensive application of MC'F technology towards re-interpreting the phylogeny and biogeography of many groups of Australian frogs. The other author (GFW) believes that these data are inappropriate and inapplicable to these problems, a point of view that is receiving increasing support in the systematic literature (for example, Scherer 1990). As these different viewpoints inevitably influence our interpretations, we have separated our systematic contributions on the myobatrachids and the hylids, which were prepared by JDR and GFW respectively. Both viewpoints are put in our consideration of regional biogeographic patterns.

MYOBATRACHIDAE

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

Relationships of Genera

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

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

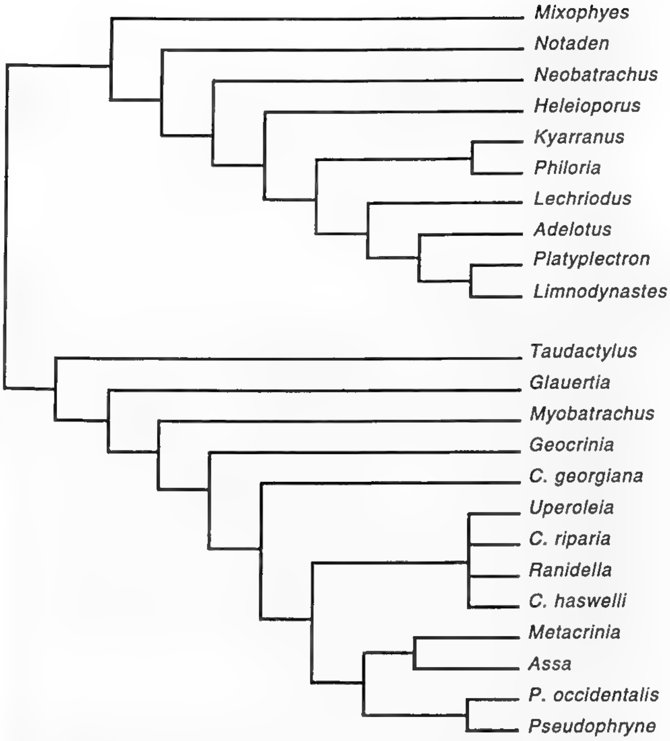

Figure 6.2 The preferred phylogenetic arrangement of Heyer & Liem (1976) of the myobatrachid genera. *Crinia georgiana*, *C. riparia*, *Crinia haswelli* and *Pseudophryne occidentalis* were named *Crinia*, *Australocrinia*, *Paracrinia* and *Kankanophryne* in the original illustration. (Modified from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

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

Farris *et al.* (1982) re-analysed both the complete and the reduced data sets in two ways. The phylogeny shown in Fig. 6.3 is their preferred tree. The same basic pattern of two subfamilies noted by Heyer & Liem is present, but there are many discrepancies. For example, their results associated *Myobatrachus* with *Assa* and *Metacrinia*, but in Heyer & Liem's analysis *Myobatrachus* was only distantly related to these other two genera. However, some of the earlier deficiencies in the data, for example, those relating to breeding biology, are perpetuated. Farris *et al.* conclude their paper with the following: 'It seems necessary to conclude that these characters offer only weak evidence on kinship. Given such weak data, we see little value in generalising further about the relationships among myobatrachid frogs'.

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

Farris *et al.* (1982) considered the genus *Rheobatrachus* as related other genera of the Limnodynastinae, but placed it as a very old derivative of this subfamily (Fig. 6.3). Heyer & Liem (1976) also saw *Rheobatrachus* as distinct and erected a new subfamily to recognise this fact. Hutchinson & Maxson (1987b) compared the albumins of the two known species, *R. vitellinus* and *R. silus*, and compared *Rheobatrachus* both with other Australian myobatrachid genera and other leptodactyloid frogs (*sensu* Lynch 1971) from South America. They concluded that the two species of *Rheobatrachus* are closely related, and that the genus is also not closely related to any other genera or lineages within the Myobatrachidae, but it is more closely related to Australian lineages than to any other leptodactyloid group. However, the data obtained are at the limits of resolution for the MC'F methodology. The distinctness of this genus is unquestioned, but its relationships are still unclear. The antiquity of the split of this genus from other Australian frogs may make this position unresolvable until techniques capable of resolving ancient divergences are applied (Hutchinson & Maxson 1987b).

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

The Subfamily Myobatrachinae

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

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

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

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

The Subfamily Limnodynastinae

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

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

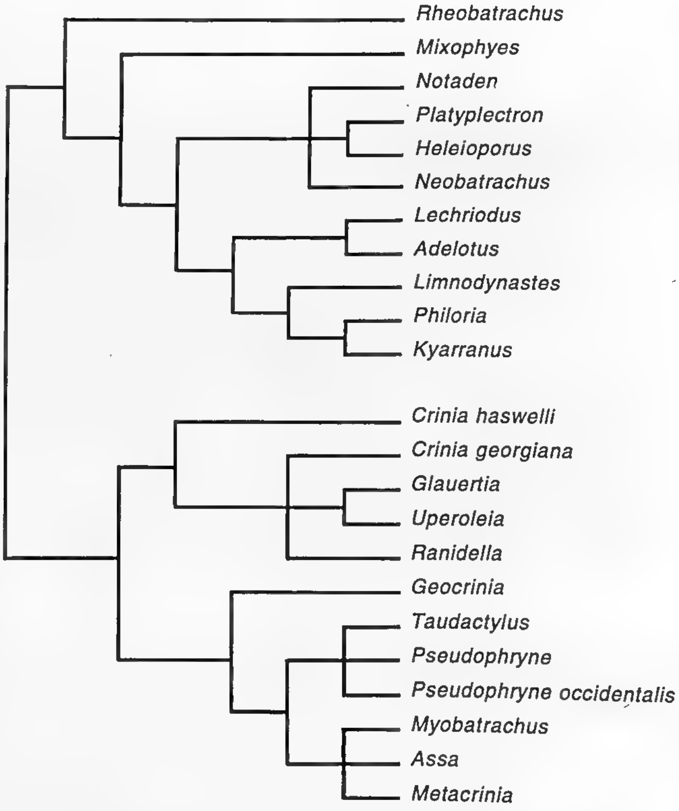

Figure 6.3 Wagner tree based on a twenty-three character, restricted dataset. *Ranidella* includes *R. riparia* (now placed in *Crinia*), *Limnodynastes* excludes burrowing species treated as *Platyplectron* (see text) and *Pseudophryne* excludes *P. occidentalis*. (After Farris, Kluge & Mickevich 1982)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

& Liem (1976, Fig. 23). These authors, however, did not list the content of this genus. Roberts & Maxson (1986) did not investigate relationships of *Limnodynastes* to *Adelotus*, *Kyarranus*, *Philoria* or *Lechriodus*, the genera that Farris *et al.* (1982) associated with *Limnodynastes* more closely than *Platyplectron* (Fig. 6.3).

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

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

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

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

HYLIDAE

The Australopapuan tree frogs of the genera *Litoria* and *Nyctimystes* form a monophyletic group defined by the presence of a supplementary apical element of the intermandibularis muscle (Tyler 1971b, 1979a). However, the status of this group relative to other hylid lineages worldwide and to the Australian myobatrachid lineages has been questioned. Tyler (1979a) suggested that Australian hylid and myobatrachid frogs might share a common ancestor. This claim was partly based on the status of *Cyclorana*, at that time considered a myobatrachid, but now clearly shown to be a hylid frog (see above, and also Tyler & Davies, Chapter 8).

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

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

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

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

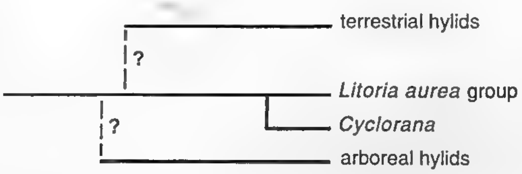

Figure 6.4 Possible phylogeny of Australian Hylidae. (After Tyler, Watson & Martin 1981) [D. Wahl]

SPECIATION MECHANISMS IN THE AUSTRALIAN ANURAN FAUNA

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

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

Main *et al.* (1958), for example, argued that the high species richness in south-western Australia in the three genera *Heleioporus*, *Neobatrachus* and *Crinia*, could be explained by repeated invasion of an eastern stock with subsequent isolation and differentiation in south-western Australia. Roberts & Maxson (1985) reviewed relationships in these south-western genera, using data from gel electrophoresis, MC'F studies and chromosome analysis. They showed that the data contradicted the relationships suggested by Main *et al.* (1958) in some instances, for example, in *Crinia* and *Heleioporus*, or that alternative modes of speciation had not been considered, such as polyploidy in *Neobatrachus*. They concluded that most of the data were consistent with an *in situ* speciation model, despite the lack of geographic barriers within south-western Australia. The possibility of speciation within this area is now clearly demonstrated, however, by the discovery of four species of *Geocrinia* in far south-western Australia. These taxa have clear differences in colour, call, and in genotype as determined by electrophoresis (Wardell-Johnson & Roberts 1991).

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

In their review, Watson & Littlejohn (1985) proposed phylogenetic relationships based on a variety of factors. Levels of genetic compatibility between taxa were determined through *in vitro* hybridization experiments (for example, Watson & Martin 1968; Littlejohn, Watson & Loftus-Hills 1971). Also examined were morphological differentiation (for example, Littlejohn & Martin 1964; Martin 1972a), quantitative differences in advertisement calls (for example, Littlejohn 1964, 1965); and the structure of the various zones of intertaxonomic interaction. The latter ranged from extensive hybridization between interacting taxa, which indicates close genetic and ecological similarity, to extensive spatial coexistence with little or no hybridization, indicating considerable genetic and/or ecological differentiation (for example, Littlejohn *et al.* 1971; Littlejohn & Watson 1985; Watson 1972; Watson *et al.* 1985). While any one of these factors may not provide strong evidence of phylogenetic relationships, together they provide a substantial body of evidence to refute the view put by Roberts & Maxson (1988).

Watson & Littlejohn (1985) considered eight groups of species in Tasmania and on the mainland of south-eastern Australia. Seven of these groups provide clear evidence of a southern taxon showing a pattern of distribution that includes the southern mainland and Tasmania, with one or more additional mainland taxa (Fig. 6.5). In the eighth group, the *Crinia signifera* complex, a more complicated but consistent pattern of distribution is evident. The proposed pattern of speciation requires the southern (Tasmanian) taxon to disperse northwards across the Bassian land bridge — a suggestion that is not unreasonable, given that the cooler glacial conditions would be expected to favour the cold-adapted southern taxon. Watson & Littlejohn (1985) considered that the commonality of these repetitive patterns provide compelling evidence of repeated patterns of allopatric speciation within south-eastern Australia, for which the sequence of Pleistocene glaciations provided an appropriate geographic and temporal framework.

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

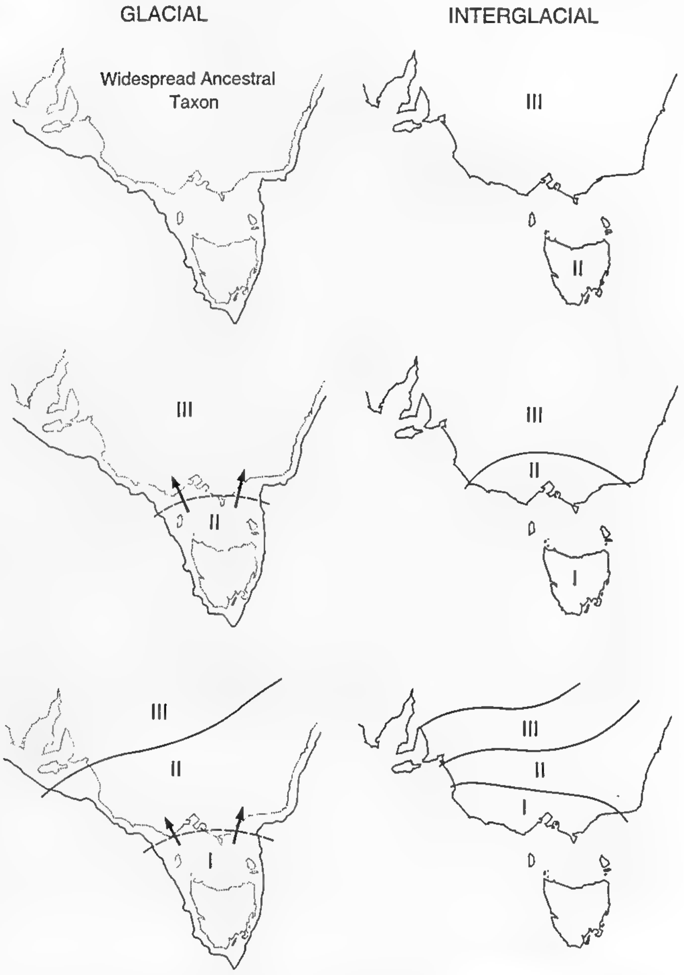

Figure 6.5 Hypothetical model of taxonomic divergence giving rise to species groups with three taxa in south-eastern Australian amphibians. (After Watson & Littlejohn 1985) [W. Mumford]

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

DISTRIBUTION PATTERNS

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

Given that the myobatrachids may be most closely related to leptodactylid lineages in South America, and previously connected to South America via Antarctica, this is not a particularly surprising suggestion.

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

FOSSIL RECORD

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

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

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

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

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

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

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

7. FAMILY MYOBATRACHIDAE

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

DEFINITION AND GENERAL DESCRIPTION

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

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

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

The following definition of the family Myobatrachidae is based on those of Lynch (1973) and Duellman & Trueb (1986). There are eight, or functionally seven, presacral vertebrae with a persistent notochord. Subadults have free intersacral discs, except in *Lechriodus* and *Mixophyes*, and these are usually fused to the posterior end of the sacrum in adults to give the procoelous condition. Ribs are lacking. The sacrum has dilated diapophyses, and a bicondylar articulation with the coccyx, which may have transverse processes proximally. The pectoral girdle is arciferal or modified arciferal (Fig. 7.1). The anterior end of the scapula is not overlain by the clavicle. Palatines are present, and a parahyoid is absent. The astragalus and calcaneum are fused proximally and distally, and there are two tarsalia. The *m. sartorius* is usually distinct from the *m. semitendinosus*, the *m. gluteus magnus* has an accessory tendon, and the *m. adductor magnus* has a small accessory head.

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

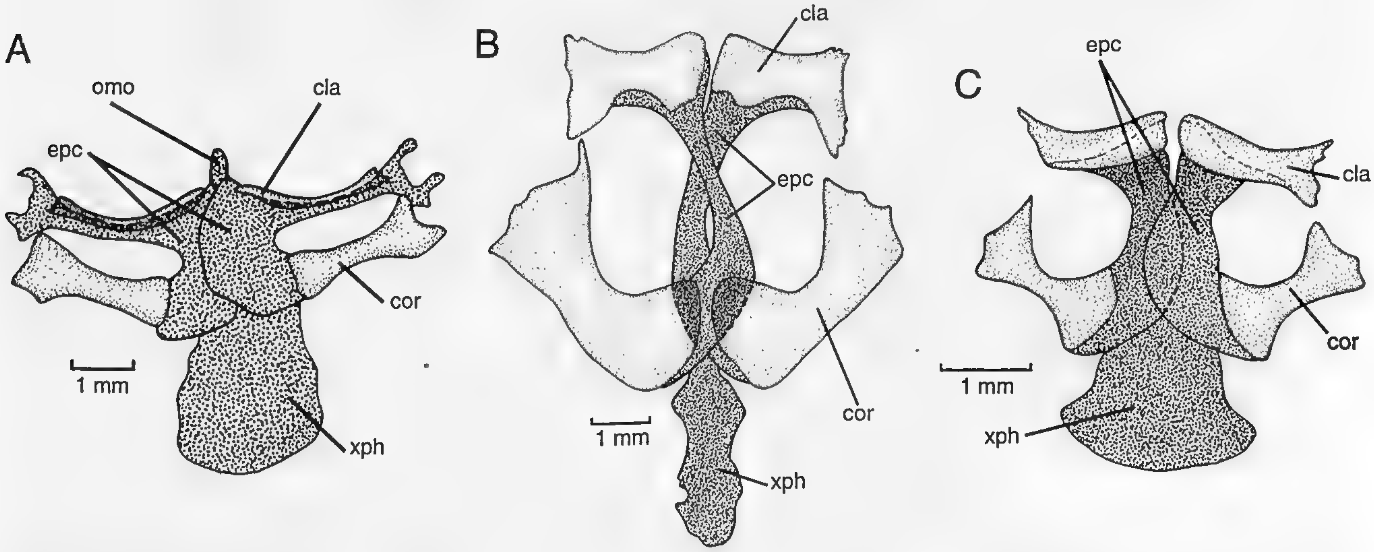

Figure 7.1 Ventral views of the arciferal pectoral girdles of Myobatrachidae. **A**, *Pseudophryne semimarmorata*, a non-burrowing species; **B**, *Myobatrachus gouldii*, a forward burrowing species; **C**, *Arenophryne rotunda*, a forward burrowing species. **cla**, clavicle; **cor**, coracoid; **epc**,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

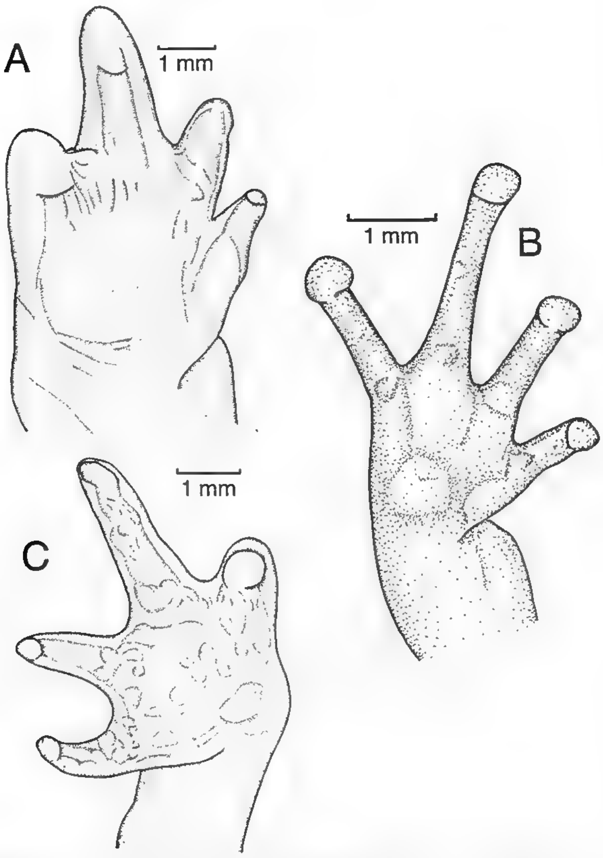

Figure 7.2 Palmar views of myobatrachid frogs. **A**, right hand of *Myobatrachus gouldii*; **B**, right hand of *Taudactylus diurnus*; **C**, left hand of *Arenophryne rotunda*. [M. Davies]

intracapsular development in *Geocrinia*, *Kyarranus*, *Pseudophryne* and *Heleioporus* (part). Complete or almost complete intracapsular development occurs in *Arenophryne*, *Myobatrachus*, *Kyarranus* and *Philoria*.

HISTORY OF DISCOVERY

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

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

The first myobatrachid species to be described was *Heleioporus australiacus* (as *Rana australiaca*) by Shaw & Nodder in 1795, on the basis of a drawing (Fig. 2.2). This was followed by the exhibition of a specimen of *Bombinator* (= *Pseudophryne*) *australis* by Gray in 1835, and the description of *Crinia georgiana* by Tschudi in 1838, from a preserved specimen collected near King Georges Sound, Western Australia. In the next three decades, six species in four genera were recognised and, by the turn of the century, species of nine or 10 of the presently accepted genera had been described.

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

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

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

A new genus and species, *Taudactylus diurnus*, was described by Straughan & Lee (1966). Tyler (1972b) erected the genus *Assa* to accomodate *Crinia darlingtoni*. Blake (1973) revised the genus *Crinia*, and re-established *Ranidella*, described *Geocrinia*, and synonymised *Metacrinia* with *Pseudophryne*. *Rheobatrachus* was described by Liem (1973) to accommodate an unusual aquatic species. Heyer & Liem (1976) established several new monotypic genera, including *Australocrinia*, *Kankanophryne* and *Paracrinia*, none of which are presently recognised. *Arenophryne* was described by Tyler (1976a) to incorporate a newly discovered forward-burrowing species. The most recent new, extant genus to be described is *Megistolotis* (Tyler, Martin & Davies 1979). Cogger *et al.* (1983) recognised the monotypic genus *Metacrinia*, as had Heyer & Liem (1976), and placed *Kyarranus* in the synonymy of *Philoria*. Heyer, Daugherty & Maxson (1982) synonymised *Ranidella* within *Crinia* on the basis of immunological distance. Tyler *et al.* (1981a) placed *Glauertia* in the synonymy of *Uperoleia*. Frost (1985) recognised *Kyarranus*, *Megistolotis* and *Paracrinia*, but not *Metacrinia* and *Ranidella*. Tyler (1991a) confirmed the status of *Kyarranus* as distinct from *Philoria* on the basis of differences in the structure of the ilium.

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

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

MORPHOLOGY & PHYSIOLOGY

External Characteristics

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

The dorsal skin ranges from smooth in species such as *Limnodynastes tasmaniensis* and *Rheobatrachus silus* (Pl. 2.7) through tubercular skin such as found in *Notaden bennettii* (Pl. 2.12), to skin that has characteristically well-developed localised glandular areas, particularly in the parotoid, inguinal and coccygeal regions as in *Arenophryne*, *Uperoleia* (Fig. 4.2) or in the supralabial and tibial regions such as in the *L. dorsalis* complex (Fig. 4.2). Examination of the dorsal skin of *R. silus* by scanning electron microscopy reveals a repetitive pattern of polygons with raised lateral cell margins and elongate depressions bounded by narrow, slightly raised ridges (Tyler & Davies 1983a). Ventral skin is smooth or granular with variations (sexually dimorphic and intraspecific) in the degree of granularity (Davies *et al.* 1986b).

Skin colouration is highly variable, but commonly drab brown or grey often highlighted with patches of ochre, gold or red. Many species are highly colourful with brilliant yellow and black stripes as in *Pseudophryne corroboree* (Pl. 2.5), or an intense yellow dorsum patterned in the form of a crucifix in black and red in juvenile *Notaden bennettii* (Pl. 2.12), or red or tan triangular head markings as in *P. australis* and *P. coriacea*. Many species have bright patches of colour (scarlet, orange, yellow) in the axillary and inguinal regions. Ventrally, many myobatrachids are highly patterned, as in examples of *Pseudophryne semimarmorata* with bold black and white marbling supplemented by brilliant orange/scarlet (illustrated by Tyler 1976b). Main (1965a) observed that *Metacrinia nichollsi* were often collected with the ventral surface uppermost, and that the ventral patterning closely resembled fungal hyphae and fruiting bodies within their habitat.

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

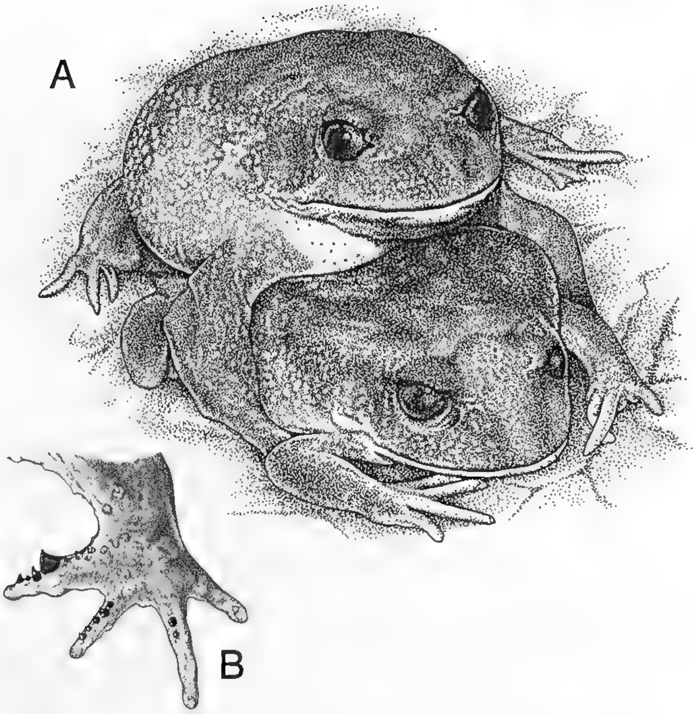

Figure 7.3 Mating behaviour A, amplexus in *Heleioporus australiascus*, B, nuptial excrescences on the hand of the male. (A, after Hoser 1989; B, after photo by F. Kristo/ANT) [K. Hollis]

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

Nuptial excrescences are usually glandular and located at the base of the first finger. In most species they are pigmented, but they lack pigment in *Uperoleia* (Davies & Littlejohn 1986). Within the Limnodynastinae, structure of the nuptial excrescences ranges from thorn-like in *Heleioporus* (Fig. 7.3B) and *Megistolotis* to numerous and very fine spines, appearing glandular to the naked eye in *Limnodynastes convexiusculus* (Davies & Watson unpub. data). Under the Scanning Electron Microscope, the nuptial excrescences appear as conical elevations (*Lechriodus fletcheri*), pads in the form of rosettes (*Neobatrachus pictus*), radial processes (*Limnodynastes spenceri*) or alary processes (*L. ornatus*; Tyler & Lungershausen 1986). The nuptial excrescences of *L. ornatus* are found on the first three fingers (illustrated by Tyler & Davies 1986) whilst in *L. spenceri* there are several pads on the first two fingers (illustrated by Tyler, Smith & Johnstone 1984).

Fossorial species, except forward burrowers like *Myobatrachus*, are characterised by compressed, shovel-shaped, keratinised, inner metatarsal tubercles (Fig. 7.2A, C; Pl. 2.1) which are melanic in most *Neobatrachus* (Fig. 7.4B) and in *Notaden melanoscaphus*. *Uperoleia* spp. also have the outer metatarsal tubercle adapted for burrowing although some species such as the toothed forms *U. tyleri*, *U. martini*, *U. laevigata* and *U. fusca* that live in temperate wet areas not subjected to the same extremes of seasonal aridity, tend to have poorer fossorial development of the outer metatarsal tubercles.

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

Body Wall

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

The only myobatrachid for which a complete description of musculature is available is *Rheobatrachus silus* (Davies & Burton 1982; Burton 1983a) although particular muscle groups have been examined in various phylogenetic studies. Tyler (1972b) examined the superficial mandibular musculature of Australopapuan myobatrachid frogs and identified three muscles: the *m. submentalis* which is ovoid and usually araphic at the apex of the mandibles; the *m. intermandibularis* which arises as a thin flat sheet from the lateral lingual surface of the mandibles between the *m. submentalis* and the jaw articulation; the *m. interhyoideus* arising principally from the anterior cornu of the hyoid uniting anteriorly with the posterior border of the *m. intermandibularis*. Tyler (1972b) showed that the nature of these muscles separates the Limnodynastinae and the Myobatrachinae (Figs 1.4F, G, 7.4F). In the limnodynastines the *m. intermandibularis* underlies the *m. submentalis* whilst in the myobatrachines, the *m. intermandibularis* has no contact with the *m. submentalis*. *Rheobatrachus*, a genus of contentious subfamilial placement, shares the limnodynastine condition (Tyler 1983c).

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

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

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

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

Skeletal System

The maxillary arch is complete and dentate in all limnodynastines except *Notaden* (Lynch 1971; Shea & Johnston 1988). The teeth form a continuous row, except in *Adelotus* in which a distinct diastema between the maxillary and premaxillary teeth corresponds to the position of the odontoid 'tusks' on the lower jaw. *Adelotus* has fang-like teeth (Lynch 1971) that are found also in *Rheobatrachus* (Liem 1973; Davies 1983). In these two genera, medio-lateral extremities of the premaxillary palatal shelf extend such that they lie medial to the anterior portion of the palatal shelf of the maxilla (Davies 1983). Within the Myobatrachinae, the maxillary arch is invariably complete, but is edentate in *Pseudophryne, Myobatrachus, Arenophryne* and many species of *Uperoleia*. Teeth occur sparsely in *U. micromeles* and *U. altissima* (Tyler *et al.* 1981a; Davies, Watson, McDonald, Trenerry & Werren 1993). Tooth complement is influenced by heterochrony (Davies 1989a).

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

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

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

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

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

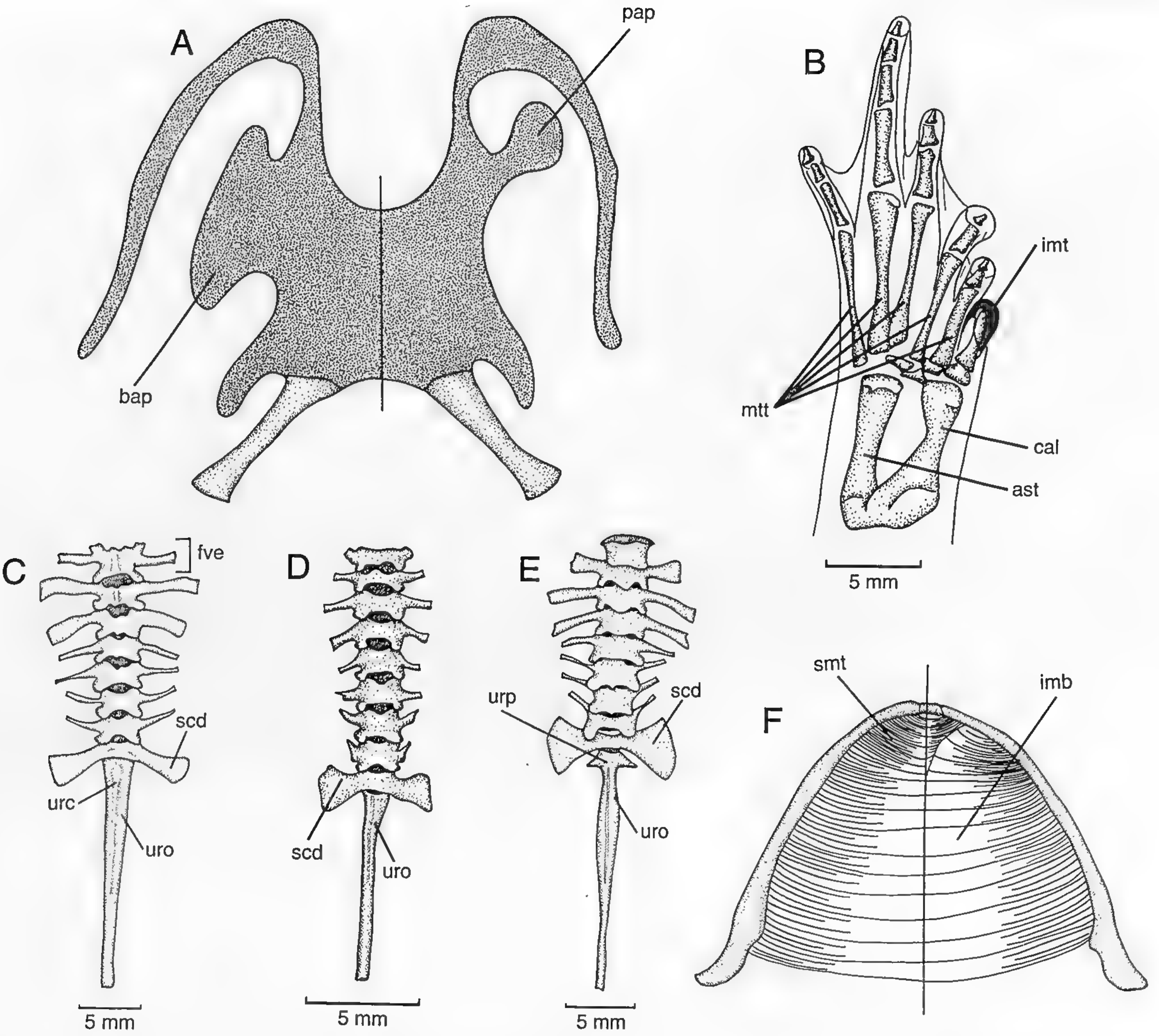

Figure 7.4 Postcranial elements of myobatrachid skeleton. A, composite diagram of hyoid to compare structure in the Myobatrachinae (left) and the Limnodynastinae (right); **B**, bones of the foot of *Neobatrachus aquilonius*, a backwards burrowing species with a melanic inner metatarsal tubercle; **C**,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

genera. Vomerine teeth are present in *Crinia georgiana*, *C. haswelli* and *Geocrinia*.

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

In the Limnodynastinae the pterygoids vary from extremely robust in for example, *Mixophyes* (Donnellan *et al.* 1990), to reduced, with only a minute posterior ramus in *Notaden weigeli* (Shea & Johnston 1988). A ventral flange occurs on the body of the pterygoid in *Rheobatrachus* (Davies & Burton 1982; Mahony *et al.* 1984). The parasphenoid is invariably robust. The columella is always present and is sinuous in shape in most genera (Davies unpub. data.). In the Myobatrachinae, the pterygoids are moderately robust, varying in the breadth of the anterior ramus, and the parasphenoid is invariably robust. The columella, where present, is straight. It is absent in *Arenophryne*, *Myobatrachus*, *Pseudophryne* and *Crinia (Ranidella) riparia*.

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

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

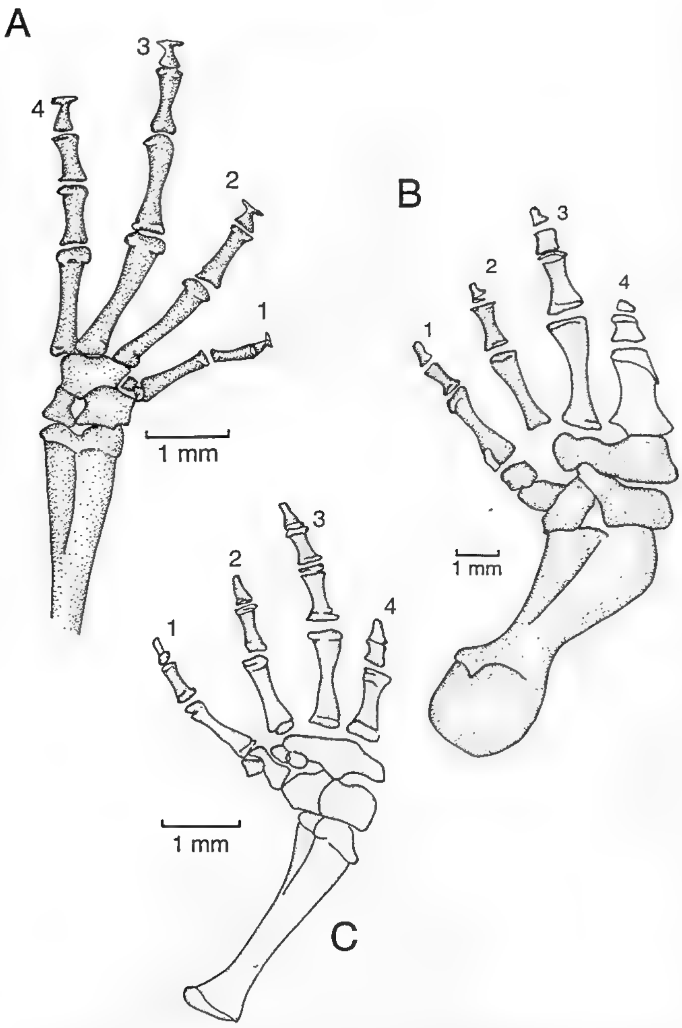

Figure 7.5 Palmar views of the bones of myobatrachid frogs. **A**, the right hand of *Taudactylus diurnus* which has no phalangeal reduction, but has T-shaped terminal phalanges; **B**, left hand of *Myobatrachus gouldii*, showing phalangeal reduction in the fourth finger; **C**, left hand of *Arenophryne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

[M. Davies]

Presacral vertebrae I and II are fused in the Limnodynastinae, except in *Mixophyes* and *Rheobatrachus*, so that there are effectively only seven presacral vertebrae (Fig. 7.4C). The ontogeny of the fusion of presacrals I and II is obscure as there are only seven cartilaginous primordia of presacral vertebrae at hatching (Davies unpub. data.). The neural arches of the presacral vertebrae are imbricate or non-imbricate. In some species, the first vertebrae are imbricate, whilst the others are non-imbricate. The majority of genera have free intervertebral discs as subadults (ectochordy) (Lynch 1971). Shea & Johnston (1988) reported dorsal fusion of fused presacral vertebrae I and II with presacral vertebra III, but this may be anomalous as it does not occur in congeners (Davies unpub. data.). Presacral vertebrae I and II are not fused in the Myobatrachinae, and there are eight presacral vertebrae (Fig. 7.4E). The vertebrae are procoelous with free intervertebral discs, in many cases persisting in the adult, and generally are non-imbricate.

Sacral diapophyses are moderately expanded in the Limnodynastinae, and transverse processes occur on the urostyle in *Rheobatrachus* (Fig. 7.4D); in the Myobatrachinae they are poorly expanded, and transverse processes have been recorded on the urostyle of *Metacrinia nichollsi* (Lynch 1971), although this occurrence has not been confirmed.

Within the Limnodynastinae, the phalangeal formula of the hand is uniformly 2,2,3,3 and of the foot 2,2,3,4,3. The terminal phalanges are knobbed. In *Limnodynastes fletcheri*, and to a lesser extent *L. peronii*, *L. salmini* and *Megistolotis lignarius*, metacarpal I is disproportionately long with an associated reduction in size of the phalanges (Parker 1940; Davies & Watson in ms). Parker associated this lengthening with an absence of nuptial excrescences in the *Limnodynastes* species, but such structures have since been located in *L. salmini* (Davies & Watson in ms), and they are spinous and prominent in *M. lignarius* (Tyler *et al.* 1979). Medial flanges are present on the first metacarpal of *M. lignarius*, *L. convexiusculus* and in *L. salmini* (Davies & Watson in ms.). The prehallux provides support for the inner metatarsal tubercle (Tyler, Davies & Walker 1985), and is large and hastate in burrowing species such as *Neobatrachus* and the *Limnodynastes dorsalis* group. The digital formulae are reduced in some myobatrachine species, including the forward burrowers (Fig. 7.5B, C). The terminal phalanges are knobbed except in *Taudactylus*, in which they are T-shaped (Fig. 1.4U, 7.5A). A modified prehallux supporting the inner metatarsal tubercle is present in *Uperoleia*, but there is no osteological support for the well-developed outer metatarsal tubercles in this genus.

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

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

Locomotion

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

Feeding & Digestive System

Tyler (1989a) tabulated the published dietary studies on Australian frogs. Diet is, to a large extent, governed by the gape of the mouth and seasonal abundance of the prey. Prey is captured by either a biting or a grabbing action, or by tongue-flicking (Regal & Gans 1976). The tongue of *Rheobatrachus* is fused to the floor of the mouth (Horton 1982), so that it cannot be flicked out. *Rheobatrachus vitellinus* appears to feed underwater, on the basis of its diet (McDonald pers. comm.), but studies on the diet of *R. silus* suggest that this species does not (Ingram 1983).

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

Excretion and Water Loss

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

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

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

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

Sense Organs & Nervous System

Duellman & Trueb (1986) note that species that have lost the columella tend to be fossorial or to live alongside streams. Although this holds true for *Arenophryne rotunda* and *Crinia (Ranidella) riparia*, the columella is lacking also in all species of *Pseudophryne*. There appears to be no adaptive significance in the loss. Other parts of the auditory system are not lost in those species lacking a columella, hence sound is received by a different route (see Duellman & Trueb 1986 for a summary of sound production). Lack of a tympanum appears not to inhibit sound reception (though see Wever 1985). The surface area of the tympanum has been suggested by Loftus-Hills (1973b) as affecting auditory sensitivity, although this does not hold true for all anurans (Frishkopf, Capranica & Goldstein 1968). Within the Myobatrachidae, the largest tympanum relative to the size of the frog is that of *Megistolotis lignarius*. The call of this species is a soft tapping sound with remarkable carrying capacity (Tyler, Davies, Watson & Martin unpub. data). Underlying neural mechanisms for acoustic behaviour have been investigated in *Limnodynastes dumerilii* (as *L. dorsalis*) and *Pseudophryne semimarmorata* (Loftus-Hills 1971, 1973a), and further investigations are reported by Loftus-Hills (1973b), Eggermont (1988) and Jaslow, Hetherington & Lombard (1988).

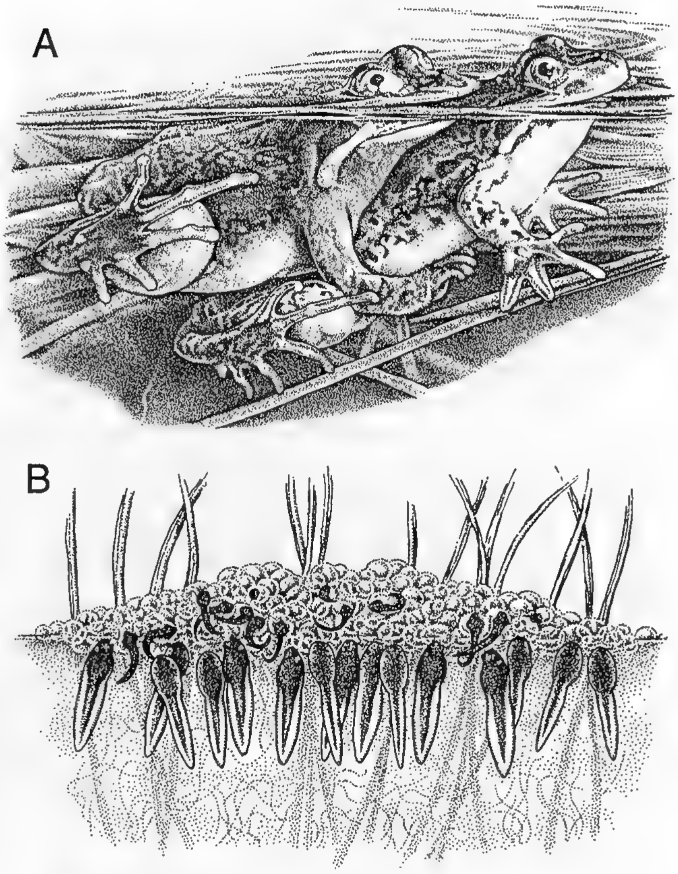

Figure 7.6 Reproduction in *Limnodynastes tasmaniensis* **A**, amplexus. Note flanged fingers of the female; **B**, tadpoles sheltering beneath foam nest. (A, B, after photos by C.A. Henley/NPIAW) [K. Hollis]

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

Exocrine Systems

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

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

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

Reproduction

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

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

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

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

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

Eggs in a foam nest out of water with an aquatic, feeding tadpole. In Western Australian species of *Heleioporus*, eggs are deposited in a foam nest at the bottom of a dry breeding burrow. These burrows are well-defined structures up to 115 cm long and up to 7 cm diameter depending on species (Lee 1967). Embryonic development proceeds in the nest until the burrow floods with the onset of winter rains. In some instnces, eggs may hatch at the bottom of the burrow before full flooding occurs (Lee 1967). In *H. australiacus* from eastern Australia, the eggs are deposited in a foamy mass floating in water or in a flooded burrow (Watson & Martin 1973), although Barker & Grigg (1977) reported calling by males from burrows in sandy banks a few metres from water, as occurs in the western species. Eggs of all species of *Heleioporus* are non-pigmented or very lightly pigmented (Lee 1967).

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

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

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

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

Terrestrial eggs with an aquatic tadpole. There are two variants on this theme. Eggs may develop out of water for long periods, as in eastern species of *Geocrinia* (up to 120 days for *G. victoriana*, Martin 1967b) and all species of *Pseudophryne* except *P. douglasi* (Main 1965a; Pengilley 1973). Eggs of *Geocrinia leai* are deposited above water in vegetation; after hatching, the tadpoles wriggle into water (Main 1965a), without an extended period of terrestrial development.

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

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

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

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

The members of the subfamily Limnodynastinae have evolved foam-nesting at least once (the *Limnodynastes*, *Adelotus*, *Megistolotis*, *Kyarranus*, *Philoria* and *Lechriodus* lineage), and possibly twice, as *Heleioporus* has a radically different form of foam production (Watson & Martin 1973). The function of foam is unclear, though possible options are protection from desiccation and aquatic predators, the ecological advantages of foam nesting in a terrestrial site (see above), and respiratory advantages where foam holds the egg mass close to the highly oxygenated water surface (Roberts & Seymour 1989). Though foam does not necessarily protect against desiccation, or against predation (see Embryonic Mortality below), there is some support for the last suggestion (Roberts & Seymour 1989; Seymour & Roberts 1991).

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

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

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

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

Embryology & Development

In terms of life history and larval morphology, the Myobatrachinae is a relatively uniform group whilst the Limnodynastinae is a more heterogeneous assemblage (Watson & Martin 1973). Members of the Myobatrachinae could be linked on the basis of their life history and larval morphology traits — eggs with discrete capsules, egg masses not foamy, no external gills at hatching, a dextral anus (Fig. 7.7B), two upper and three lower rows of labial teeth, and anterior and posterior gaps in the papillary border (Fig. 1.9G). The few exceptions that Watson & Martin (1973) recorded were in *Assa*, *Crinia* and *Taudactylus* in which larvae are modified for development in specialist niches. Odendaal & Bull (1980) showed experimentally that *Crinia (Ranidella) riparia* has a body and mouth form adapted for living in fast flowing streams and this has been inferred for *Mixophyes* species (Moore 1961; Watson & Martin 1973; Davies 1991).

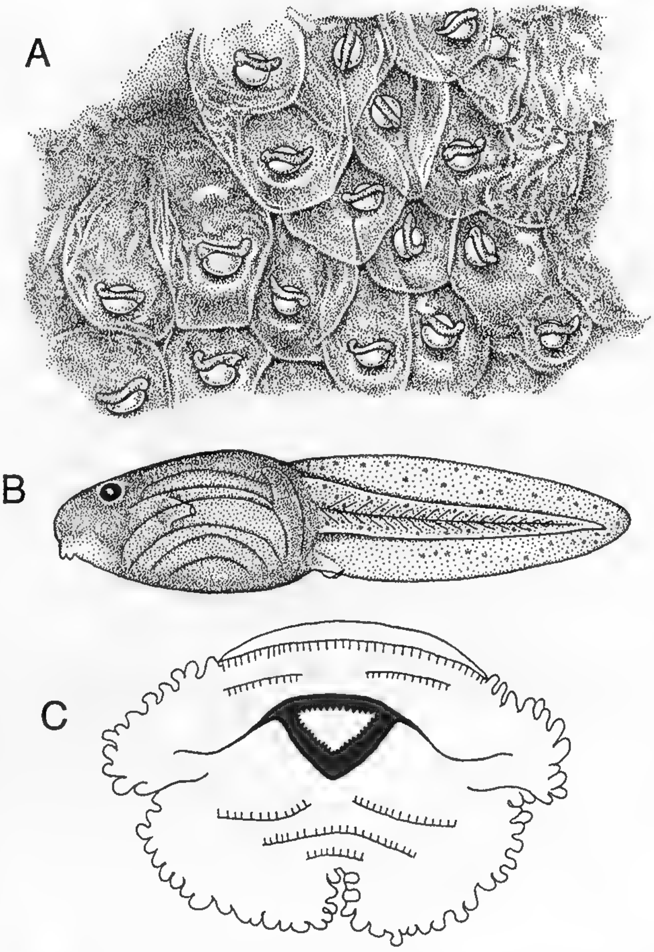

Figure 7.7 Eggs and larvae of *Taudactylus*. **A**, aquatic egg mass deposited on the underside of a rock; **B**, lateral view of tadpole; **C**, mouth disc of tadpole. (A, after photo by D. Parer & E. Parer-Cook/Auscape; B, C, after Heyer & Liem 1976) [K. Hollis]

Larvae of the genera *Arenophryne* and *Myobatrachus* develop directly (Roberts 1981, 1984). The myobatrachine tooth row complement of *Taudactylus acutirostris* (Fig. 7.7B) is unlike that of its congeners *T. diurnus* and *T. eungellensis* that lack tooth rows (Watson & Martin 1973; Liem & Hosmer 1973). Given that habitat of *T. acutirostris* is riparian and similar to that of the described congeneric species, the form of the mouth disc appears somewhat anomalous (Fig. 7.7C). There is no gap in the labial papillae, either posteriorly or anteriorly. *Crinia georgiana* is the only myobatrachine recorded as having more than two upper rows of labial teeth (Main 1968).

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

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

Standard developmental schemes for anurans (for example, Gosner 1960) apply to many myobatrachids. However, for species with terrestrial eggs or direct development, the large yolk mass may complicate the normal patterns of development. Initial cleavage and gastrulation are slower in *H. eyrei* than in *Rana*, presumably because of the relatively large yolk in *H. eyrei* (Packer 1966). Gollman & Gollman (1991) described developmental stages of *Geocrinia laevis*, *G. victoriana* and their hybrids. They noted differences from Gosner's scheme in stages 20 to 26. Gollman (1991) also described development in *Crinia (Ranidella) signifiera.* In these two genera, the only major variation from Gosner's scheme is that *Geocrinia* hatch at a later stage than expected. Roberts (1984) did not report any special adaptations or variations from expected developmental patterns in the direct-develping eggs of *Arenophrune rotunda*, except that the tail seemed to be heavily vascularised.

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

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

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

NATURAL HISTORY

Life History

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

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

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

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

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

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

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

Ecology

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

The distributions of some species are relatively broad, covering a wide range of habitats, and those of others are restricted. For example, *Arenophryne rotunda* is common in coastal sand dunes, but also occurs on adjacent red sands in mallee scrub on the edge of the arid zone at Shark Bay, Western Australia (Anon. 1980; Roberts 1985, 1990). *Myobatrachus gouldii* is common in coastal and inland areas with reliable winter rainfall in south-western Western Australia, but is absent from the wetter forested areas, and the arid zone (Roberts 1981). *Geocrinia vitellina* and *G. alba* occur only in a limited number of flat-bottomed creek systems in far south-western Western Australia, where there are seepage systems that can supply excess soil moisture during spring breeding seasons (Wardell-Johnson & Roberts 1991).

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

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

Frogs are commonly exposed to extreme temperatures. Brattstrom (1970) reported the results of an extensive study of thermal acclimation in Australian frogs, including 20 species of myobatrachids. Cold tolerant (cryophilic) species tend to have a more southerly distribution and heat tolerant (thermophilic) species a more northerly one; but species with wide (eurythermic) or narrow (stenothermic) temperature tolerances were found across all latitudes. Extent of geographic range appeared to be related to ability for thermal acclimation, and species that have restricted ranges (for example, *Kyarranus sphagnicolus* and *Philoria frosti*), show no physiological ability to adjust their temperature tolerances. Even so, Marshall & Grigg (1980) found that tadpoles of the wide-ranging species *Limnodynastes peronii* show little evidence of ability to adjust temperature tolerances physiologically and they concluded that any adaptations of tadpoles to regimes of fluctuating temperatures are probably behavioural rather than physiological.

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

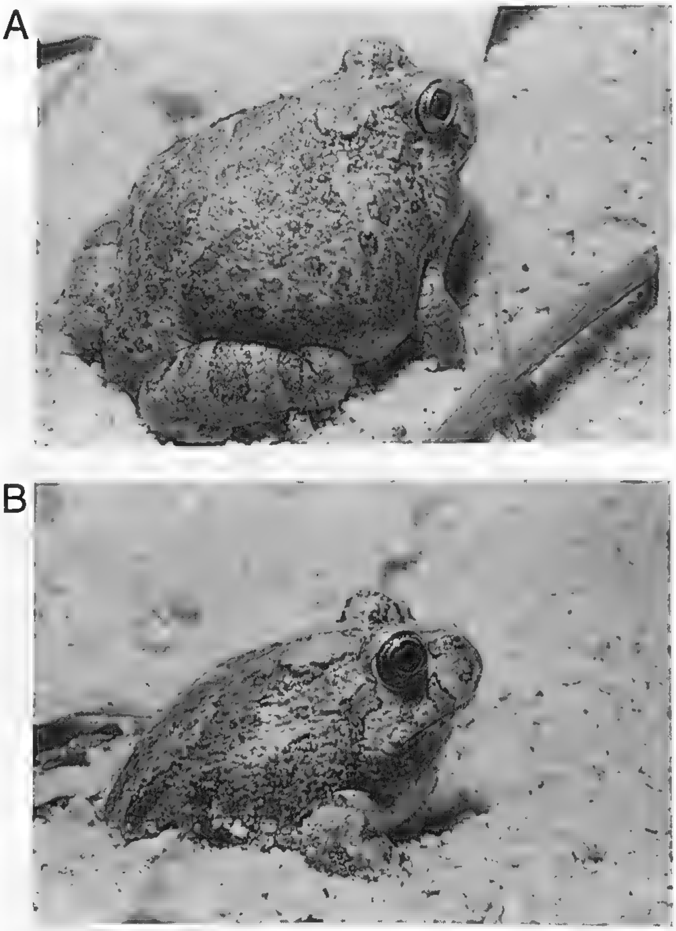

Figure 7.8 *Limnodynastes spenceri* a 'backward sliding burrower'.
[Photo by M. Davies]

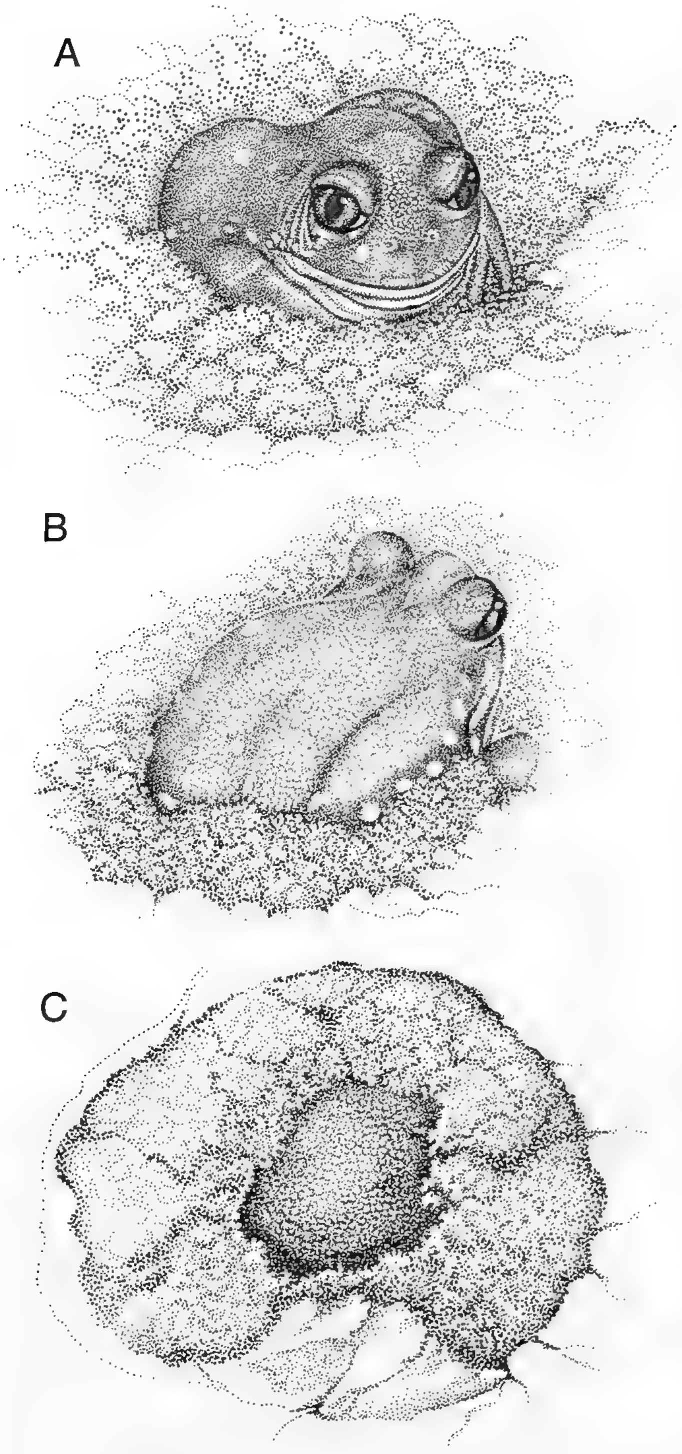

Figure 7.9 Circular burrowing mode of *Heleioporus albopunctatus*, which turns around as it progresses into the substrate. (After photos by G.E. Schmida/ANT) [T. Wright]

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

Behaviour

Burrowing, which is common in myobatrachids, is the most fundamental and widespread means of avoiding periods of aridity (Tyler 1989a). Three groups are recognised on the basis of burrowing pattern. *Limnodynastes dumerilii*, *L. ornatus* and *L. spenceri* (Fig. 7.8) are 'backwards sliding burrowers'. *Neobatrachus* spp., *Notaden bennettii*, *N. melanoscaphus*, *N. nichollsi* and *Heleioporus albopunctatus* (Pl. 3.8) are 'circular burrowers' (Fig. 7.9; Sanders & Davies 1984). *Arenophryne rotunda* and *Myobatrachus gouldii* are the two members of a 'forward burrowing' group (Pl. 2.1–2.3; Tyler 1989a).

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

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

Myobatrachids demonstrate specificity of female response to calls of conspecific males. For example, females of *Geocrinia laevis* always approached broadcast calls of a conspecific male when given a choice between that and a call from *G. victoriana* (Littlejohn & Watson 1974). Females of *G. victoriana* were almost as successful, but about 12% of females chose incorrectly. In sympatric myobatrachids, call differentiation is marked. For example, five species of *Heleioporus* that breed synchronously in the same swamps in south-western Australia have distinct calls (Littlejohn & Main 1959; Lee 1967; Bailey & Roberts 1981) ranging from a slow moan in *H. eyrei* to a highly pulsed call in *H. psammophilus*. However, calls of related, allopatric species may retain strong similarity in structure. For example, *Geocrinia alba* and *G. vitellina* both have short pulse trains, although they differ slightly in pulse rate, pulse number, and in dominant frequency (Roberts *et al.* 1990).

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

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

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

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

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

Choruses may be spatially organised. MacNally (1979) showed that males of two species of *Crinia (Ranidella)* were regularly spaced, and that males held specific calling-sites over extended periods. Non-calling, satellite males were common in these choruses. Satellites often took over calling sites when they were abandoned by resident callers. In *Uperoleia laevigata* (as *U. rugosa*), males actively defend an exclusive calling zone (Robertson 1984, 1986). In this species, there are also many satellite males who cannot hold calling territories. The status of males changes predictably over time. The heaviest males hold territories; however, as calling and territorial defence are energetically costly activities, the territorial males lose weight rapidly, and hence their ability to hold territories if challenged.

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

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

Economic Significance

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

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

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

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

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

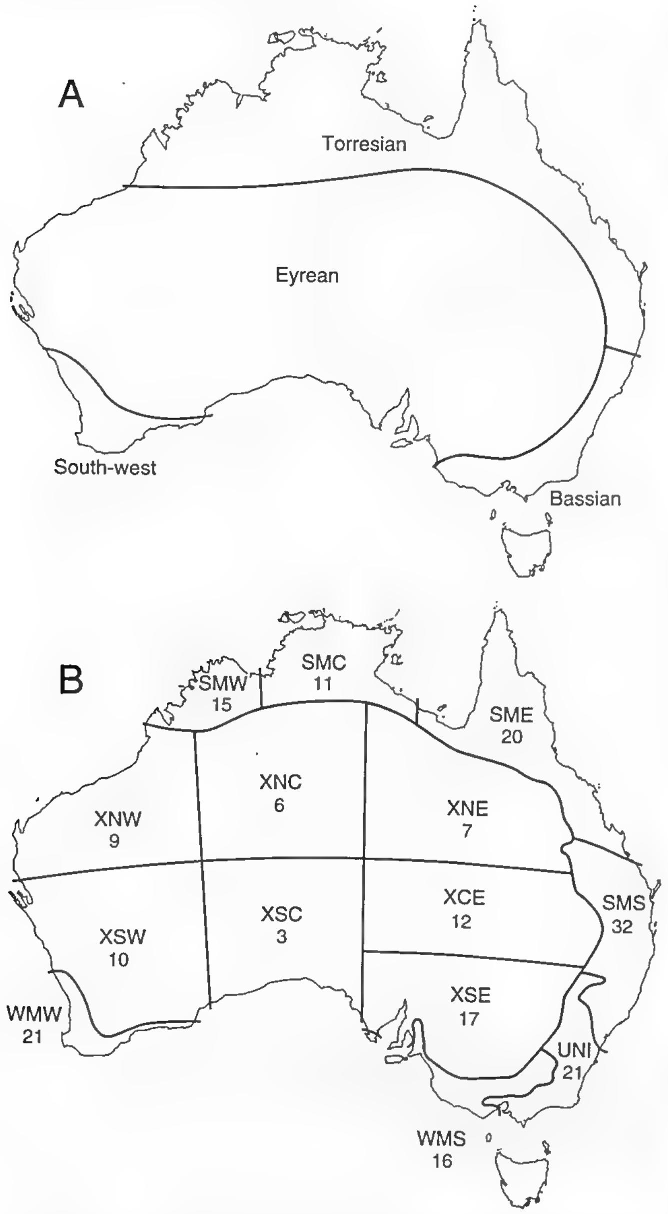

Figure 7.10 Australian zoogeographical regions. A, the faunal subregions of Spencer; B, zoogeographic areas for myobatrachid frogs. Division of three eastern areas (SMS, UNI, WMS) is based on seasonal rainfall incidence — the ratio of median rainfalls in summer and winter. The crescentic belt of summer-maximum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

of south-western Western Australia, especially on the destruction of breeding habitats (in low-lying water courses). Main concluded that salination, in particular, had caused a decline in the distribution and/or abundance of *H. albopunctatus*.

BIOGEOGRAPHY & PHYLOGENY

Distribution

The division of the terrestrial biota of the Australian Region (*sensu* Wallace 1876) into subregions has been a continuing process since its initiation by Tate (1889). Main, Lee & Littlejohn (1958), and Jenkins (1982) have provided historical accounts for both the flora and the fauna. The major schemes are the faunal subregions of Spencer (1896), as modified by Serventy & Whittell (1951) (Fig. 7.10A); the floristic zones of Burbidge (1960); the avian divisions of Kikkawa & Pearse (1969); the bioclimatic regions of Nix (1982); and the botanical regions of Barlow (1984; 1985). However none of the recent, objectively-based schemes is appropriate to the anurans, usually because the mesic zones are too extensive, so that their boundaries are placed in areas that are too dry for many anuran taxa.

The amount, seasonal distribution and reliability of precipitation are critical factors in determining the geographic ranges of frog species, because of their relatively permeable integuments, and the requirement for free water or sustained high humidities to complete their life cycles (Littlejohn 1981). These factors were used in establishing a zoogeographic map for the Myobatrachidae (Fig. 7.10B). Boundaries to zoogeographic regions were established using isopleths for precipitation and broad climatic patterns following the criteria of Littlejohn (1981). The Seasonal Rainfall Zones established by the Bureau of Meteorology (1975, 1989) provided the basis for delimitation of climatic regions.

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

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

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

Affinities with other Groups

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

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

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

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

(Lynch 1973). The Sooglossidae were retained as a separate family.

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

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

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

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

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

Affinities within the Taxon

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

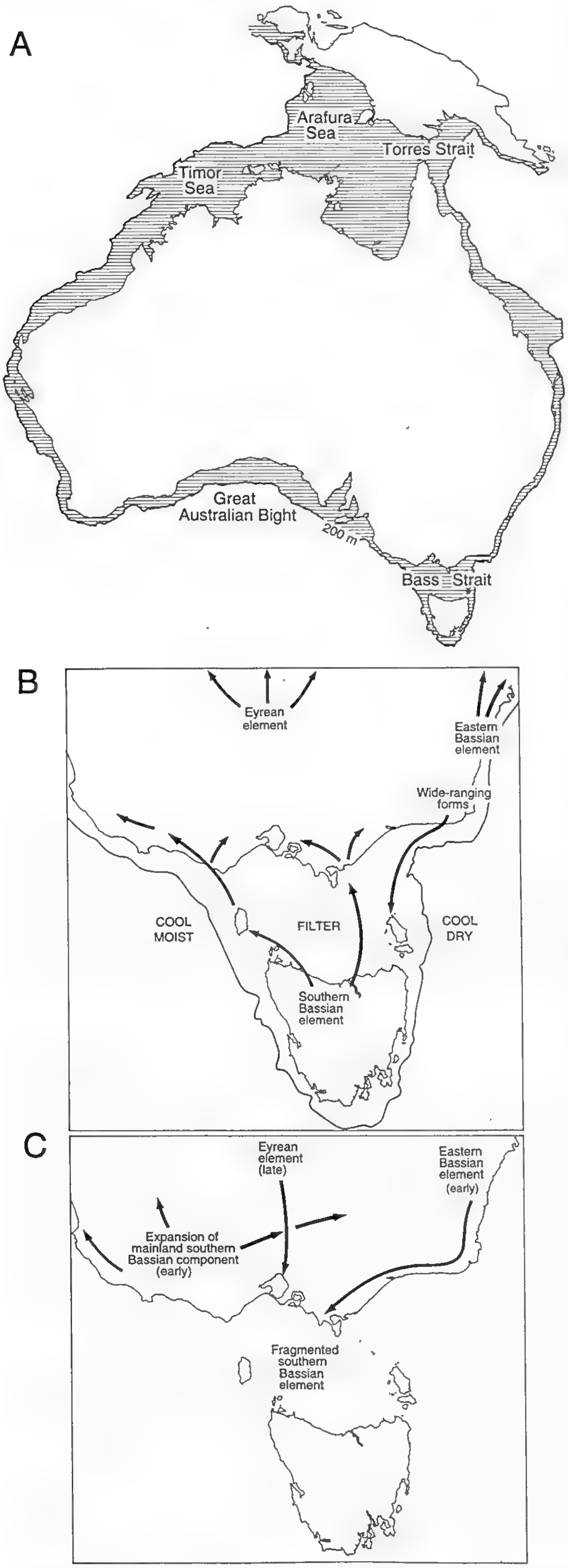

Figure 7.11 Scenarios for distributional changes in south-east Australian faunal elements. **A**, the present coastline of Australia and southern New Guinea, in which the 200 m isobath approximates the coastline some 20 000 years ago; **B**, expansion of cool-temperate (Bassian) elements, and probable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

At the height of the last glaciation, about 20 000 years ago, the global temperatures were lower than at present (by 5 to 7°C at sea level in middle latitudes) and much of the Earth's water was incorporated into expanded polar ice-caps and continental ice-sheets. As a consequence, the world sea level was lowered by some 130 to 150 metres (Chappell 1983b). Most of the continental shelf was exposed, and many of the adjacent islands were linked to the Australian mainland (Fig. 7.11A).

Evidence from isotope-dated changes in lake levels, stream flows, pollen profiles, etc., suggests that effective precipitation was higher than at present during the first part of the glacial period, and possibly lower than at present in the last part (see Edney, Kershaw & De Deckker 1990; Singh & Luly 1991; Nanson, Price & Short 1992 and references cited). As the glacial period ended and temperatures increased, the ice sheets began to melt, and the sea level rose at about one metre per century until the present mean sea level was reached about 6 000 years ago (Chappell 1983b). In the mid-Holocene Epoch (about 5000 years ago), the climate of southern Australia probably was warmer and moister than at present (De Deckker, Kershaw & Williams 1988).

During the early stage of glaciation, the cool-temperate adapted faunal elements (Bassian) could expand their ranges to the north and west, facilitated by the land bridges and extensive coastal plains, while the distributions of warm temperate xeric-adapted elements presumably contracted to the north. During the dry phase, mesic-adapted, or moisture-sensitive taxa would have reduced geographic ranges (Fig. 7.11B). Subsequently, during the warmer mid-Holocene, warm-temperate mesic elements could have expanded their ranges, presumably at the expense of the cool-temperate mesic elements — which would then have contracted their ranges and may have become fragmented, leading to the present patterns of distribution (Fig. 7.11C).

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

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

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

A similar scenario was also adopted by Keast (1958) when explaining speciation in whip birds (*Psophodes*).

Main *et al.* (1958) adopted the model of Serventy & Whittell (1951), and extended it to include three successive east-west migrations during the Pleistocene Period to explain the high diversity of south-western species in three genera of myobatrachid frogs (*Heleioporus*, *Neobatrachus* and *Crinia (Ranidella)* in the absence of obvious local geographic barriers. The model of Main *et al.* (1958) was also employed by Mackerras (1962) for tabanid flies, Main (1962) for trap-door spiders, and Horton (1972) for skinks of the genus *Egernia*. Rawlinson (1974) noted the presence of eastern and western conspecific populations and species pairs of reptiles, as did Hutchinson (1990). Thus, there seemed to be a considerable amount of supporting data from disjunct conspecific populations, and cognate species-pairs in a number of taxonomic groups that reflected recent continuous distribution across southern Australia. Lee (1967) re-examined the application of the multiple migration model to *Heleioporus*, and also considered the likelihood of *in situ* speciation in the south-west. He was also swayed against the latter model because of the apparent lack of suitable geographic barriers.

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

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

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

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

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

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

8. FAMILY HYLIDAE

Michael J. Tyler & Margaret Davies

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.infrafrenata* 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 Pelodryadinae is confined to Australia, New Guinea and adjacent islands.

In the Australian region, the endemic subfamily Pelodryadinae comprises the genera *Litoria*, *Nyctimystes* and *Cyclorana*. Pelodryadines 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

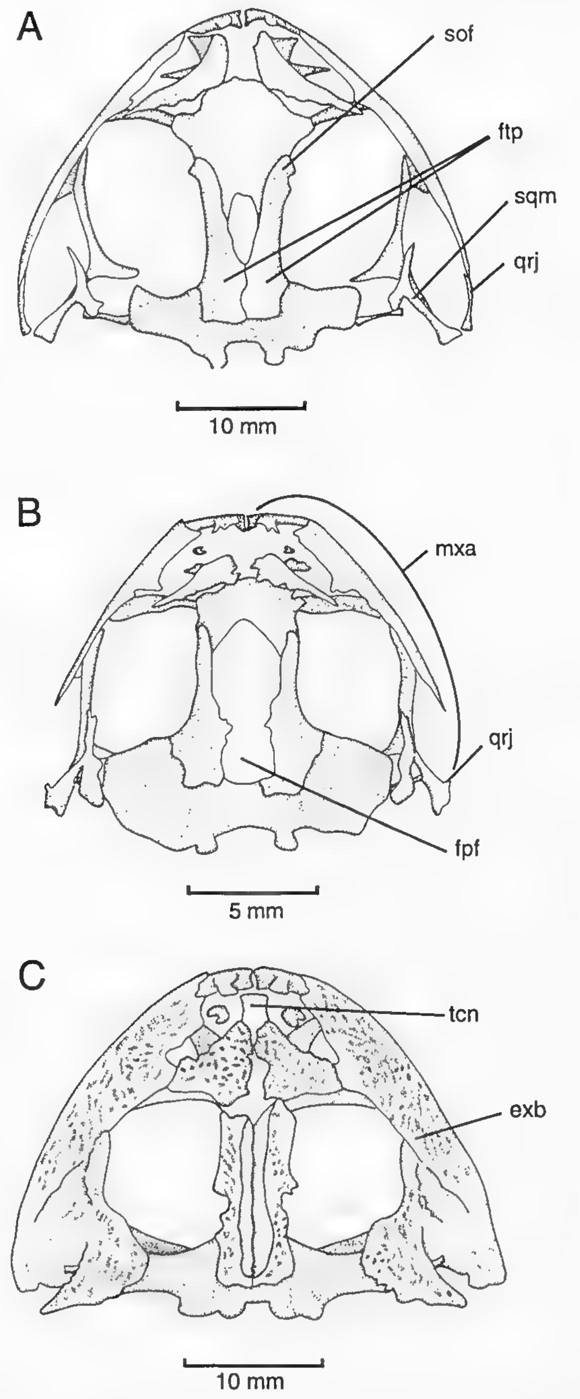

Figure 8.1 Dorsal view of the hylid skull. A, *Litoria splendida*; B, *Litoria verreauxi*; C, *Cyclorana novaehollandiae*. **exb**, exostosed bone; **fpf**, frontoparietal fontanelle; **ftp**, frontoparietal; **mxa**, maxillary arch; **qrj**, quatratojugal; **sof**, supraorbital flange; **sqm**, squamosal;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

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, nomencalture 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 Kestevan'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 (Fig. 8.1C). It is absent in other *Litoria* species and in *Nyctimystes*. The prootic is complete in all hylids and the columella is present.

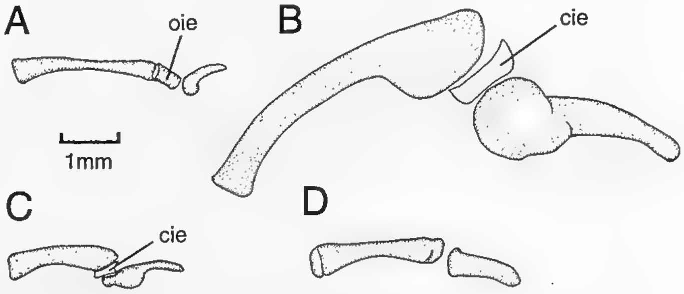

Figure 8.2 Terminal phalanges of hylid frogs. **A**, *Litoria nasuta*; **B**, *L. caerulea*; **C**, *Nyctimystes dayi*; **D**, *Cyclorana australis*. **cie**, cartilaginous intercalary element; oie, ossified intercalary element. [M. Davies]

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) (Fig. 8.1A) and in *L. infrafrenata*.

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 (Fig. 8.2).

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, 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).

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

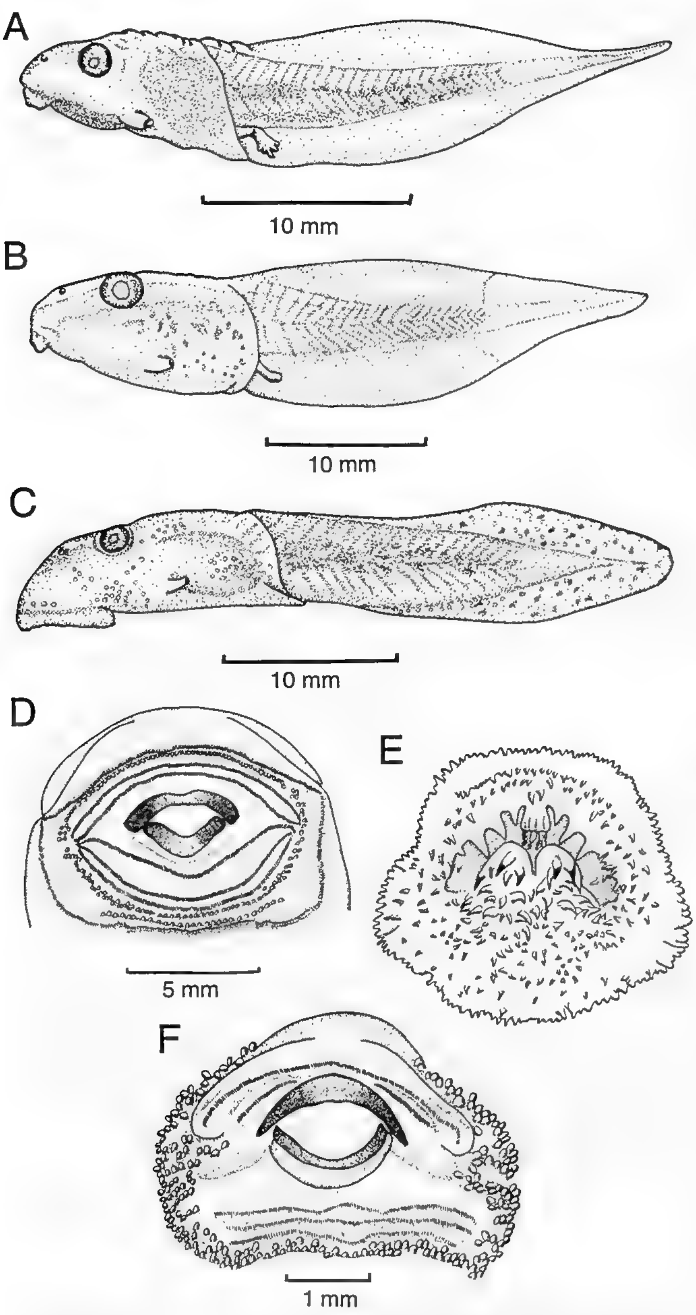

Figure 8.3 Lateral views (A–C) and oral discs (D–F) of hylid tadpoles. Lateral view of A, *Litoria rubella*; B, *L. infrafrenata*; C, *L. nannotis*. Oral disc of D, *L. nannotis*; E, *L. subglandulosa*; F. *L. infrafrenata*. (E, After Tyler & Anstis 1975) [M. Davies]

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 1967; 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* (Fig. 8.3B), whilst those of the mountain stream type have flattened bodies, narrow tail fins, a well-developed tail musculature and a large suctorial mouth with numerous labial papillae, for example, *L. lesueuri* (Martin 1967); *L. eucnemis* (Davies 1989b), *Nyctimystes dayi* (Davies & Richards 1990) and *L. nannotis* (Fig. 8.3C).

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

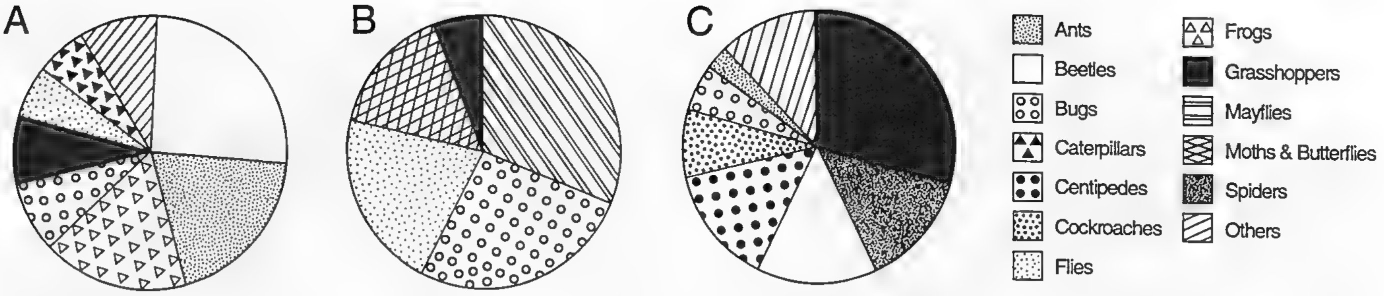

Figure 8.4 Frequency of occurrence of prey categories in the diet of *Litoria dahlii* during three periods over five months at Jabiru, Northern Territory. A, mid wet season; B, late wet season; C, late dry season. (From Tyler 1989a) [D. Wahl]

& 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 $\frac{1\ ^{1}\ 1}{1\ 2\ 1}$ and $\frac{2}{3}$ $\frac{2\ \ 2}{3}$ $\frac{1\ ^{1}\ 1}{2}$ $\frac{1\ ^{2}\ 1}{2}$ $\frac{1\ ^{1}\ 1}{2\ 1\ 2}$ 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).

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. gracilenta*, *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 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. nigritarsus* 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. paraewingi* 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. dahlii* 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 (Fig. 8.5).

Fletcher (1890, 1891, 1892, 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 Pelodryadinae.

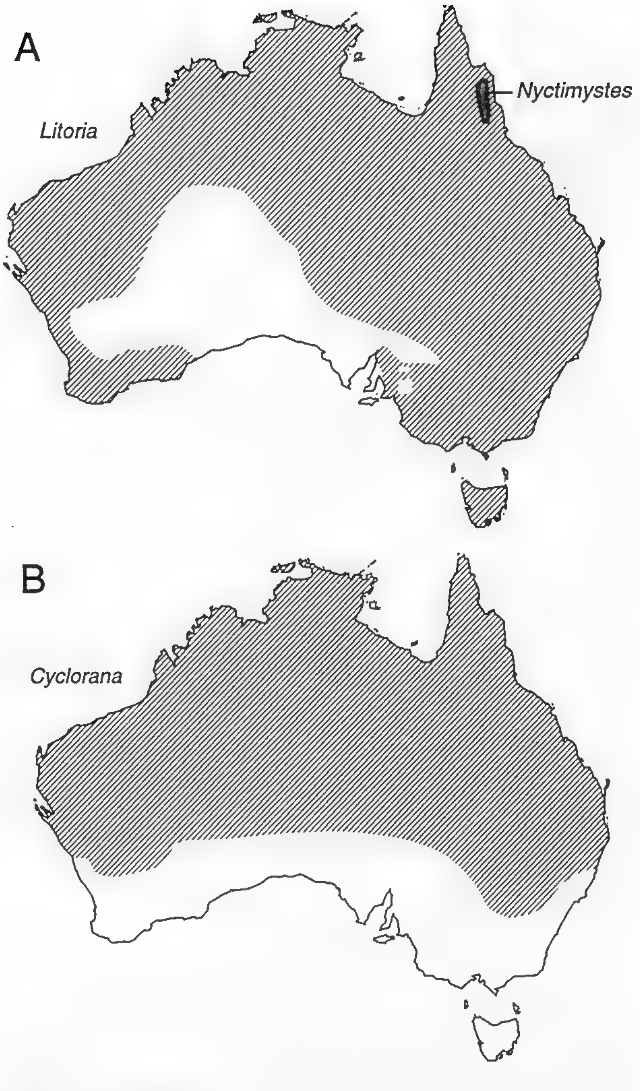

Figure 8.5 Distribution of hylid genera. A, *Litoria* and *Nyctimystes*; B, *Cyclorana*. [K. Maurice-Jones]

Savage (1973) interpreted these data as refuting the confamilial rather than the congeneric status of the Australopapuan element and erected the family Pelodryadidae to accomodate them. This view was followed by Laurent (1979), Dubois (1983, 1984), and reiterated by Savage (1986). Duellman (1975), who did not feel that available evidence warranted recognition of the Pelodryadidae 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. dahlii* (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 accomodate 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. infrafrenata* as being anomalous, an observation supported by its unique karyotype within the Pelodryadinae of 2n = 24 (Menzies & Tippett 1976).

Resolution of phylogenetic relationships within *Litoria* awaits further data analyses. It is highly likely that the number of pelodryadine 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 1991). 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.

9. FAMILY MICROHYLIDAE

Thomas C. Burton

DEFINITION AND GENERAL DESCRIPTION

The Microhylidae is a family of firmisternal frogs, which have broad sacral diapophyses, one or more transverse folds on the surface of the roof of the mouth, and a unique slip to the abdominal musculature, the *m. rectus abdominis pars anteroflecta* (Burton 1980). All but one of the Australian microhylids are small (snout to vent length less than 35 mm), and all have procoelous vertebrae, are toothless and smooth-bodied, with transverse grooves on the tips of their variously expanded digits. The terminal phalanges of fingers and toes of all Australian microhylids are T-shaped or Y-shaped (Pl. 1.3) with transverse grooves.

The Microhylidae consists of eight subfamilies, of which two, the Asterophryinae and Genyophryninae, occur in the Australopapuan region. Only the Genyophryninae occurs in Australia, represented by *Cophixalus* (11 species) and *Sphenophryne* (five species). Two newly discovered species of *Cophixalus* await description (Tyler 1989a). As both genera are also represented in New Guinea, information available from New Guinean species is included in this chapter to remedy deficiencies in knowledge of the Australian fauna.

HISTORY OF DISCOVERY

The Australian microhylids generally are small, cryptic and tropical, and so it was not until 100 years after European settlement that the first species, *Cophixalus ornatus*, was collected, in 1888 (Fry 1912). As the microhylids are much more prominent and diverse in New Guinea than in Australia, Australian specimens have been referred to New Guinean species from the time of the early descriptions by Fry (1915), whilst revisions by Parker (1934) and Loveridge (1935) minimised the extent of endemism in Australia.

The most important factors in the development of understanding of the nature and extent of the Australian microhylid fauna were an acceleration of faunal surveys of the northern rainforests and the involvement of Dr R.G. Zweifel, who in a series of papers described most of the known species, and explored their relationships, ecology and behaviour (Zweifel 1962, 1965, 1985; Zweifel & Parker 1969, 1977).

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

The main features of the external morphology are listed above. Although with experience it is possible to identify a frog as a microhylid by its general appearance, the only diagnostic external character is the presence of transverse grooves at the tips of the digits. Nor are there any reliable external characters to distinguish microhylid genera, as intrageneric variation outweighs intergeneric variation.

External characters are, however, the basis of a key to the Australian microhylid species prepared by Zweifel (1985). Variation between species occurs in size, breadths of finger and toe discs, proportions of leg length and of the snout, and the size of the thumb in *Sphenophryne*. As specimens, alive or dead, are difficult to measure reliably or consistently, even when the measuring equipment is good and the researcher experienced, there is often a degree of uncertainty in identifications based on proportions. Moreover, two pairs of Australian microhylid species are distinguishable by call alone.

Australian species range from reddish brown to grey brown, and sometimes pale yellow in colour dorsally, and are usually marked with darker streaks, W-, or H-shaped blotches, and mottling. The ventral surface may be white, yellow, orange, brown or grey in colour, sometimes with paler or darker flecks. Snout-vent length for all species ranges from 15 to 40 mm.

Body Wall

Tyler (1974b) demonstrated the importance of musculature as a source of taxonomically useful variation in Australopapuan microhylids. *Cophixalus* and *Sphenophryne* conform in most important respects to the generalised microhylid pattern exemplified by the New Guinean asterophryine *Phrynomantis stictogaster* (Burton 1983b), except in those features that distinguish the subfamilies Asterophryinae and Genyophryninae. These are the presence of a dorsal slip of the *m. intermandibularis* (Burton 1986) and the origin, in part, of the *m. acromiohumeralis* from the coracoid (Burton 1990) in genyophrynines, and overlap in the asterophryines of *m. intermandibularis* and *m. interhyoideus* (Tyler 1979).

The submandibular musculature of the genera differs (Burton 1984). In *Sphenophryne* the supplementary slip of the *m. intermandibularis* is a broad muscle, orientated medially, while

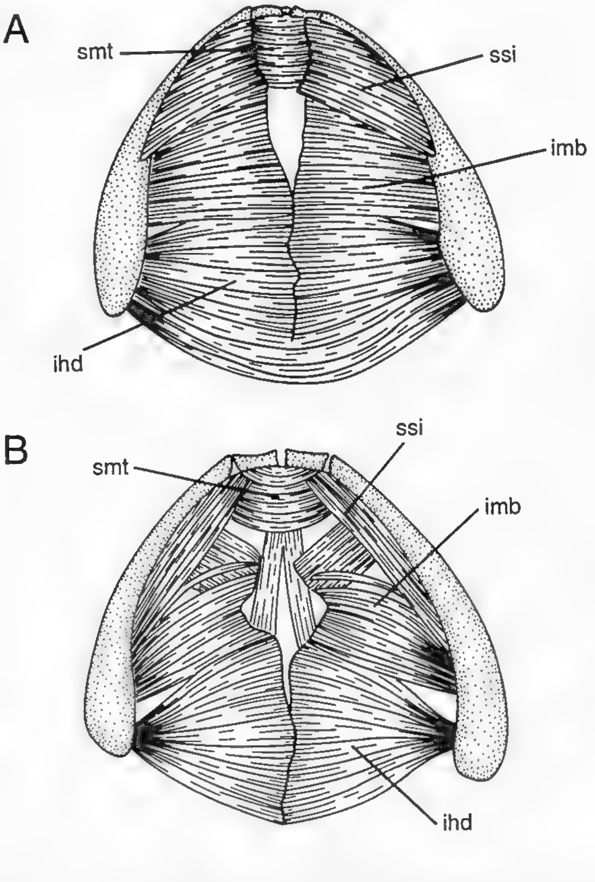

Figure 9.1 The submandibular musculature of microhylids. A, *Cophixalus ornatus*; B, *Sphenophryne* sp. **ihd**, *m. interhyoideus*; **imb**, *m. intermandibularis*; **smt**, *m. submentalis*; **ssi**, supplementary slip of the *m. intermandibularis*. (After Burton 1984) [C. Eadie]

in *Cophixalus* the same slip is narrow and orientated parallel to the mandible (Fig. 9.1A, B).

Skeletal System

In both genera the pectoral girdle is reduced: *Sphenophryne* possesses clavicles and procoracoid cartilages but no presternal elements (Fig. 9.2A, B); *Cophixalus* lacks clavicles and procoracoids (Fig. 9.2C, D).

The skulls of Australian *Cophixalus* and *Sphenophryne* are generally well-developed, toothless, and the maxillae do not meet anteriorly to the premaxillae (the eleutherognathine condition). In both genera there is variation in the degree of ossification of the prootic region and the development of the vomer. Zweifel (1985) believed that paedomorphosis explains much of the evolution of the Australian fauna. He ascribes to paedomorphosis the poor ossification found in some species, for example, *C. hosmeri*, *C. infacetus* and *S. robusta*, and the relative lack of ossification of the extremity of the vomer in *Cophixalus*.

Paedomorphosis is invoked also to explain the non-imbricate condition of the vertebrae observed in both genera. As Zweifel (1985) points out, variation in the postcranial skeleton has not yet been documented sufficiently in either genus for useful generalisations to be made.

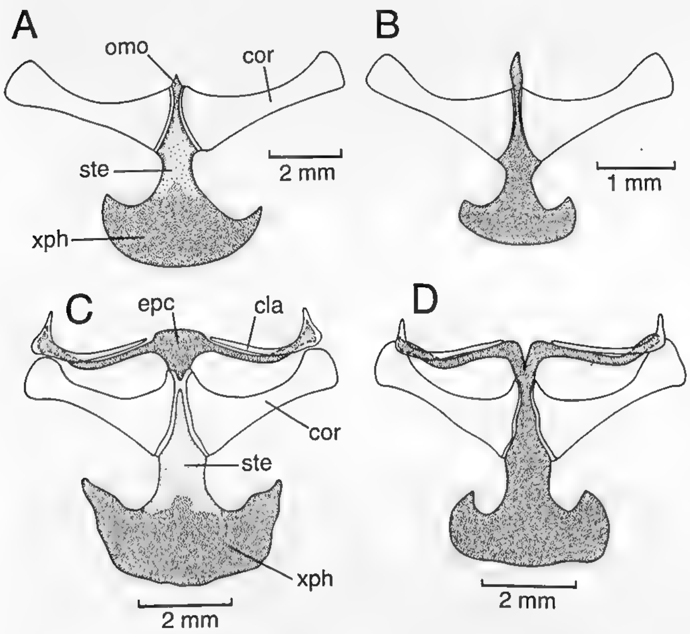

Figure 9.2 Pectoral girdles of Australian microhylids. A, *Sphenophryne fryi*; B, *S. pluvialis*; C, *Cophixalus hosmeri*; D, *C. saxatilis*. Dense stippling indicates cartilage, sparse stippling calcified cartilage, clear areas bone. **cla**, clavicle; **cor**, coracoid; **epc**, epicoracoid cartilages; **omo**, omosternum; **ste**, sternum; **xph**, xiphisternum. (After Zweifel 1985) [C. Eadie]

Locomotion

Australian microhylids are walkers rather than leapers. All *Sphenophryne* and most *Cophixalus* appear to be predominantly leaf-litter dwellers, but some *Cophixalus* are at least partially scansorial, and males of six *Cophixalus* species are known to call from elevated sites (Zweifel 1985). There appears to be a loose correlation between the tendency to climb and the width of finger-discs (but not toe-discs), but too little is known of the habits of most species to generalise (Zweifel 1985).

Feeding and Digestive System

As far as is known, the Australian microhylids are generalised feeders on leaf-litter invertebrates. No specialisation, such as the earthworm-feeding of *Xenobatrachus* (Blum & Menzies 1988), has been observed. All genyophrynines possess densely muscled tongues which are free posteriorly (Zweifel 1971; Horton 1982; Burton 1986). Captive specimens of *Cophixalus ornatus* and *Sphenophryne fryi* have been observed to flick their tongues long distances, almost to a body length (Burton pers. obs.).

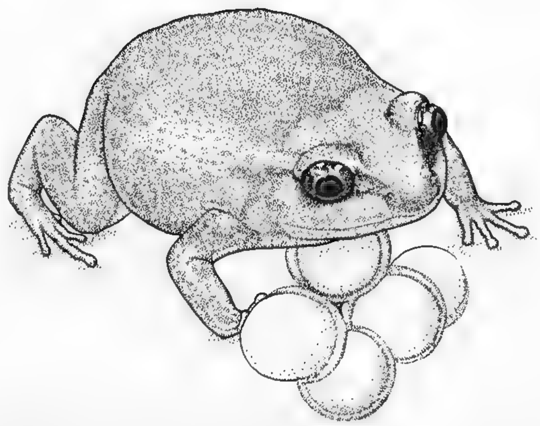

Figure 9.3 Adult *Sphenophryne fryi* attending egg mass. The eggs are held together by a string of jelly. (After photo by A. Dennis/ANT) [M. Cilento]

As in other Genyophryninae and Asterophryinae, the Australian microhylids that have been examined possess a denticulate transverse fold on the posterior surface of the roof of the mouth. The function of this fold is not known. It may provide mucus to the tongue before or during feeding, lubricate food, or it may wipe the tongue after feeding. There has been no study of the morphology or physiology of the digestive system of microhylids.

Reproduction

Little is known of the reproduction of the Australopapuan microhylids. A small number of macrolethical (large-yolked) eggs are laid on land, the eggs being held together by a string of jelly so that the egg mass resembles a string of beads (Fig. 9.3).

When egg masses are discovered by accident under leaf-litter, almost always they have been accompanied by an adult male (Fig. 9.3). In New Guinea also it is rare for a female to be collected with an egg mass (Simon 1983). The function of this apparent parental behaviour is unknown. Tyler (1976b) discusses fungal attack of microhylid eggs and suggests similarity to salamanders that sit on eggs and have antibacterial and antifungal agents in ventral skin. Simon (1983) found high mortality among embryos from which the adult was removed, usually due to fungal attack.

Horton (1984) examined the female reproductive tracts of five *Cophixalus* species, including *C. neglectus* and *C. ornatus* from Australia, and one *Sphenophryne*. She found that these species possess reproductive tracts characterised by few convolutions of the oviducts, a small ovarian complement and large egg diameter, few lobes of the ovary, and completely united ovisacs.

Embryology and Development

All available data suggest that microhylid larvae develop directly, completing metamorphosis within the egg capsule, and a miniature frog ultimately emerges from the egg (Fig. 9.4). The larva lacks adhesive organs, external gills, branchial clefts, internal gills, an operculum, spiracles and keratinous denticles (Parker 1934). Parker noted also that respiration is achieved through a vascular tail which is apposed to the inner surface of the egg capsule (Parker 1934). Simon (1983) found that the time between egg-laying and hatching varied from 85 to 100 days in *Cophixalus parkeri* from New Guinea.

NATURAL HISTORY

Ecology

Of the 16 Australian microhylid species, 13 are restricted to rainforest, and two occur in rainforest in part of their range. *Sphenophryne adelphe* occurs also on the Arnhem Land escarpment, where it is found under spinifex (*Triodia irritans*), and on Melville Island where it has been recorded from lawns and the floors of pine plantations (Tyler, Davies & Watson 1991).

Sphenophryne gracilipes occurs in open forest (Zweifel 1985), and *Cophixalus saxatilis* is unique among the Australian microhylids in its habitat, as it occurs only in granite boulder country, never in rainforests.

The altitudinal range occupied by a species appears at least in part to be related to temperature tolerance. Zweifel (1985) was unable to keep specimens of the high altitude frog *Cophixalus neglectus* alive whilst transporting them down from Mount Bellenden Ker to Cairns. On the other hand, Brattstrom (1970) found specimens of the low altitude species *Sphenophryne pluvialis* intolerant of temperatures as low as 10°C.

Behaviour

Most of the Australian microhylids are cryptic by day. All of the rainforest species are found by day under logs or leaf-litter, but *Cophixalus saxatilis* calls during the day from deep in crevices in a jumble of granite boulders (Zweifel 1985). *Sphenophryne adelphe* also calls by day (Tyler *et al.* 1991).

Rainforest species call at night from a variety of sites. All rainforest *Cophixalus* call from elevated positions, such as in shrubs, but seldom at a height much above two metres. Of the five *Sphenophryne* species, only *S. gracilipes* calls from an exposed position (Zweifel 1985).

Figure 9.4 Adult *Cophixalus parkeri* with hatchlings. (After Simon 1983) [M. Cilento]

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Only one of the 16 Australian species, *Sphenophryne gracilipes*, occurs in New Guinea (Zweifel 1985). Within Australia, 15 of the 16 species are apparently restricted to northern Queensland, between Mount Elliot, 30 km south of Townsville and the tip of Cape York. The only species recorded in the Northern Territory, *Sphenophryne adelphe*, occurs on the Cobourg Peninsula, in western Arnhem Land and on Marchinbar Island in the Wessel group. Of the north Queensland microhylids, only *Cophixalus saxatilis* occurs exclusively outside of the rainforest areas, in the vicinity of Black Gap, south of Cooktown, in a habitat of granite boulders.

Few species have a widespread distribution, and these tend also to have a wide altitudinal distribution. *Cophixalus ornatus*, found at altitudes of 20 to 1520 m, has a north-south range extending over more than 300 km. The other *Cophixalus* species have restricted distributions and generally occur over a narrow altitudinal range, about half of them above 900 m. All of the *Sphenophryne* species have relatively broad geographic and altitudinal distributions. Czechura (1978) suggested that altitudinal displacement occurs between *S. pluvialis* and *S. robusta* near the headwaters of the Russell River. McDonald (1992) pointed out that these two species are not found sympatrically.

Affinities with other Groups

There are two issues of the historical biogeography of the Australian Microhylidae to consider: the origins of the Australopapuan fauna as a whole, and the origins of the Australian component of that fauna.

The origins of the Australopapuan microhylids have been canvassed by Savage (1973) and Tyler (1979), who came to radically different conclusions. Savage saw the microhylids of the Oriental region as Gondwanan frogs which rafted northwards on the then-forested Australia and subsequently invaded Asia via New Guinea and the Indonesian Archipelago. In his view, the present Australian fauna is the product of a Pliocene reinvasion from New Guinea, after extinction of the family in Australia. Tyler, using modern distributional data, saw the reverse, and hypothesised an Asian origin and dispersal through Indonesia, followed by entry into New Guinea after the Miocene collision of the Australian plate with the Sunda Arc.

Only a discovery of appropriate fossils or a phylogenetic analysis of the Microhylidae could determine which of these hypotheses can be rejected. Currently fossil frogs are classified on the basis of the form of the ilium, which appears to be the most durable and taxonomically useful bone in fossils (Tyler 1989a). Unfortunately, the microhylid ilium is variable and not distinctive (Burton 1986), so that a fossilised ilium would be difficult to recognise. It is unlikely that fossils will yield evidence of past microhylid distribution in the foreseeable future.

Evidence of the monophyly of the Australian representatives of the two genera comes from the analysis of calls. Zweifel (1985) pointed out that there is very strong similarity of call structure in both genera of Australian microhylids compared with the congeners in New Guinea, and argued, albeit tentatively, that this indicates the monophyly of the Australian component of each genus. Zweifel allowed that the similarity of call may be due to the retention of primitive calls by the Australian microhylids, but this appears less likely than the derivation of the fauna from single invasions of Australia by one species each of *Cophixalus* and *Sphenophryne.*

The timing of the entry of the microhylids into Australia is open to debate. The Pleistocene (Tyler, Watson & Martin 1981), Pliocene (Savage 1973) or an earlier period (Zweifel 1985) have all been proposed. If the Australian microhylids are monophyletic, the time of entry must have been sufficient for at least some speciation to have occurred before the re-entry into New Guinea of *Sphenophryne gracilipes*, the only species to occur both in Australia and New Guinea.

Affinities within the Taxon

Zweifel's (1985) hypotheses of the phylogeny of each genus, based on external morphology are tenuous, as he expressed little confidence in assigning polarities to characters. McDonald's (1992) discussion of the prevalence of mountain top endemism suggested that *in situ* speciation of isolated populations may have been important in the evolution of the genera.

Parker (1934) referred the New Guinean species *Copiula fistulans* to *Cophixalus*, on the basis of its lack of a clavicle and procoracoids. Menzies & Tyler (1977) resurrected *Copiula* to accommodate *C. fistulans* and two other morphologically similar species, but the implication that *Copiula* and *Cophixalus* are close relatives persisted, and Zweifel (1985) pointed out the paucity of objective characters to distinguish the genera. Burton (1990) claimed that the unique, broad, transverse supplementary slip to the *m. intermandibularis* shared by *Sphenophryne* and *Copiula* is a more reliable indicator of relationships than the reduction of the pectoral girdle, which has clearly happened many times in the course of microhylid evolution (Jones 1933; Menzies & Tyler 1977). If the affinities of *Sphenophryne* have now been clarified, those of *Cophixalus* remain obscure.

10. FAMILY RANIDAE

Glen J. Ingram

DEFINITION AND GENERAL DESCRIPTION

Australian Ranidae, or 'True frogs', are ground-dwelling frogs characterised by the following features. The pectoral girdle is firmisternal, with the sternum fused to the pectoral arch and the epicoracoidal cartilages fused (Fig. 1.5B; Duellman & Trueb 1986). The phalangeal formula is normal in that there are no intercalary cartilages, the toes and fingers have grooved, dilated tips and the toes are webbed. There is a dorso-lateral skin fold from behind the eye to the hindlimb (Pl. 1.1). Maxillary teeth are present. The sacral diapophyses are cylindrical and the sacrum has a bicondylar articulation with the coccyx. The ilial shaft bears a large, tapering, fin-like, dorsal crest (Tyler 1976c). The tadpole has an emarginated oral disc with a fringe of elongated papillae along the posterior margin of the disc (Fig. 10.1; Richards 1992).

The family is cosmopolitan, though very poorly represented in southern South America and Australia (Frost 1985). In Australia only one species, *Rana daemeli*, is recorded from northern Queensland and north-east Northern Territory. It also occurs in New Guinea.

HISTORY OF DISCOVERY

The presence of ranid frogs in Australia was first noted by Günther (1867), British Museum. He examined two female specimens (see Boulenger 1882), found by Edward Dämel on Cape York in the latter half of 1866. However, he identified them as *Hylorana erythraea*, a South-East Asian species. Dämel was a collector for the Godeffroy Museum, Hamburg (Musgrave 1932; Monteith 1987). Steindachner (1868) of Vienna, described a further nine of Dämel's specimens and correctly assigned them to a new species, *Hylorana daemeli* (Boulenger 1920). The species was to be 'discovered' twice again at Cape York. Macleay (1877) of Sydney, named a species *Hylarana nebulosa* from a specimen collected during the *Chevert* cruise and de Vis (1884b), Queensland Museum, Brisbane, named *Hyla nobilis* from specimens collected by Kendall Broadbent.

MORPHOLOGY AND PHYSIOLOGY

Little has been published on the morphology and physiology of the Australian *Rana*. However, the Ranidae has been much studied in Europe and America (see Noble 1931; Porter 1972; Duellman & Trueb 1986 and references therein). A pair of lateral vocal sacs can be inflated externally as separate pouches (Fig. 10.2A; Tyler 1989a).

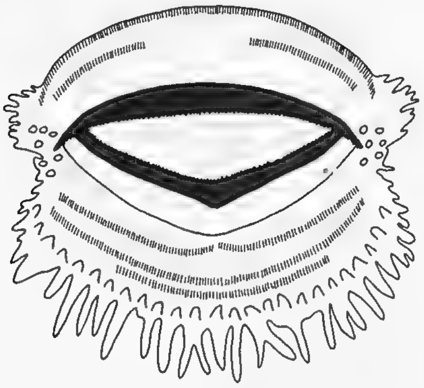

Figure 10.1 Mouth disc of *Rana daemeli* tadpole. (After Richards 1992)
[T. Wright]

REPRODUCTION AND DEVELOPMENT

The species of Australian and Papuan ranids that have been karyotyped have a diploid chromosome number of 26 and are similar in chromosome morphology (Menzies 1987). According to Richards (1992), tadpoles belong to the Benthic (Type 2: Profundal) ecomorphological guild of Altig & Johnston (1989). The length of time from egg to metamorphosis is unknown.

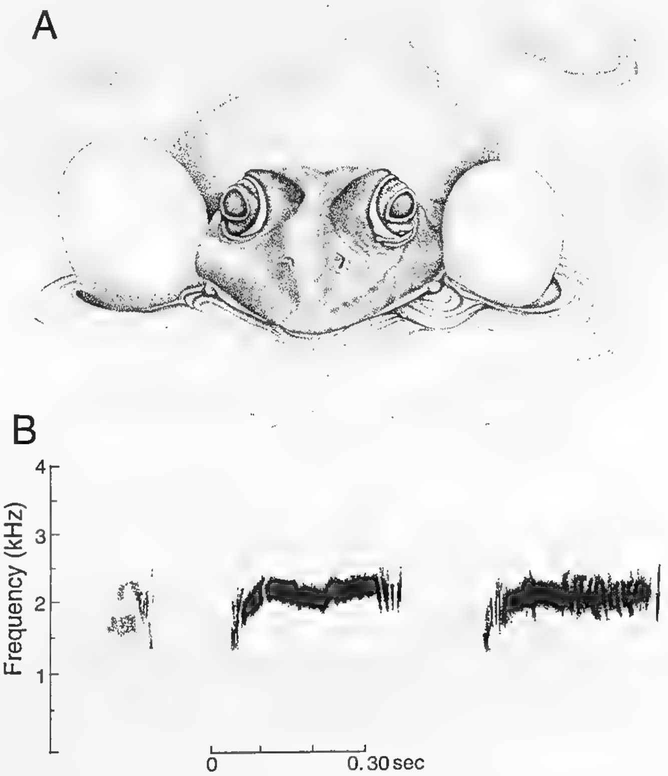

Figure 10.2 Vocalisation in *Rana*. A, calling male of a European species, *Rana esculenta*, showing the distended pair of vocal sacs characteristic of Ranidae; B, sound spectrogram for a New Guinean population of *Rana daemeli*. (A, after Cochran 1961; B, after Menzies 1987)
[A, T. Wright; B, W. Mumford]

NATURAL HISTORY

Like most frogs, the Australian ranid lives on land and returns to water to breed. The males call (Fig. 10.2B) from beside water, usually in late spring, summer and early autumn. Amplexus is axillary. Eggs are deposited in water and float in large, loosely attached clumps at the surface.

Rana daemeli occurs mostly along streams, rivers and swamps, in a variety of vegetation types from open woodland through to monsoon forest and rainforest.

Spiders, a shrimp, cockroaches, grasshoppers, a beetle, a moth, one *Litoria pallida* and the legs of two unidentified frogs were found in stomach contents examined by Cameron & Cogger (1992) at Weipa, Cape York.

Rana daemeli has been the subject of several investigations for internal parasites. Delvinquier & Jones (1988) recorded the gut flagellate *Trichomitus batrachorum* and Delvinquier (1988) recorded an undetermined gut ciliate of the family Sicuophoridae. Several species of nematode are also parasites of *R. daemeli.* Sprent (1985) recorded the gut ascaridoid *Seuratascaris numidica,* Owen & Moorhouse (1980) recorded the gut physalopterid *Pseudorictularia disparilis* and Moravec (1990) recorded the lung parasite *Rhabdias australiensis.* Cameron & Cogger (1992) noted acanthocephalans and species from three orders of nematodes in the intestine of *R. daemeli.*

Heatwole and Shine (1976) recorded female mosquitoes *Uranotaenia argyrotarsis* biting the head of *R. daemeli* at night, especially on the eyelids. Numerous simultaneous bites resulted in raised whitish swellings. No mosquitoes were seen biting the body or legs. Marks (1980) recorded one female *U. novaguinensis* and six *Culex* (*Lophoceraomyia*) spp. (representing two or three species) biting a *R. daemeli.*

Sources of mortality and behaviour of Australian ranids are largely unknown. Although species of *Rana* are the major source of frog legs for the food and restaurant market, the Australian species has not been considered for farming, apparently because its small legs would be uneconomical (Maclean 1975).

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Australian *Rana daemeli* occurs on Cape York Peninsula, Queensland, south to Kowanyama (15° 19′S) in the west and near Townsville (19° 16′S) in the east (Ingram & Raven 1991; Fig. 6.1), and has been recorded recently in eastern Arnhem Land, Northern Territory (N. Gambold pers. comm.).

Ranidae are regarded as very recent colonisers of Australia, probably during the Pleistocene (Kikkawa, Monteith & Ingram 1981; Savage 1973).

Affinities within the Taxon

Boulenger (1920) reviewed the subgenera and species of *Rana* in southern Asian, New Guinea, Melanesia and Australia. He allocated the Australian species to the subgenus *Hylarana.* Savage (1973) placed the Australian and New Guinean ranid species in the subfamily Platymantinae. However, the contributors to Frost (1985) preferred to be conservative and only recognised Raninae (including Platymantinae). Menzies (1987) revised the species of *Rana* in Papua and Australia and placed *R. daemeli* in the *R. papua* group.

Australian and Papuan species of ranids are very conservative in their morphology. However, they differ in their advertising call and habitats. Even so, it is difficult to gather this information. Donnellan, Adams & Aplin (1989) found that it was easier to identify genetic groups by biochemical analysis.

Fossil Record

No fossil ranids have been recorded from Australia (Tyler 1991e).

11. FAMILY BUFONIDAE

Simon Easteal

DEFINITION AND GENERAL DESCRIPTION

The skin of bufonids is thick, glandular and contains pustular warts in many species, including *Bufo marinus*. In *Bufo* and some other genera, large parotoid glands are present (Pl. 1.2). The toes do not end in discs. The upper jaw is edentate. Bufonidae can be distinguished from all other anurans by the presence of Bidder's organs in males (Fig. 11.1), although the absence of these does not exclude Bufonidae since they are not always present in mature individuals of some species (Griffiths 1963). All *Bufo* species have a diploid chromosome complement of 2n = 22, except members of the *B. regularis* species group, in which 2n = 20.

Twenty-three recent genera are included in the Bufonidae (Frost 1985). *Bufo* is the only genus found in Australia, represented by the introduced *B. marinus*.

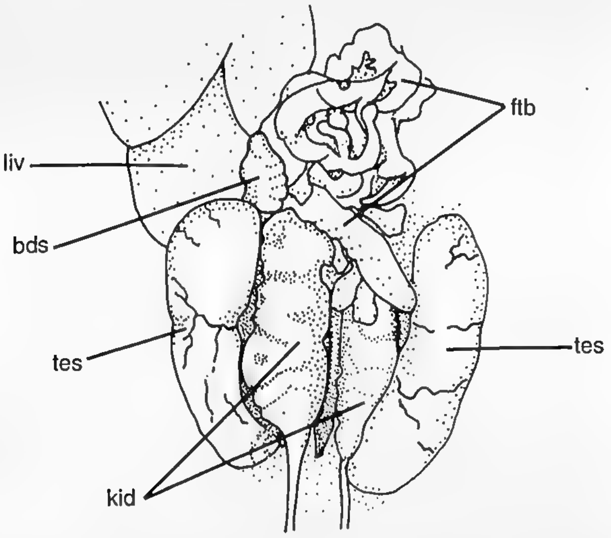

Figure 11.1 Bidder's organ in a small male *Bufo marinus*. **bds**, Bidder's organ; **ftb**, fat bodies; **kid**, kidney; **liv**, liver; **tes**, testis. [J. Courtenay]

HISTORY OF DISCOVERY

In 1935, 101 individuals of *Bufo marinus* were introduced deliberately into Queensland, in an attempt to control the greyback cane beetle, *Dermolepida albohirtum*, in sugar cane fields. Initially they were released in the Cairns, Gordonvale, Innisfail and Tully districts of Queensland. Over the next two years, further releases were made in nine districts between Mossman, north of Cairns, and Isis, near Bundaberg (Sabath, Boughton & Easteal 1981; Seabrook 1991).

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Individuals of *B. marinus* are among the largest toads. Adult females can weigh over 1.5 kg and have snout-vent lengths greater than 22.5 cm (Reed & Borowsky 1966). Females are generally larger than males, and most adults range in size from about 8.5 to 15.0 cm snout-vent length.

The head is broader than it is long, the snout is rounded in dorsal view and truncated in profile. Well-developed cranial crests form ridges above the eyes and join above the snout. The eyes are large and prominent and have horizontal pupils. The diameter of the distinct tympanum is slightly less than half that of the eye. The parotoid glands are extremely large, triangular and swollen. The limbs are short. The toes are partially webbed, but the fingers are not. The first finger is longer than the second.

There is obvious sexual dimorphism. Irregularly scattered warts and tubercles cover both sexes. However, the skin of the female is much smoother than that of males, which has the texture of rough sandpaper, caused by the presence of numerous horny spicules on the warts and tubercles. The venter of the female and young male is creamy white; the dorsum is covered with irregular blotches of various shades of brown. The skin of adult males is more uniformly yellowish-brown in colour; the yellow is pronounced laterally and around the throat (Pl. 1.2). The first finger and the inner surfaces of the second and third fingers of sexually mature males bear brown nuptial pads, and a median vocal sac opens on each side of the mouth.

The black larvae are small (up to 35 mm S–V), and the round body is slightly wider than it is deep. The tail fins are non-pigmented and transparent, and the tail is rounded. The dental formula is $\frac{1\ ^{1}\ 1}{3}$.

Body Wall

The skin of *B. marinus* is permeable to water, and absorption of water through the skin is an important rehydration mechanism, particularly in the ventral pelvic region. There is an active ion transport system in the skin with a net inward movement of sodium ions. The skin is also important in gas exchange (Hutchinson, Whitford & Kohl 1968).

Skeletal System

In most *Bufo* species, including *B. marinus*, there are eight presacral vertebrae. The atlas is not fused to the adjoining distal vertebra, the pectoral girdle is arciferal and the prezonal omosternum is absent.

Locomotion

Bufo tadpoles are weak swimmers. Adults are primarily terrestrial, but are capable of swimming. On land they walk and hop, but do not leap. Miller & Zoghby (1986) have shown that adult *B. marinus* move fastest at 22°C and that their speed of movement is enhanced if they are acclimated at this temperature. Dehydration appears to have less impact on the locomotion of *B. marinus* than on other anurans (Moore & Gatten 1989).

Feeding and Digestive System

The larvae of *B. marinus* feed on the surface layers of submerged vegetation and detritus. The rasping mouth parts are used to generate fine nutrient particles that are ingested by filter feeding. During their early development, the larvae feed on the gelatinous string from which they have emerged.

The well-developed tongue of the adult bears sticky, mucous secretions and is used actively to catch prey. *Bufo marinus* eat almost any prey of appropriate size, and the diet appears to reflect the food available in a particular location. Prey consists mainly of

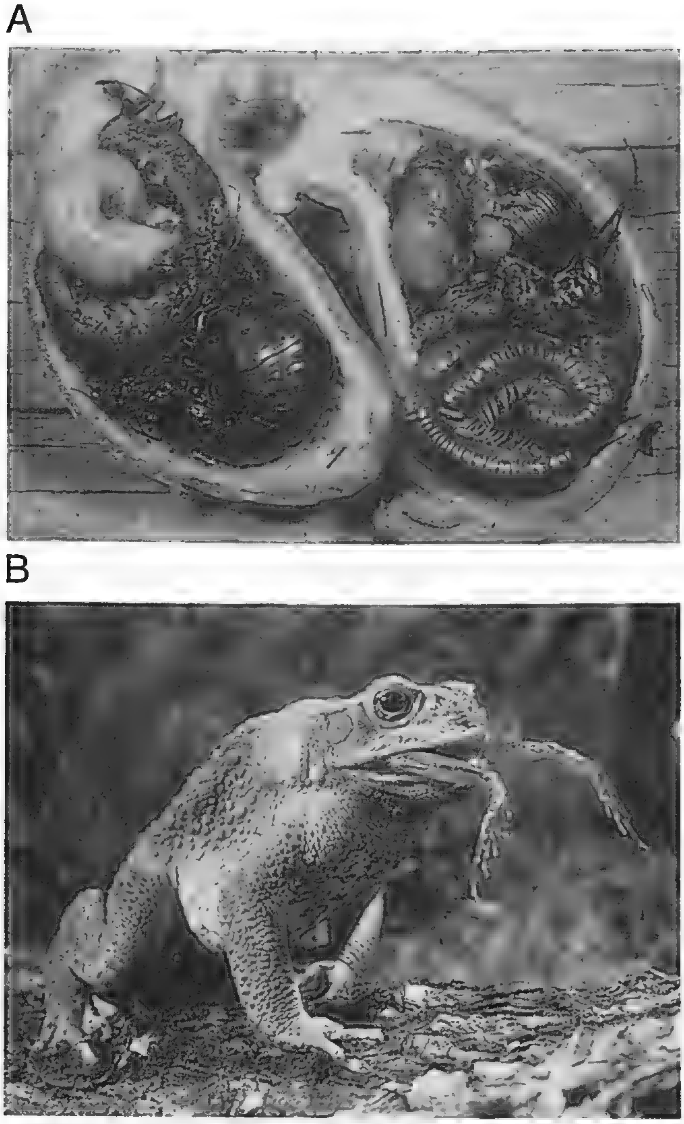

Figure 11.2 *Bufo marinus* preys on a wide variety of animal groups. **A**, bisected stomach, containing typical prey remains of several millipedes, spiders, beetles and other insects; **B**, indigenous frogs also form part of the diet of *B. marinus*.
[A, photo by M. Trenerry/NPIAW; B, Kathie Atkinson/Auscape]

small terrestrial arthropods, including crabs, spiders, centipedes, millipedes, scorpions and a wide range of insects (Fig. 11.2A). Additional dietary items include earthworms, planarians, molluscs, small vertebrates (Fig. 11.2B) including its own young, rotting fruit, dog and cat food and human faeces. Quantities of plant material and stones found often in the stomach of toads are probably ingested accidentally (Krakauer 1968; Covacevich & Archer 1975; Tyler 1975; Zug, Lindgren & Pippett 1975; Zug & Zug 1979; Niven 1988). Heatwole & Heatwole (1968) have shown that the upper size threshold of prey selected increases, following long-term food deprivation, but the lower size threshold remains the same.

Circulatory System

The heart of the *Bufo* larva has one atrium and one ventricle. In adults there are two atria and one ventricle. The resting heart rate is approximately 13.5 beats/minute, which increases in response to feeding and visual and tactile stimuli (Dumsday 1990). Heart rate also increases in response to desiccation, possibly due to increased peripheral circulation (Sherman 1980). Cardiovascular function of *Bufo marinus* is described in more detail in Chapter 4. The dense vascularisation of the ventral pelvic integument probably reflects the importance of this region in water uptake (Roth 1973). *Bufo marinus* can survive in salinities of up to 40% sea-water by increasing plasma sodium, chloride and urea to levels that are hyperosmotic to the environment (Liggins & Grigg 1985).

Respiration

In adults, gas exchange occurs through skin, lungs and the buccal cavity. The lungs are the most important and their relative contribution increases with increasing temperature (Hutchison, Whitford & Kohl 1968).

Excretion

Toads excrete urea through mesonephritic kidneys. Water, sodium and other ions can be actively resorbed from the urinary bladder, in which up to 30% of total body water can be stored (Ruibal 1962). Water uptake from the urinary bladder is thought to occur intracellularly (Shi & Verkman 1989). Shoemaker & Waring (1968) have shown that hypothalmic lesions interfere with the normal mechanisms of both the renal and cutaneous water balance.

Sense Organs and Nervous System

Much of the extensive literature on the neuroanatomy and neurophysiology of *Bufo* is referred to in Llinas & Prechts (1976) and Ewert & Arbib (1989). Recent detailed neuroanatomical studies were reported by Brown, Everett & Bennett (1989), and Hiscock & Straznicky (1989), and studies on forelimb muscle, the retina and gut were described by Oka, Ohtani, Satou & Ueda (1989), Nguyen & Straznicky (1989) and Anderson & Campbell (1989) respectively. *Bufo marinus* uses visual, olfactory and auditory (Jaeger 1976) cues to locate prey. The toad appears to use a triangulation system to assess prey distance (Collett, Udin & Finch 1987), and has a 200° horizontal visual field. Its relatively poor image quality does not decrease substantially towards the visual periphery (Jagger 1988).

Endocrine and Exocrine Systems

Water permeability of the urinary bladder of *Bufo* species is largely under hormonal control. Peptides potentially involved in this process have been isolated and partially characterised (Dassouli, Chevalier & Ripoche 1989; Rouille, Michel, Chauvet, Chauvet & Acher 1989). As in other toads, the skin of *B. marinus*, particularly the parotoid glands, is very poisonous. The anatomy and histology of these glands (Hostetler & Cannon 1974) and the nature of their poison (Gregerman 1952; Chen & Osuch 1969) have been well studied.

Reproduction

Chromosome differences associated with gender are not detectable cytologically (Schmid 1978). Gender can be reversed either by hormonal treatment or testectomy. The gender of sub-adults is often ambiguous. During embryonic and larval development, differences in a number of environmental factors, including temperature and water composition, can affect gender-ratio (Foote 1964). The male mating call is a low-pitched trill (Blair 1956, Easteal 1986). Males congregate at breeding sites, where they compete actively for females, and it is not uncommon for more than one male to attempt amplexus with a female simultaneously. Females release up to 30 000 eggs at a time, in a long, gelatinous string. The small, black eggs are approximately 2 mm in diameter. Amplexus may last for many hours.

As with most tropical toad species, breeding in *B. marinus* is opportunistic. There is no obvious breeding season and breeding occurs throughout the year, usually coinciding with periods of rain. Breeding sites include lakes, ponds, ditches and streams. Where these are permanent, breeding is not dependent on rain.

Plasma androgen and corticosterone concentrations are increased in male toads during amplexus. Corticosterone, but not plasma androgen concentrations, are also increased during periods of intense sexual activity, and following rain (Orchinik, Licht & Crews 1988).

Bidder's organs (Fig. 11.1) are rounded structures at the anterior end of the testes, which consist of small oocytes and a vestigial ovarian cavity. Experimental removal of the testes in *Bufo* causes the Bidder's organ to develop into a functional ovary (Ponse 1926).

Embryology and Development

In most bufonids and in all members of the genus *Bufo*, development from aquatic eggs to generalised aquatic larvae precedes metamorphosis to largely terrestrial adults. Embryonic cleavage is radial. A staged series of *B. bufo* embryonic and larval development was given in Fox (1983).

NATURAL HISTORY

Life History

The rate of growth and development at all stages of the life cycle is temperature-dependent. Tadpoles of *B. marinus* hatch from one to three days after spawning and metamorphose from 15 to 70 days after hatching (Straughan 1966; Floyd 1983a). The tadpoles swim in large aggregations of some 2500 individuals (Mares 1972). Growth is rapid following metamorphosis. Individuals reach adult size within a year in tropical regions (Zug & Zug 1979), but may take two years in more temperate regions. Zug & Zug (1979) found some evidence of individuals which lived for four or more years, and Pemberton (1949) maintained one in captivity for nearly 16 years.

Ecology

Though *Bufo marinus* occurs in a great variety of habitats, it is most abundant around human habitation and, to a lesser extent, in grasslands. It occurs only rarely in forested areas and is especially rare in rainforests (Zug *et al.* 1975). Duellman (1978) reports that it is often common along rivers and in clearings in forested areas within its natural range.

Speare (1990) has compiled a comprehensive list of *B. marinus* parasites. Many of these are potentially pathogenic, but their pathenogenicity in *B. marinus* is poorly understood. *Bufo marinus* could act as a vector of human helminth parasites, including *Ascaris lumbricoides*, presumably by ingesting human faeces containing eggs.

Covacevich & Archer (1975), Niven (1988), Tyler (1976b), Zug *et al.* (1975) and Zug & Zug (1979) have summarised much of the information on predators. These include mongooses (in Fiji and Hawaii), various bird species, the keelback snake, *Amphiesma mairii*, freshwater crayfish of the genera *Cherax* and *Euastacus* (Hutchings 1979), and the snapping tortoise, *Elseya latisternum* (Hamley & Georges 1985).

Despite many reports of native animals being preyed on or poisoned by *B. marinus*, the species' impact on natural communities may not be substantial (Fig. 11.2). In the Northern Territory, *B. marinus* appears to have little or no impact on the native frog community (Freeland & Kerin 1988).

Estimates of population density range from 0.5/ha in rainforest (Zug *et al.* 1975) to 2138/ha in newly colonised areas of the Northern Territory (Freeland 1986). In Australia (Freeland 1986; Freeland, Delvinqueir & Bonnin 1986a) and elsewhere (Easteal 1981), population numbers have increased rapidly in newly colonised areas and then declined after 10 to 20 years. The densities of native (Zug & Zug 1979) and long-established introduced (Freeland 1986) populations in semi-urban areas have been estimated to be approximately 80/ha. In old introduced populations, individual toads have been observed to have relatively small body size and to be in poor condition, despite a high food intake and a low incidence of parasitism (Freeland *et al.* 1986a, Freeland, Delvinquier & Bonnin 1986b). This may be the result of microbial infections.

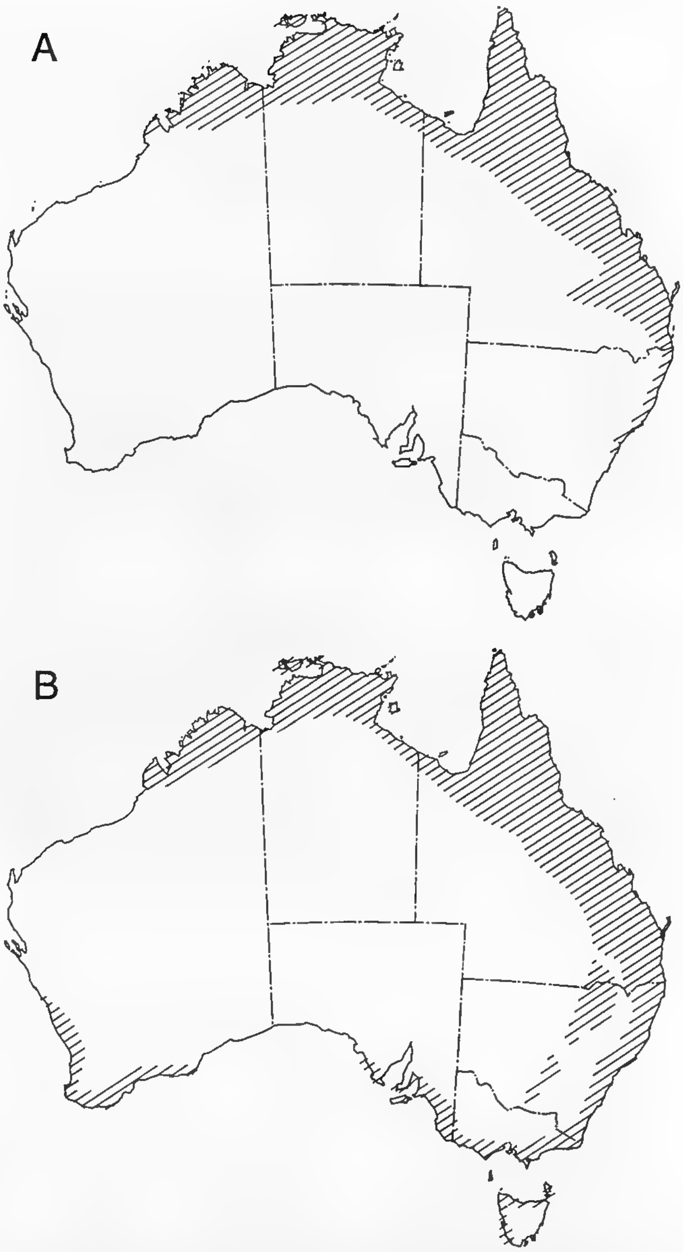

Figure 11.3 Predicted expansion of the range of *Bufo marinus*. Predictions based on A, the thermal physiology of embryos and larvae; B, bioclimatic variables of van Beurden (1981). (A, after Floyd 1983a)
[W. Mumford]

Populations well-removed from breeding sites, where males tend to predominate, can exhibit marked gender-ratio disparity even among sexually immature individuals (Zug & Zug 1979; Easteal & Floyd 1986).

The thermal physiology of *B. marinus* larvae (Floyd 1983b, 1984, 1985) and adults (Brattstrom 1968; Krakauer 1970) has been well described. The dessication tolerance of adults is 52.6% body water (Krakauer 1970). On the basis of the thermo-physiological characteristics of the species, Floyd (1983a) and van Beurden (1981) have made predictions of the areas in Australia in which *B. marinus* populations would be viable and thus of the potential limits to the continuing range expansion of the species (Fig. 11.3).

Behaviour

Bufo marinus juveniles are active both day and night. Adults are usually nocturnal, though sometimes they feed and breed during the day. Adults take refuge in holes, crevices and burrows during the day, and may remain in these for long periods in dry conditions and during the winter months. Even when conditions are warm and wet, and thus favourable, individual toads are not active every night (Brattstrom 1962; Zug & Zug 1979; Floyd &

Benbow 1984). *Bufo marinus* exhibits homing behaviour (Brattstrom 1962; Carpenter & Gillingham 1987).

Bufo species respond to prey with a behavioural pattern that has four distinct stages: orienting, approaching, fixating, and snapping (Ewert 1987). Although this response is instinctive, it is subject to maturation and modification (Ewert & Ingle 1971; Brzoska & Schneider 1978; Ewert & Kehl 1978).

Economic Significance

Many of the introductions of *B. marinus* were made with the intention that the species should control a variety of insect pests. Nowhere was this successful. In most cases the introductions are regarded as having had a net detrimental effect. Although little is known about the species' ecological impact, *B. marinus* is not a serious economic pest. It is known to prey on domestic bees and there are numerous reports of domestic animals being poisoned, and sometimes killed, as a result of eating or mouthing toads. Small enterprises have developed to supply toads for research and teaching purposes, and to produce leather goods made from toad skin.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Bufonidae occur naturally on all continents except Australia and Antarctica. Natural populations of *B. marinus* occur continuously from southern Texas and north-western Mexico to central Brazil (Cei 1968; Zug & Zug 1979). Upper altitudinal limits vary with latitude from 1600 m in Venezuela to 500 m in Sinaloa, Mexico (Zug & Zug 1979). *Bufo marinus* is the only member of the *marinus* species group to occur naturally outside South America.

Deliberate introductions have spread *B. marinus* widely throughout the Caribbean and Pacific regions (Easteal 1981). The species was introduced to Australia from Hawaii in June 1935. The subsequent geographical spread of the species has been described by van Beurden & Grigg (1980), Easteal & Floyd (1986), Easteal, van Beurden, Floyd & Sabath (1985), Freeland & Martin (1985) and Sabath *et al.* (1981), and is shown in Figure 11.4. Range expansion continues in New South Wales and the Northern Territory.

The species has probably reached the potential western limits of its distribution in central and south Queensland. Freeland & Martin (1985) estimated that, at the current rate of active range expansion, *B. marinus* will have colonised the 'Top End' of the Northern Territory by 2027. However, they suggest that colonisation may be more rapid than this as a result of occasional long-distance passive transport by humans. The potential southern limit of the distribution will probably take longer to reach because of a relatively slower rate of spread.

Affinities with Other Groups

The family Bufonidae is thought to have evolved from an ancestral group of terrestrial leptodactylids (Griffiths 1963; Hecht 1963).

Affinities Within the Taxon

Comparative immunological studies (Maxson 1984) indicate that *Bufo* existed in Gondwana before the separation of Africa and South America at the end of the Cretaceous. They cast doubt on the earlier view (Blair 1972) that *Bufo* originated in South America and radiated from there to occupy the rest of its extensive distribution during the Late Tertiary.

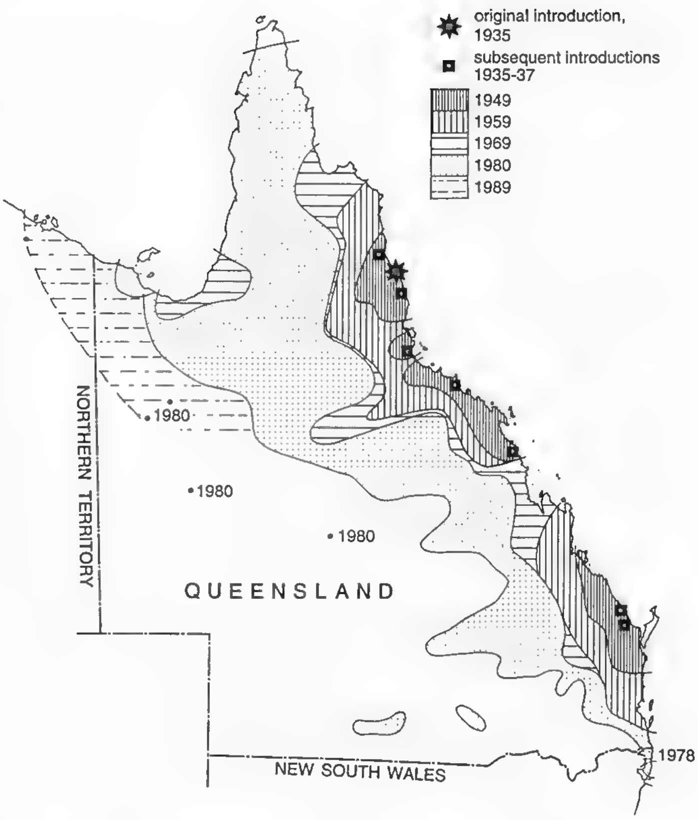

Figure 11.4 Present distribution of *Bufo marinus*. Borroloola, Northern Territory marks the western limit, and the southern limit is the Broadwater, New South Wales. (Modified from Sabath *et al.* 1981; Easteal *et al.* 1985; van Beurden & Grigg 1980; Freeland & Martin 1985; Seabrook 1991, with additional data from Davies pers. comm.) [W. Mumford]

The genus has been divided into 'broad skulled' and 'narrow skulled' species (Martin 1972b). However, immunological comparisons (Maxson 1984) indicate that the osteological characters on which this division is based are plesiomorphic. The broad skulled *marinus* species group is most closely related to other South American species groups, including some that are narrow-skulled.

The *marinus* species group includes *Bufo arenarum*, *B. ictericus*, *B. marinus*, *B. paracnemis*, and *B. rufus*. *Bufo marinus* comprises two subspecies, *B. m. marinus* and *B. m. poeppigi* (Henle 1985). Throughout its extensive natural range, *B. m. marinus* appears to be genetically and morphologically uniform (Zug & Zug 1979; Maxson 1981).

Fossil Record

Bufo fossils are known from Miocene to Pleistocene deposits in Europe, and North and South America (Estes & Reig 1973). There are two *B. marinus* fossils. One is from the Lower Pliocene of Kansas, well outside the species present distribution (Wilson 1968). The other is from the late Miocene La Venta fauna of the upper Magdelana Valley, Huila, Colombia (Estes & Wassersug 1963).

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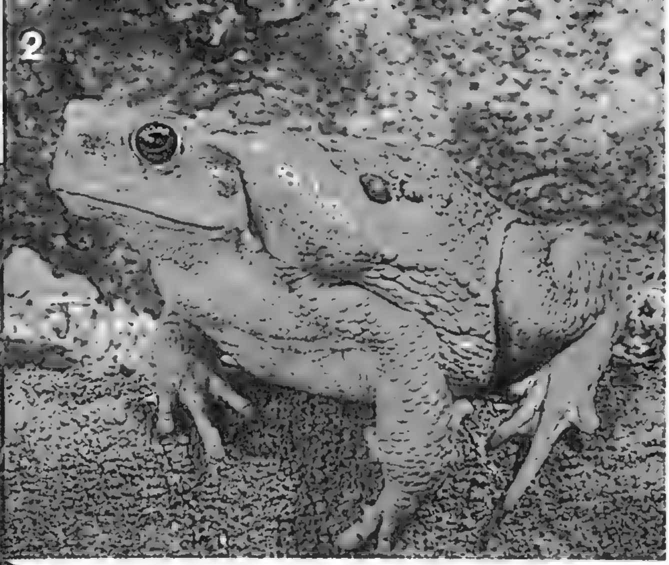


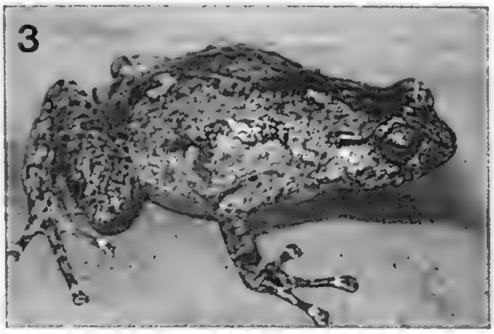
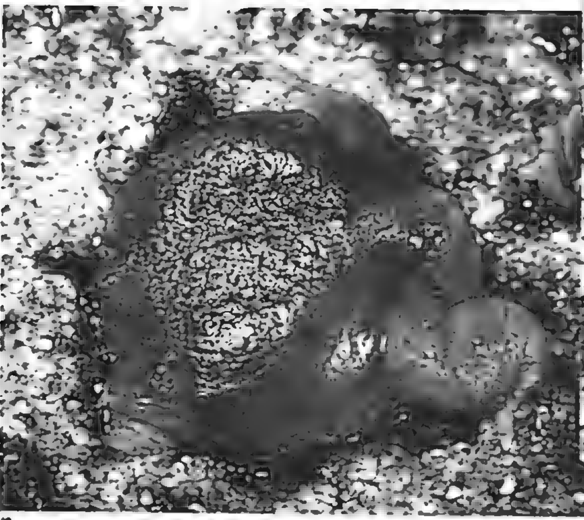


PLATE 1. RANIDAE (1), BUFONIDAE (2) MICROHYLIDAE (3), HYLIDAE (4-7)

1 *Rana daemeli*, the only member of the Ranidae in Australia; Cape York and Arnhem Land.
2 *Bufo marinus*, introduced; the range of the cane toad has expanded from north-eastern Australia into the Northern Territory and New South Wales.
3 *Cophixalus ornatus*, usually found in leaf litter; endemic to the wet tropics of northern Queensland.
4 *Litoria infrafrenata*, a mainly coastal species that frequents houses; Cape York.
5 *Litoria wotjulumensis*, a ground dwelling species of northern Australia.
6 *Cyclorana novaehollandiae* burrows in a wide range of habitats in Queensland and New South Wales.
7 *Nyctimystes dayi*, a large-eyed, arboreal species endemic to the wet tropics of northern Queensland.



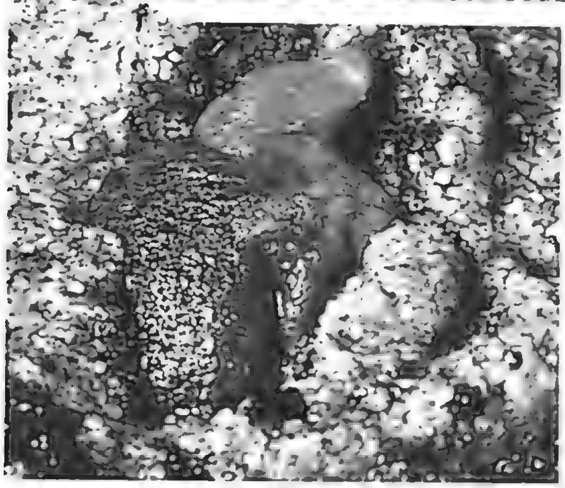


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PLATE 2. MYOBATRACHIDAE

1-3 *Myobatrachus gouldii* burrows head first into the soil, and feeds on termites; occurs in Houtman Abrolhos and south-western Australia.

4 *Adelotus brevis* lives under stones and logs along the coast and in mountain ranges from New South Wales to central Queensland.

5 *Pseudophryne corroboree* is found in alpine, grassy marshes and along forest streams and breeds in sphagnum bogs; Mt Kosciusko to the Brindabella Ranges, south-eastern Australia.

6 *Megistolotis lignarius* has a large and distinctive tympanum; it lives among rocks and in boulder fields near water; Kimberleys to Arnhem Land.

7 *Rheobatrachus silus* is fully aquatic, with eyes high on the head; mainly nocturnal; only in the Blackall and Conondale ranges, south-eastern Queensland.

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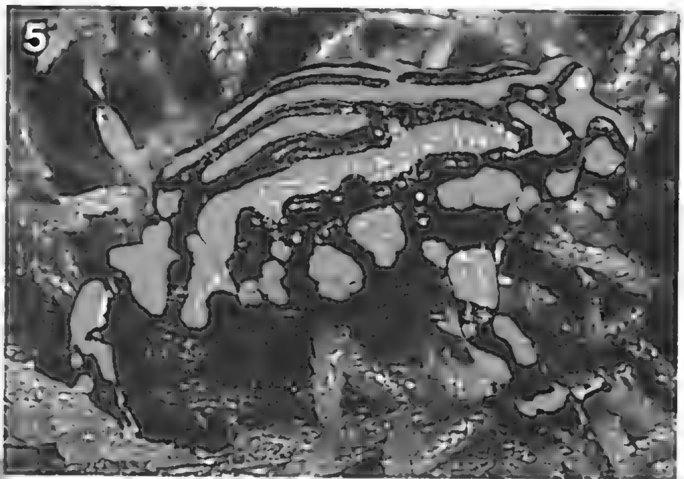

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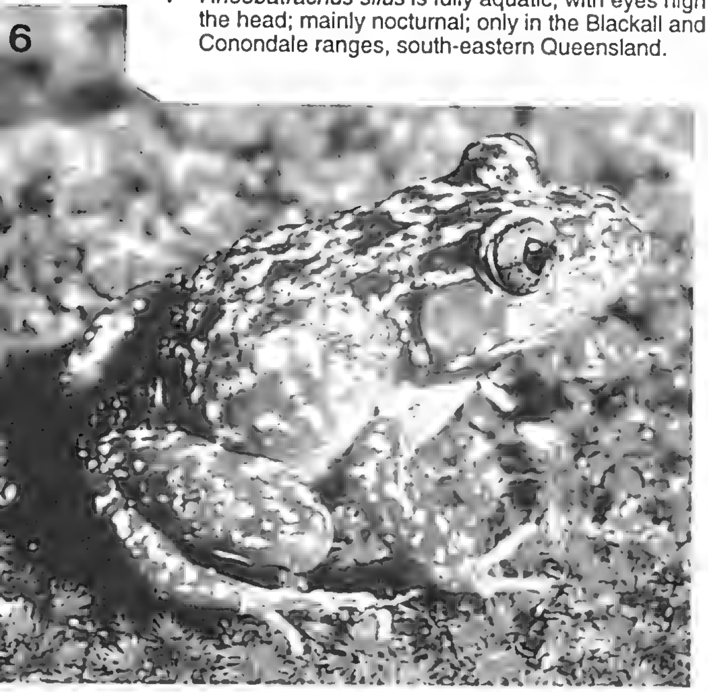

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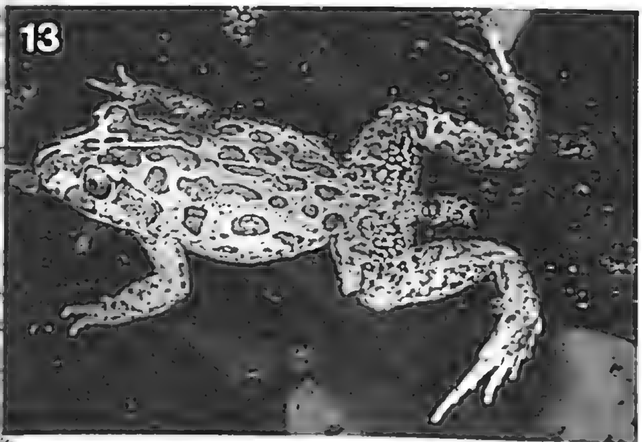
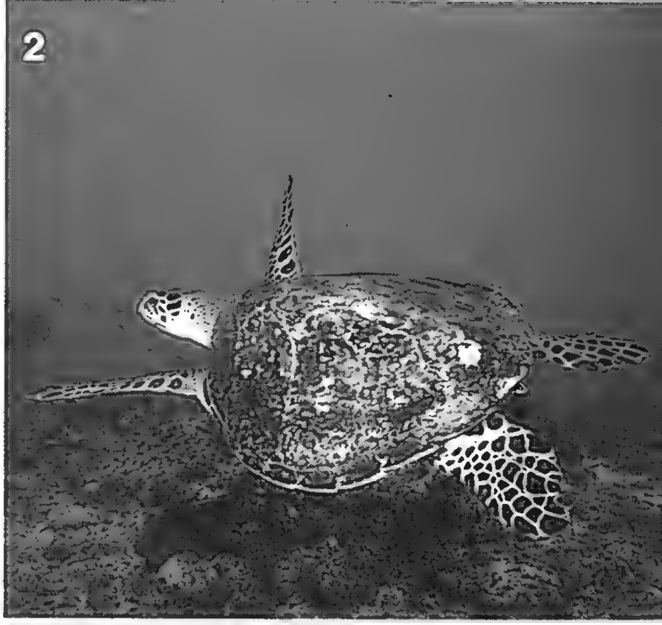
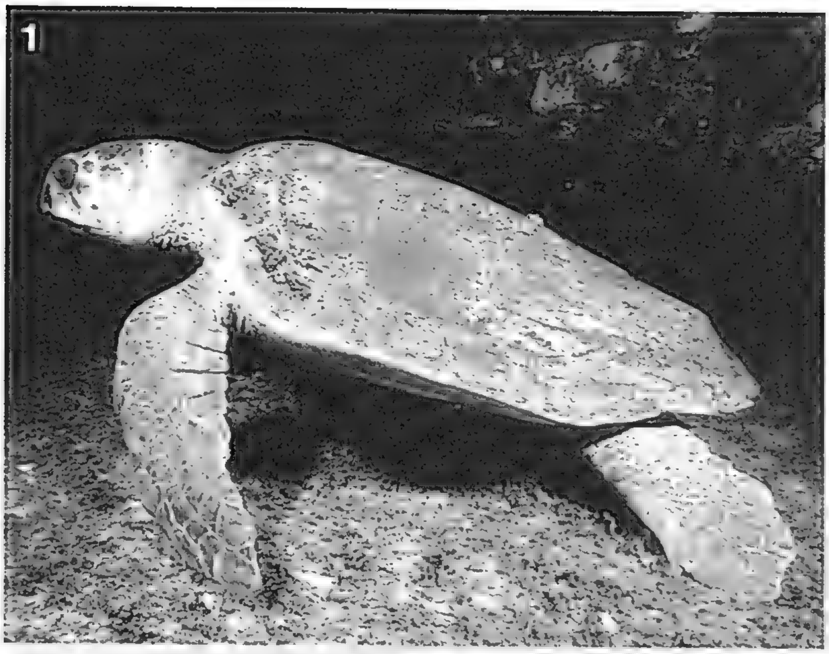
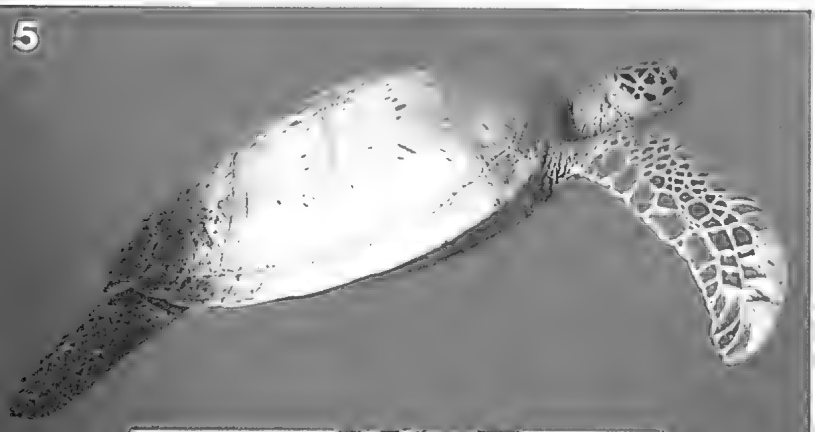
8 *Heleioporus albopunctatus*, a burrowing frog which breeds in ephemeral waters; coast and ranges of south-western Australia.
9 *Taudactylus acutirostris*, a ground-dweller near mountain streams; endemic to the wet tropics.
10 *Lechriodus fletcheri*, a ground dwelling frog of wet forests along the eastern Australian coast.
11 *Philoria sphagnicola* inhabits wet mountain forests, in north-eastern New South Wales.
12 *Notaden bennettii* burrows in flood plains and woodland in central eastern Australia.
13 *Limnodynastes convexiusculus*, a ground dwelling frog of coastal savannah and shrub; Kimberleys to central Queensland.









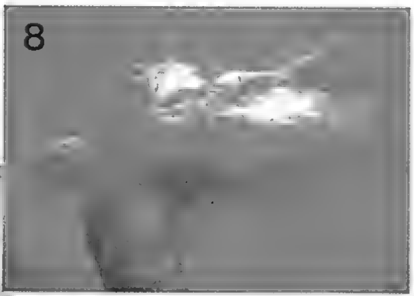


PLATE 3. CHELONIIDAE (1-6), DERMOCHELYIDAE (7-8)

1 *Caretta caretta* rarely breeds in Australia; tropical and warm temperate seas; entire northern Australian coast.

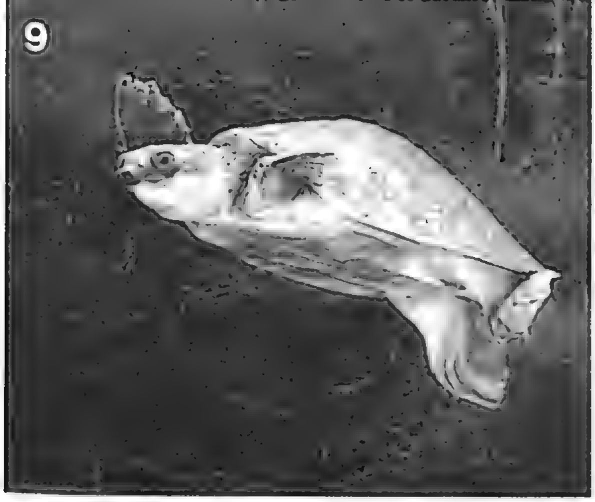
2 *Eretmochelys imbricata*, common on coral reefs; rarely breeds in Australia; tropical and warm temperate seas; entire northern Australian coast.

3-4 *Natator depressus* leaving breeding ground (3); hatchlings heading for the sea (4); often breeds along the north coast.

5 *Chelonia mydas*, adults mainly herbivorous; circumtropical; common from Shark Bay to south-eastern Queensland.

6 *Lepidochelys olivacea* nests in western Arnhem Land; common along north coast and northern Cape York.

7-8 *Dermochelys coriacea* at nesting ground (7) and with diver (8); tropical and temperate seas; rarely breeds in Australia.



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CARETTOCHELYIDAE (9), CHELIDAE (10-15)

9 Fleshy proboscis and large flippers distinguish *Carettochelys insculpta* from other Australian freshwater turtles; nests in sandbanks of rivers, northern Australia.

10 A Western Australian *Emydura* species.

11 *Chelodina longicollis* showing characteristic, elongate neck; carnivorous; in wetlands of eastern Australia.

12 *Rheodytes leukops* occurs in fast flowing waters of the Fitzroy River system, eastern Queensland.

13-14 *Pseudemydura umbrina*, Australia's most endangered reptile; one or two ponds in Western Australia; head covered with solid shield (14).

15 *Elseya dentata* lives in large rivers and lagoons of northern Australia.

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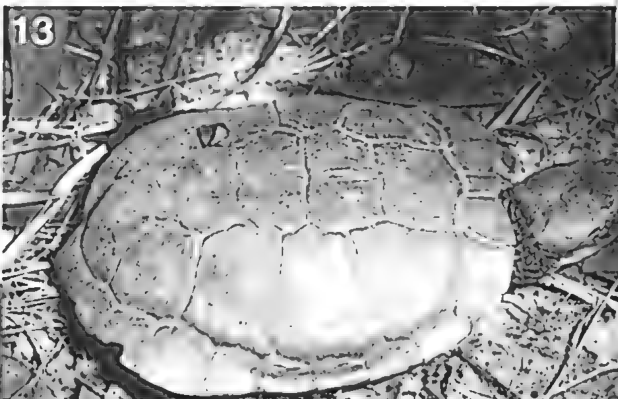

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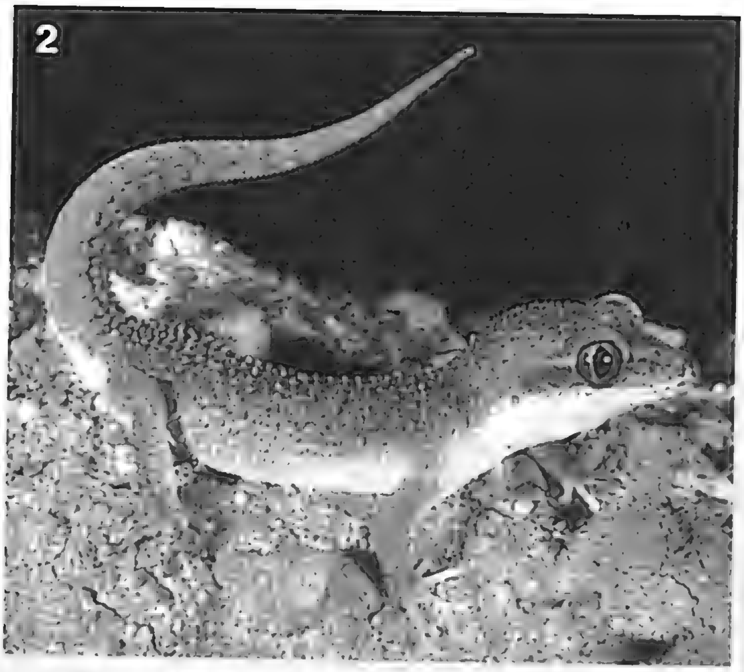

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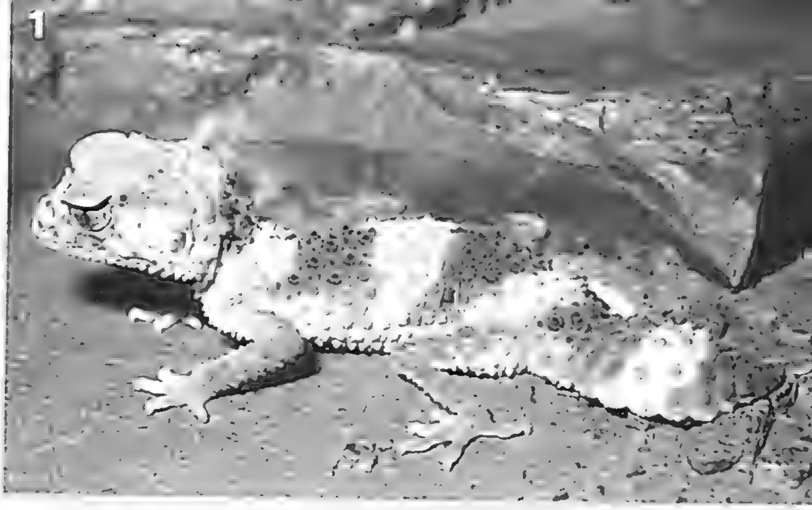

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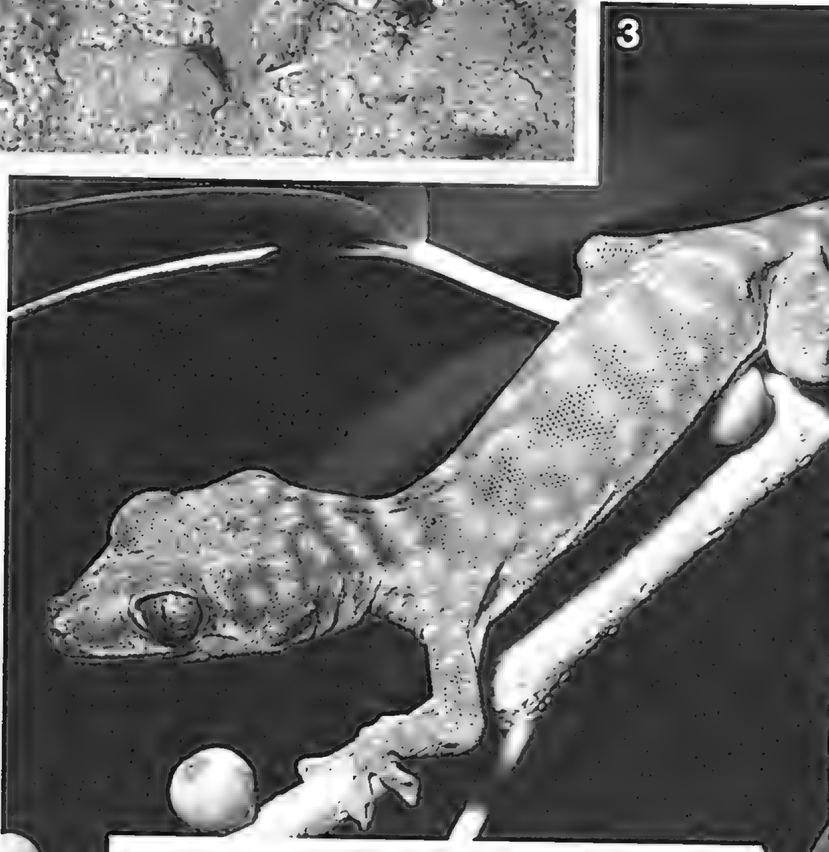

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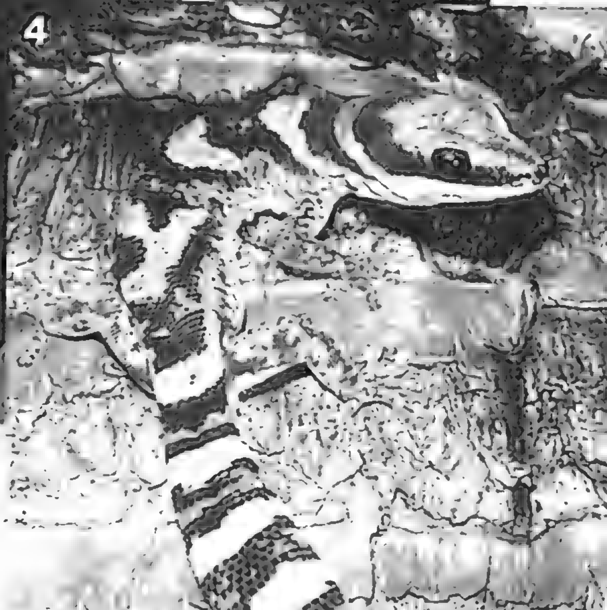

PLATE 4. GEKKONIDAE (1-8), PYGOPODIDAE (9-12)

1 *Nephrurus wheeleri;* in members of this genus the tail ends in a rounded sensory knob; found among shrub and in stone fields in the arid central west.
2 *Nactus pelagicus* is usually found under ground debris in forests and woodlands, Cape York.
3 *Pseudothecadactylus lindneri* lives in sandstone caves and crevices in far north-western Australia.
4 *Oedura castelnaui* has a moderately depressed tail; arboreal under bark and debris, Cape York.
5 *Diplodactylus ciliaris* ranges from coastal forests of north-western Australia to the arid interior.
6 *Gehyra pilbara* hides during the day in the crevices and tunnels of termite mounds in north-western Australia.

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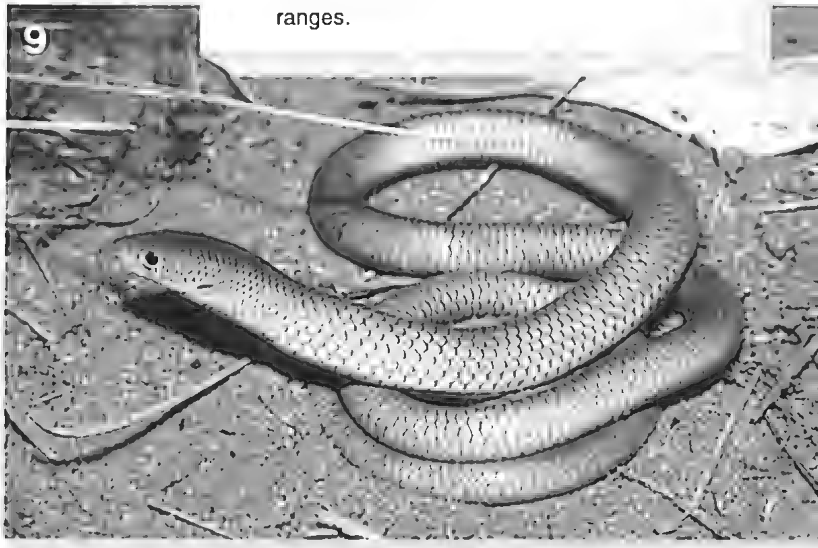
7-8 *Phyllurus cornutus* has a strongly flattened leaf-like tail (7); the same animal showing excellent camouflage (8); the species is found in wet forests from Cape York to the central east coast.

9 *Delma nasuta* is legless; it preys on insects and spiders in dry grasslands and shrub in stony deserts of northern and western Australia.

10 *Lialis burtonis* is found throughout Australia except in the extreme south-west and south-east; highly variable in colour and pattern; inhabits low vegetation and ground litter; feeds mainly on small lizards.

11 *Aprasia smithi* is a little known species which burrows in dry soil around Shark Bay in Western Australia.

12 *Pygopus nigriceps* showing characteristic black head bands; a nocturnal insectivore found throughout Australia, except along the wetter south and south-east coasts and ranges.



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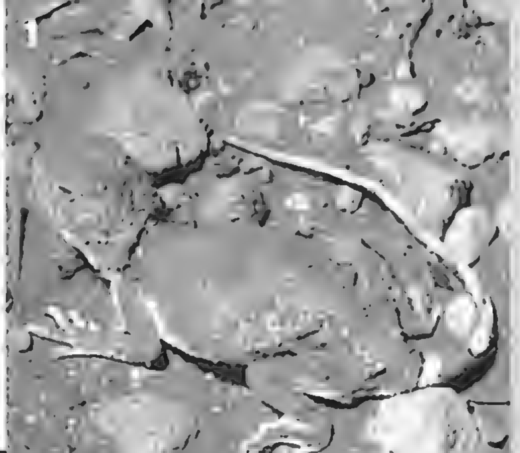

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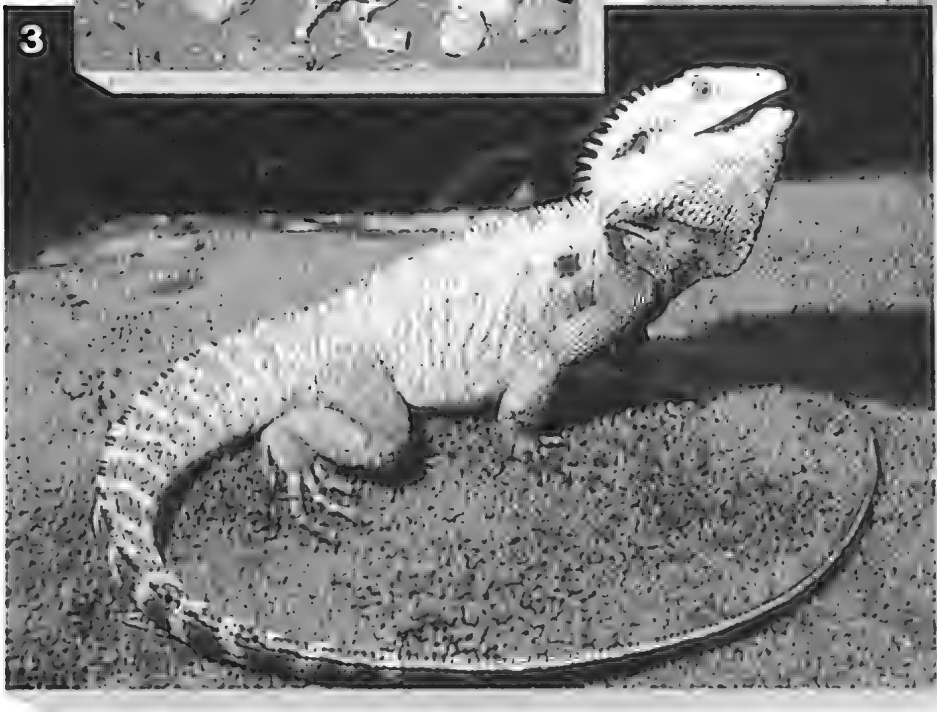

PLATE 5. AGAMIDAE (1-9), VARANIDAE (10-13)

1 *Tympanocryptis cephalus*; its cryptic colour matches its habitat in arid central and western Australia.
2 *Lophognathus longirostris* lives in shrub and on the ground along streams in arid central and western Australia.
3 *Physignathus lesueurii*, an omnivorous, arboreal water dragon common along creeks and rivers of the east coast.
4 *Ctenophorus vadnappa* panting as a result of heat stress; among rocks and boulders in and around the Flinders Ranges.
5 *Diporiphora superba*, the most slender Australian agamid; found among acacias and spinifex, Kimberleys.
6 *Moloch horridus* is easily recognised; feeds only on ants; occurs in central and western Australian deserts.
7 *Hypsilurus boydii*, a forest dragon with distinctive head ornamentation; endemic to the wet tropics, northern Queensland.
8 *Pogona barbata*, showing defensive display; a semi-arboreal species commonly found in south-eastern and eastern Australia.

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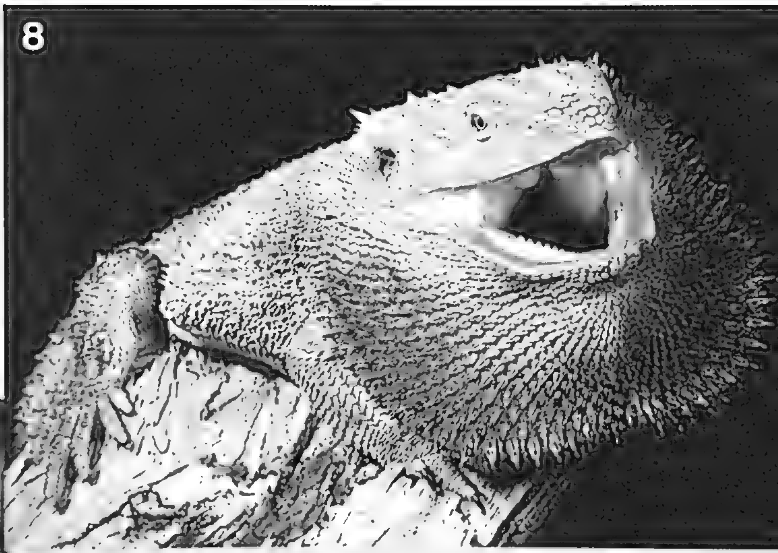

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9 *Chlamydosaurus kingii* in upright defensive posture with raised frill and open mouth; in dry forests in the north and north-east.

10 *Varanus gouldii* foraging actively in the arid interior; one of the largest goannas in Australia, it grows to 1.6 m overall; common throughout the mainland except in the wettest parts; also on Lizard Island.

11 *Varanus glauerti* is a rock dwelling species which is known only from the Kimberley region.

12 *Varanus panoptes* is a large ground dwelling goanna which grows to 1.2 m overall; found in the arid north and west of Australia.

13 *Varanus brevicauda*, the smallest member of the family in Australia, inhabits sandy deserts with spinifex grass in central and western areas of Australia.

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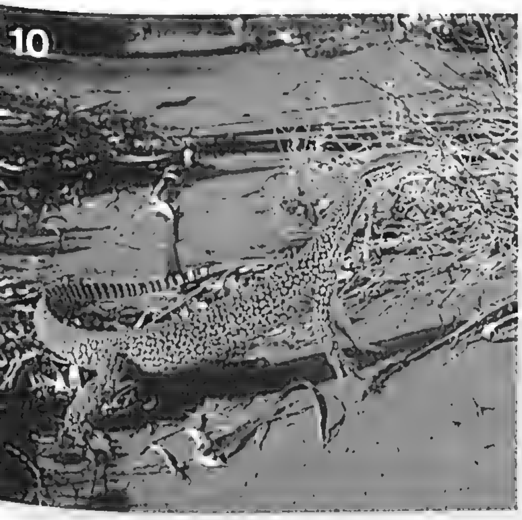

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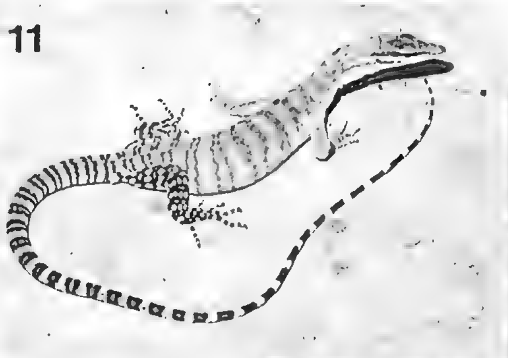

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PLATE 6. SCINCIDAE

1-2 *Trachydosaurus rugosus*; very common and easily recognisable by its short, rounded tail and large, coarse scales (1) and blue tongue (2); dry habitats in southern and eastern Australia.

3 *Hemisphaeriodon gerrardii*, a nocturnal insectivore, found mainly in wet temperate to tropical forests in eastern Australia.

4 *Tiliqua occipitalis* is found in a variety of dry habitats in southern Australia from New South Wales to the west coast.

5 *Egernia stokesii* in characteristic 'family' group; among rocks and boulders in central and western Australia.

6 *Gnypetoscincus queenslandiae* is nocturnal and hides under rotting logs during the day; endemic to the wet tropics.

7 *Carlia rhomboidalis* occurs in rainforest, stream margins and in similar moist habitats in north-eastern Queensland.


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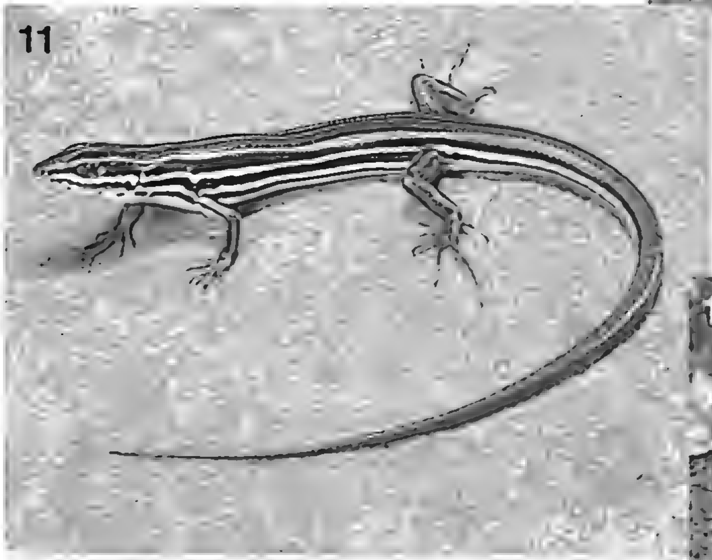
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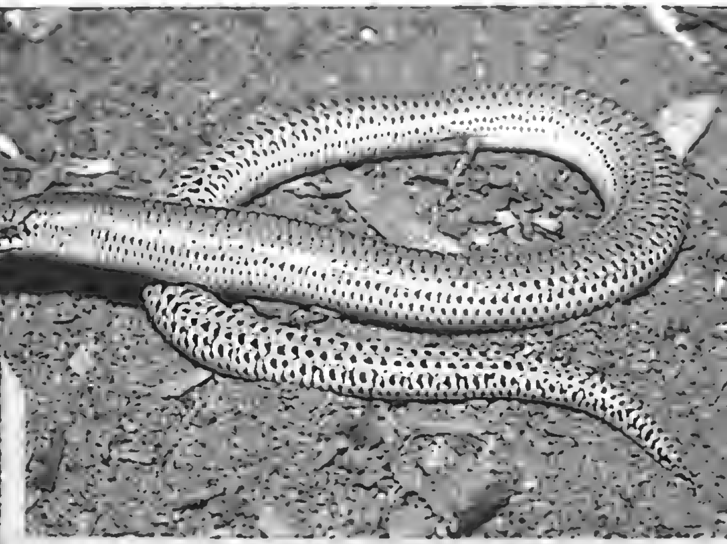
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8 *Glaphyromorphus nigricaudis* is nocturnal; found in coastal dunes to marginal rainforest in Cape York and Torres Strait Islands.

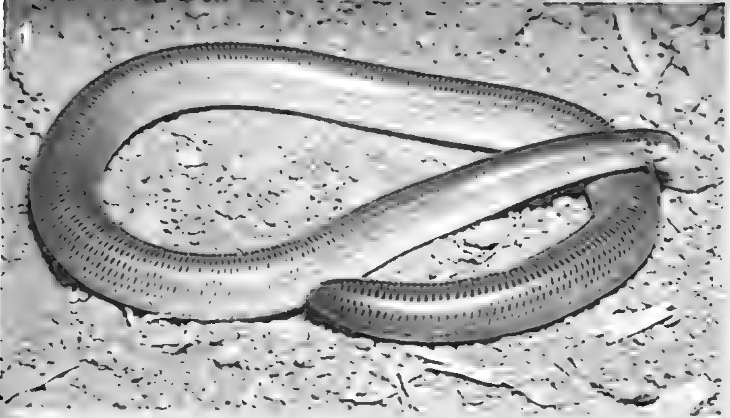
9 *Cryptoblepharus egeriae*, arboreal, forages in the ground litter; endemic to Christmas Island, Indian Ocean.

10 *Morethia ruficauda* uses its bright tail to distract predators; found in dry to arid areas near streams and water-holes in central and north-western Australia.

11 *Ctenotus taeniolatus*, from coastal heathland to montane forests in eastern Australia.

12 *Lerista punctatovittata* lacks forelimbs and has reduced hindlimbs; burrows in dry, open forests, inland south-eastern Australia.

13 *Anomalopus verreauxi* (two colour morphs) has strongly reduced forelimbs and tiny, styliform hindlimbs; found in humid coastal and montane habitats, central east coast.



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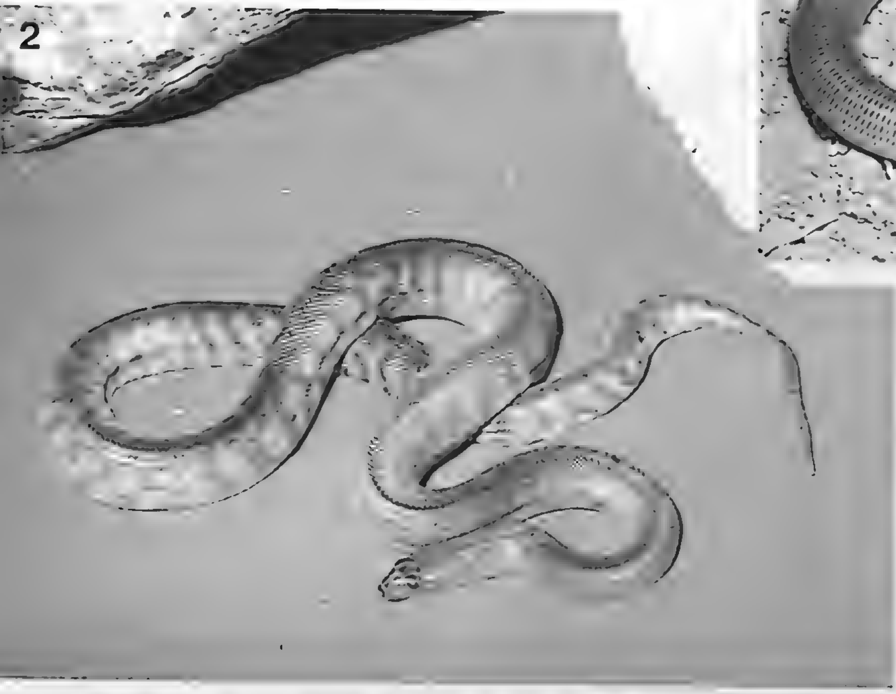

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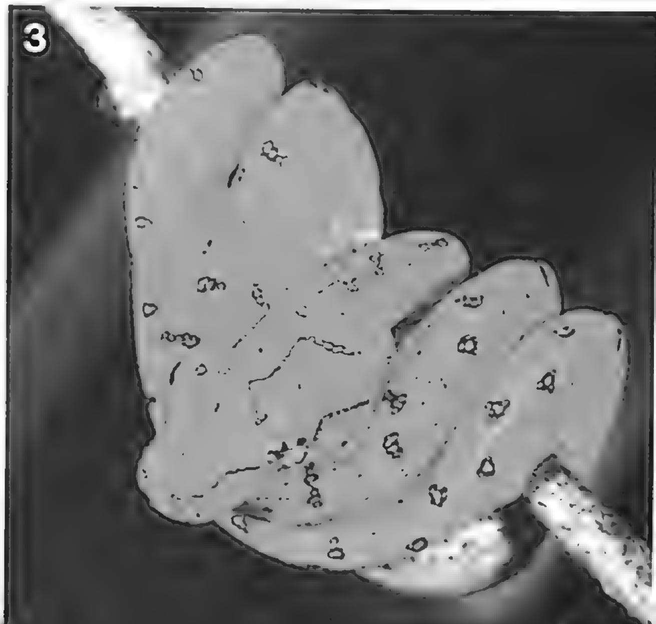

PLATE 7. TYPHLOPIDAE (1), BOIDAE (2-5), ACROCHORDIDAE (6)

1 *Ramphotyphlops australis* is a small, worm-like, burrowing snake; small, black spots indicate the eyes in these blind snakes; found in the drier parts of southern Australia.

2 *Aspidites ramsayi*, a nocturnal, terrestrial snake, often found sheltering in hollow logs or thick vegetation; occurs in dry areas and deserts across central Australia.

3-4 *Chondropython viridis*; juveniles (3) are often yellow, adults (4), bright green; a nocturnal, arboreal python of the rainforests, north-eastern Cape York.

5 *Liasis stimsoni* is found frequently near rock outcrops, in stone fields, around large trees or other isolated features in sandy deserts; throughout arid central and western parts of Australia.

6 *Acrochordus arafurae*, a strictly aquatic snake that feeds almost exclusively on fishes; note the small, pointed scales characteristic of file snakes; coastal streams and lagoons in the north.

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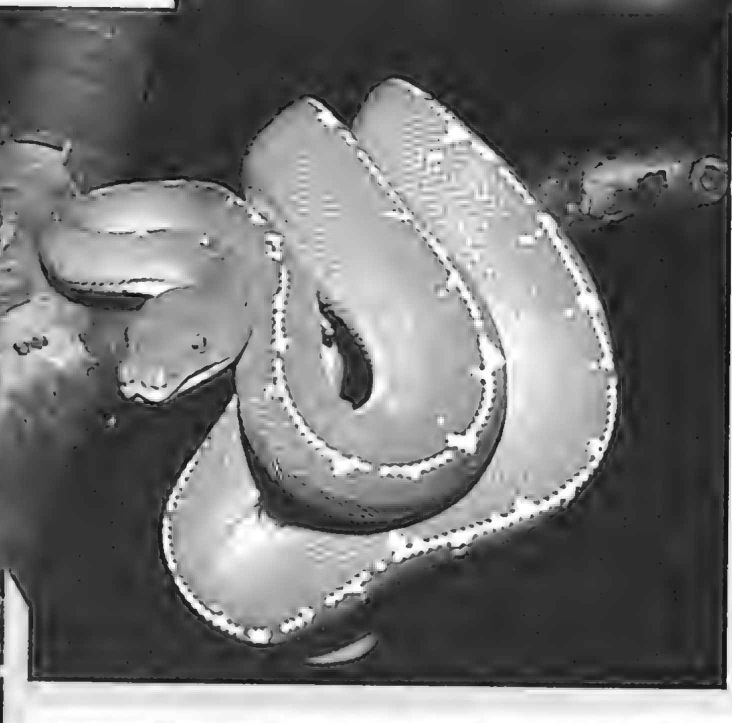

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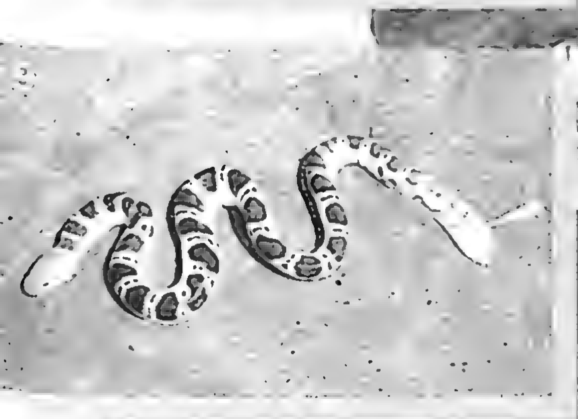

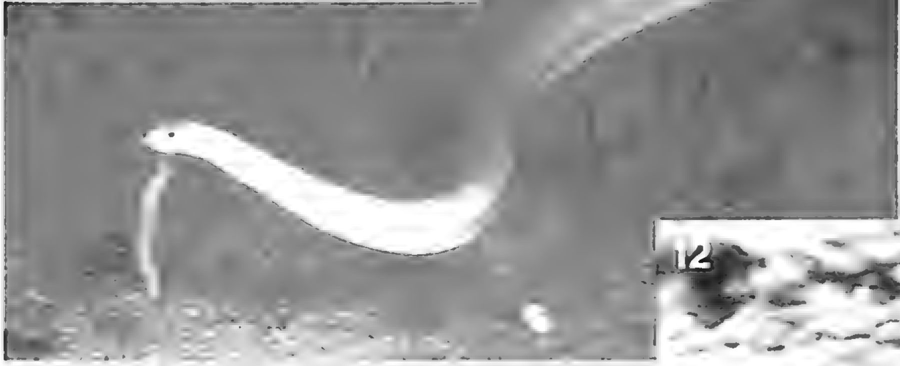
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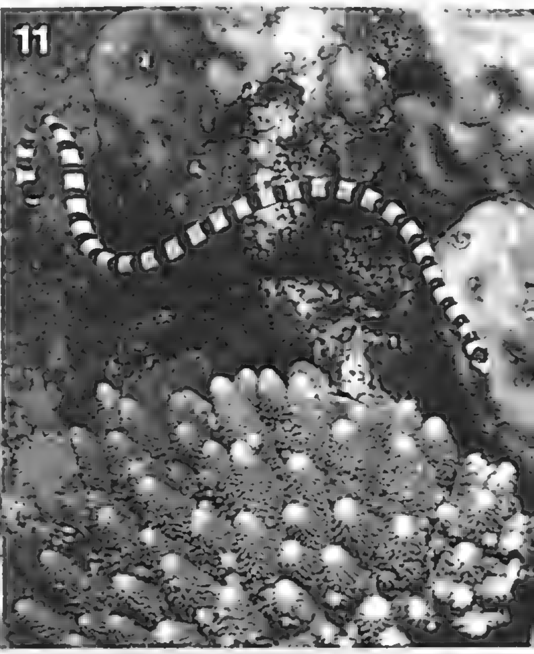
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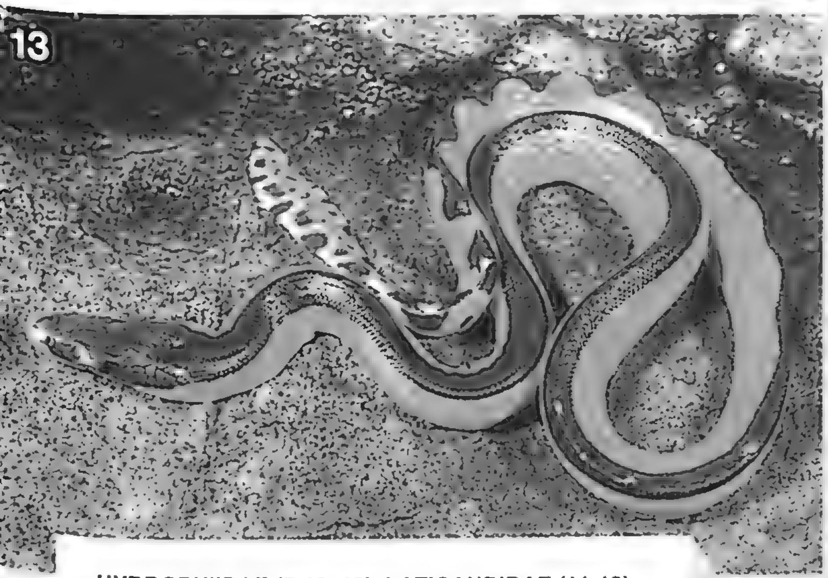
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HYDROPHIIDAE (7-10, 13), LATICAUDIDAE (11-12)

7-8 *Aipysurus laevis* is one of the most abundant sea snakes in coral reefs (7); members of the family close the nostrils (8) when submerged; feeds mainly on fishes; occurs from Shark Bay in the west to the central east coast of Australia.

9-10 *Astrotia stokesii* on the shore showing tail flattened for swimming (9); typical of shallow tropical waters (10); in Australia it occurs from Shark Bay in the west to the central east coast.

11-12 *Laticauda colubrina*, swimming in tropical coral reef (11), and on land (12) where it rests, mates and nests; infrequently recorded from north-eastern Australia.

13 *Pelamis platurus* has a unique colour pattern; it is fully pelagic and feeds on fishes; found around Australia except along the south coast.

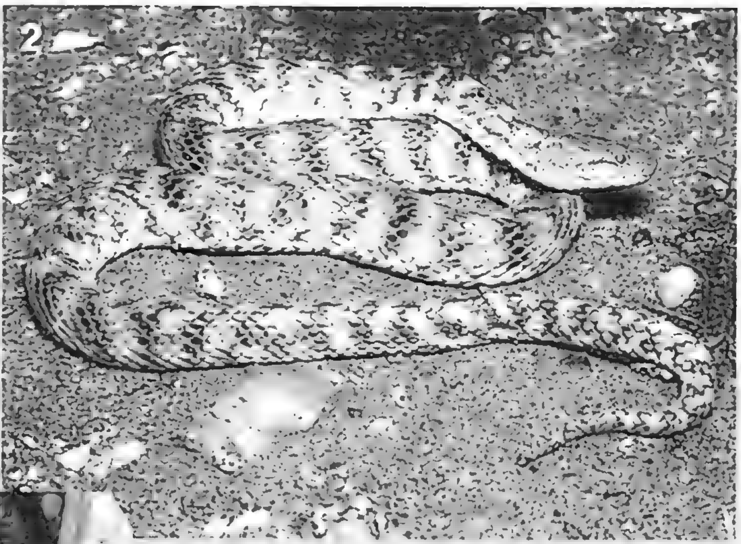
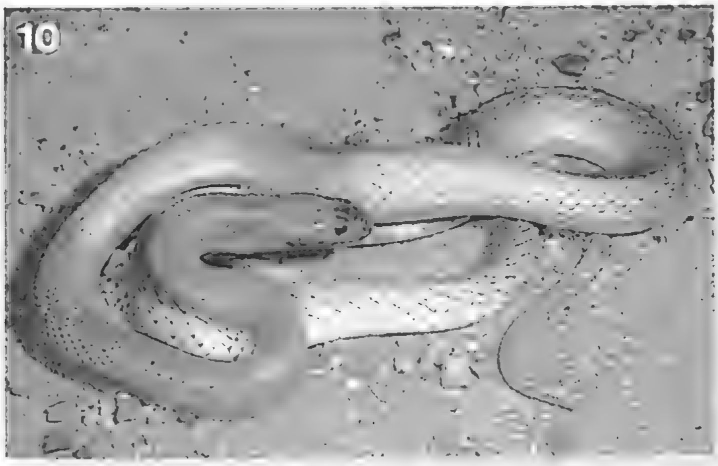
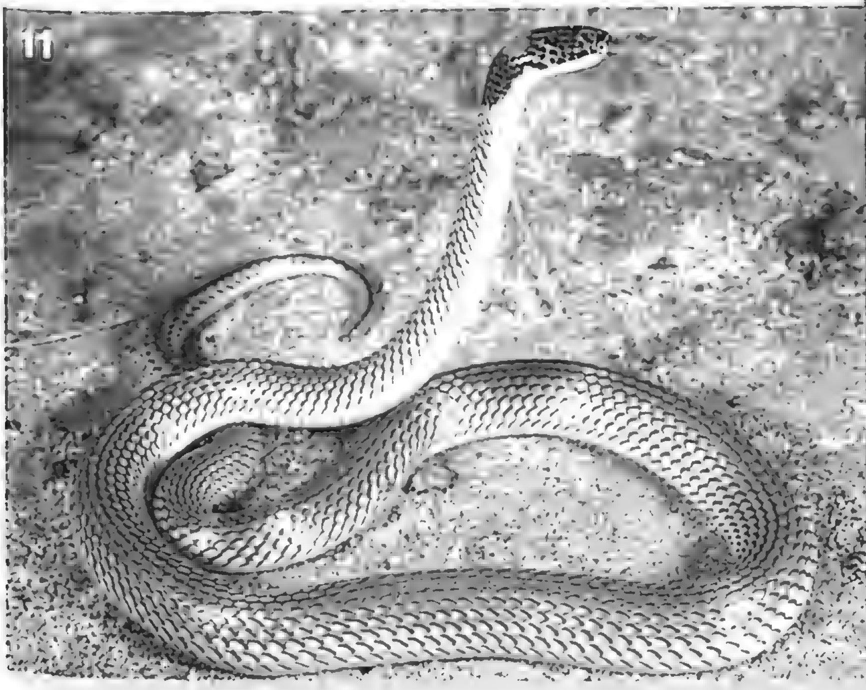


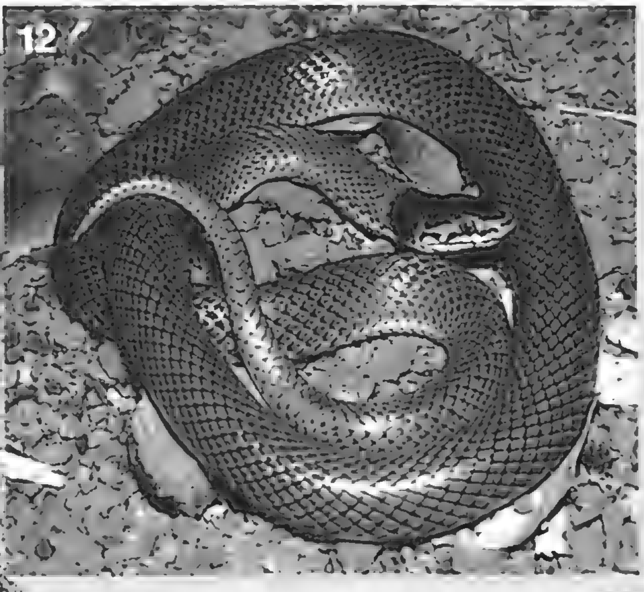
PLATE 8. COLUBRIDAE (1-3), ELAPIDAE (4-12)

1 *Boiga irregularis* is mainly arboreal; diverse habitats from coastal heaths to rainforests in northern and eastern Australia.
2 *Myron richardsonii* inhabits mangrove flats and tidal creeks; central north coast.
3 *Fordonia leucobalia* feeds on crabs and fishes on mudflats and among mangroves; north coast to eastern Cape York.
4 *Vermicella annulata*, a burrower, feeds on blind snakes (Typhlopidae); diverse habitats, wet coastal forests to spinifex deserts; central and eastern Australia to central west coast.
5 *Simoselaps warro*, a nocturnal burrower, lives in forests and woodland; north-eastern coast and ranges of Queensland.
6 *Demansia psammophis*, found from coastal habitats to the arid interior, is widespread in mainland Australia except in the central north.



7 *Notechis scutatus*, occupies a wide range of habitats from rainforests to open woodlands and floodplains; its main food is frogs; found in south-eastern mainland Australia.
8 *Pseudonaja guttata* in aggressive posture; inhabits tussock grassland of interior north-eastern Australia.
9 *Acanthophis pyrrhus*, occurs in desert regions and adjacent arid lands in central and western Australia.
10 *Oxyuranus microlepidotus*, Australia's most venomous snake, feeds mainly on rats and occurs on floodplains in the central east of the continent.
11 *Furina diadema* raises its characteristically coloured head high when alarmed; often associated with ants and termites in eastern Australia.
12 *Suta suta* in coil-spring offensive posture; found in sandy-stony deserts to savannah woodlands in central and eastern Australia.





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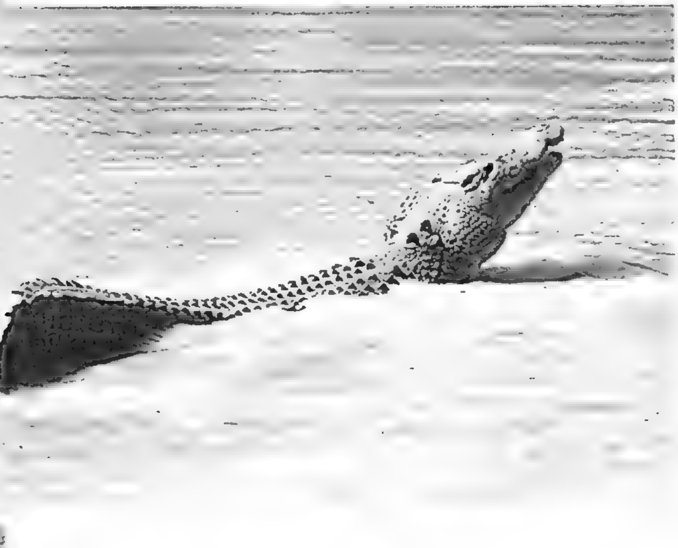

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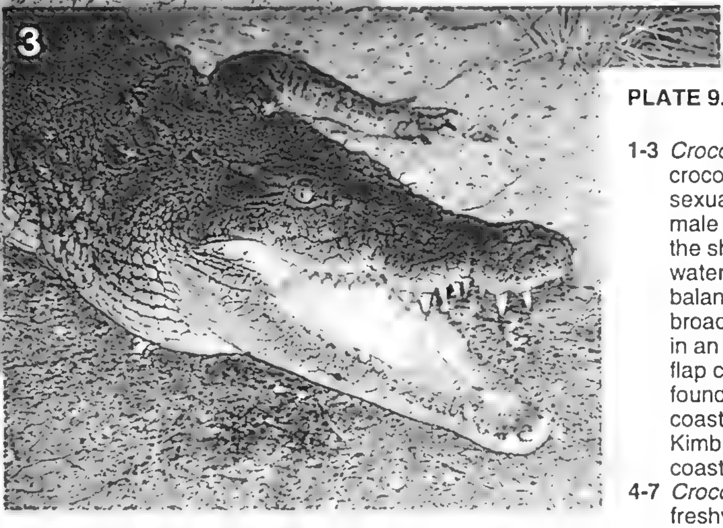

PLATE 9. CROCODYLIDAE

1-3 *Crocodylus porosus*, the salt water crocodile, shows pronounced sexual dimorphism, as seen in this male (left) and female resting on the shore (1); when feeding in water the tail is lifted to counter balance the head (2); the snout is broad and rounded, the teeth set in an irregular row (3); note palatal flap closing entrance to the throat; found in rivers, billabongs and coastal waters from the Kimberleys to the central east coast of Australia.

4-7 *Crocodylus johnstoni*, the freshwater crocodile, basking on a rock, with mouth open to aid temperature regulation through evaporation (4); body inflated in threat display (5); snout long and slender with a more regular row of nearly equal sized teeth (6); the eyes and the slit-like ears set high on the head can be closed during diving (7); found in rivers and billabongs from the Kimberleys to eastern Cape York.

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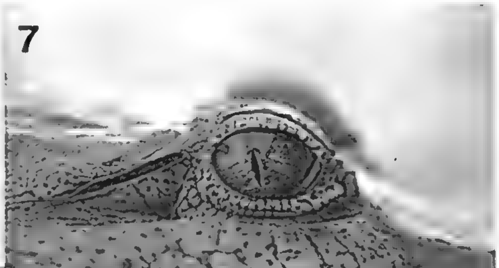

6

12. GENERAL DESCRIPTION AND DEFINITION OF THE CLASS REPTILIA

Harold G. Cogger

Both in numbers and taxonomic diversity, living reptiles represent but a remnant of the enormous variety of reptiles which we know from the fossil record have previously inhabited the earth. While these earlier radiations consisted mostly of groups of reptiles which were not significantly different in size range from extant reptilian groups, popular knowledge and culture has emphasised one or two fossil groups containing megareptiles — the orders Saurischia and Ornithischia. A general overview of this past diversity, and of the classification of fossil reptiles, can be found in Romer (1956) and Carroll (1988b).

The first recognisable reptiles appeared in the Carboniferous, some 340 million years ago. By the middle of the Mesozoic, about 170 million years ago, they had evolved and adapted to occupy most of the world's ecotopes. In terms of species richness, biomass and physical dominance, they became the dominant vertebrates during this period.

Reptiles are amniotes, a group containing the reptiles, birds and mammals and characterised by the presence of a series of three extra-embryonic membranes. The amnion and chorion start as two-layered outgrowths of the body wall at each end of the embryo and grow around the embryo to eventually meet and fuse; the allantois begins as an outgrowth of the lower gut. The amnion forms a fluid-filled sac in which the embryo develops, cushioned from the external world and largely safe from dehydration. The chorion is a vascularised membrane lying just beneath the egg shell where its primary function is gas exchange. The allantois stores the embryo's metabolic wastes. These membranes first evolved in conjunction with a shelled egg, allowing reptiles to breed in less-humid areas than their amphibian progenitors, or even in areas without free water. Later amniotes have retained these membranes, albeit often in a form modified for viviparity. The reptiles were the first vertebrates to be freed from reproductive dependence on water, by providing a 'pond' inside a relatively impervious eggshell, within which the developing embryo could be cushioned from the outside world, it could avoid desiccation, and into which it could safely void the poisonous waste products of metabolism.

The amniotes are believed to represent a true clade. They are a monophyletic group containing an ancestral species and all of its descendant species of reptiles, birds and mammals.

The Class Reptilia, the 'reptiles', has for nearly two centuries had a clear meaning to neontologists. Living reptiles are readily distinguished from the other amniote tetrapod vertebrates — the birds and mammals — simply by virtue of the combination of ectothermy (often known colloquially as being 'cold-blooded'), scaly (rather than furred or feathered) skins and the possession of intromittent sex organs for internal fertilisation.

For palaeontologists, struggling with a disjointed and discontinuous record of mostly bony fragments extending over 450 million years, assigning a given fragment to the Reptilia has often proved surprisingly difficult. The distinctions between many early reptiles and contemporaneous amphibians, or between reptiles and the early ancestors of birds and mammals, are often blurred in the fossil record.

Consequently, for nearly two centuries three living Classes have been recognised within the amniotes — mammals (Mammalia), birds (Aves) and reptiles (Reptilia). Indeed, this Volume implicitly

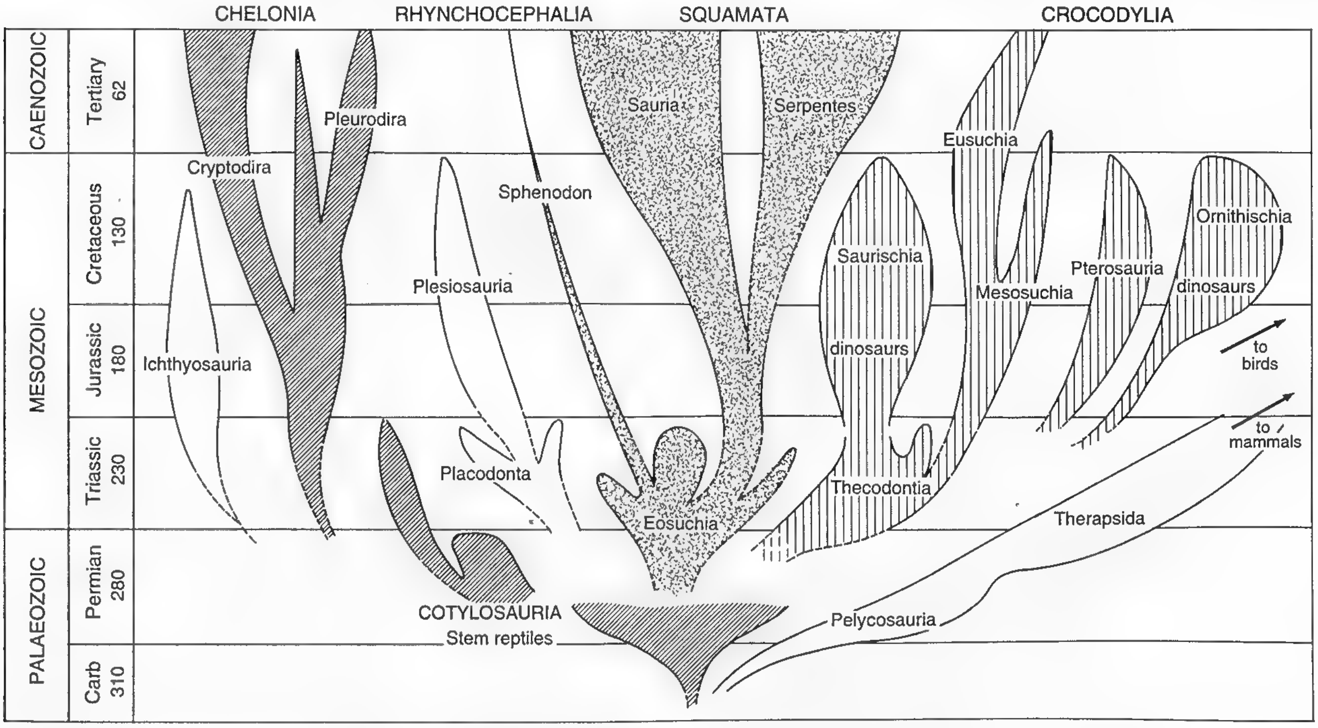

Figure 12.1 The evolutionary history and relationships of the Class Reptilia. The diversity of each subclass through time is indicated by its relative width in the diagram. (Modified after Bellairs 1969) [W. Mumford]

Table 12.1 The higher classification of the Class Reptilia. (After Romer 1956)

	Subclass Anapsida
	Order Cotylosauria
'Sauropsid' orders	Order Chelonia
	Subclass Lepidosauria
	Order Eosuchia
	Order Rhynchocephalia
	Order Squamata
	Subclass Archosauria
	Order Thecodontia
	Order Crocodylia
	Order Saurischia
	Order Ornithischia
	Order Pterosauria
'Theropsid' orders	Subclass Uncertain
	Order Mesosauria
	Subclass Ichthyopterygia
	Order Ichthyosauria
	Subclass Euryapsida
	Order Protorosauria
	Order Sauropterygia
	Subclass Synapsida
	Order Pelycosauria
	Order Therapsida

supports this conventional classification. However, under this traditional treatment of the Class Reptilia, the group is clearly paraphyletic, as it excludes one of its descendant groups, the birds.

In his classic work on the osteology of the reptiles, Romer (1956) provided a brief, but highly informative account of the history of the classification of the Reptilia. The classification Romer adopted in this work has remained in place with minor modifications until the present day, although recently it has been overtaken by new studies of fossil forms and their relationships, and by the cladistic methods of analysis of Hennig (1966) and his successors. This essentially phenetic classification is represented in Figure 12.1 (after Bellairs 1969).

Whereas earlier methods of classification tended to give more or less equal weight in phylogenetic analysis to both primitive (plesiomorphic) and advanced (apomorphic, or derived) features, cladistics is based on the use of shared derived characters (synapomorphies). While theoretically rigourous, cladistics depends absolutely on the ability to assign polarity to a character, that is, to determine whether the expression of that character in any given taxon is closer to its primitive or advanced condition. Carroll (1988b) discussed the problems of applying cladistic methodologies and criteria to groups whose phylogenies are primarily constructed from the fossil record.

Romer recognised seven subclasses of reptiles (Table 12.1), three of which are represented by modern reptiles: Anapsida (turtles), Lepidosauria (tuataras, lizards and snakes) and Archosauria (crocodilians). One of the remaining subclasses was tentatively erected for one major fossil group, the mesosaurs. The remaining two subclasses, the Euryapsida and Synapsida, contained only fossil forms, including (in the Synapsida) the ancestors of mammals.

Because of the great diversity of fossil reptiles, which reached a peak during the Mesozoic, early classifications tended to be based on cranial features which are evident in the fossil record. The higher classification of reptiles has long been based on the number and location of openings in the skull (Fig. 12.2). In modern reptiles only the anapsid (turtles) and diapsid (lizards, snakes, tuataras and crocodilians) conditions persist, albeit in a modified form.

Though the evolutionary relationships of many fossil forms continue to be debated, the above higher classification of extant reptiles has varied surprisingly little during the past century. Not until the post-1960s application of methods of phylogenetic systematics (cladistics), with its rejection of paraphyletic groups, was the traditional view of modern reptilian relationships challenged (for example, Gauthier, Estes and de Quieroz 1988). This revised classification removed the synapsids entirely from the Reptilia, retained the anapsid turtles within the order Chelonia, and placed the birds, with crocodilians, in the subclass Archosauria. The remaining extant reptiles were assigned to the subclass Lepidosauria.

A key element of recent studies of reptilian evolutionary relationships has been the issue of the monophyly of the diapsid reptiles (the subclass Diapsida of some classifications). Romer (1956) and others believed that the diapsid condition of the skull had evolved independently in archosaurs and lepidosaurs. Gauthier (1984), Gauthier *et al.* (1988), and others have argued for the monophyly of the Diapsida.

The following key distinguishes the living orders of reptiles found in Australia. These orders include all extant reptiles except the

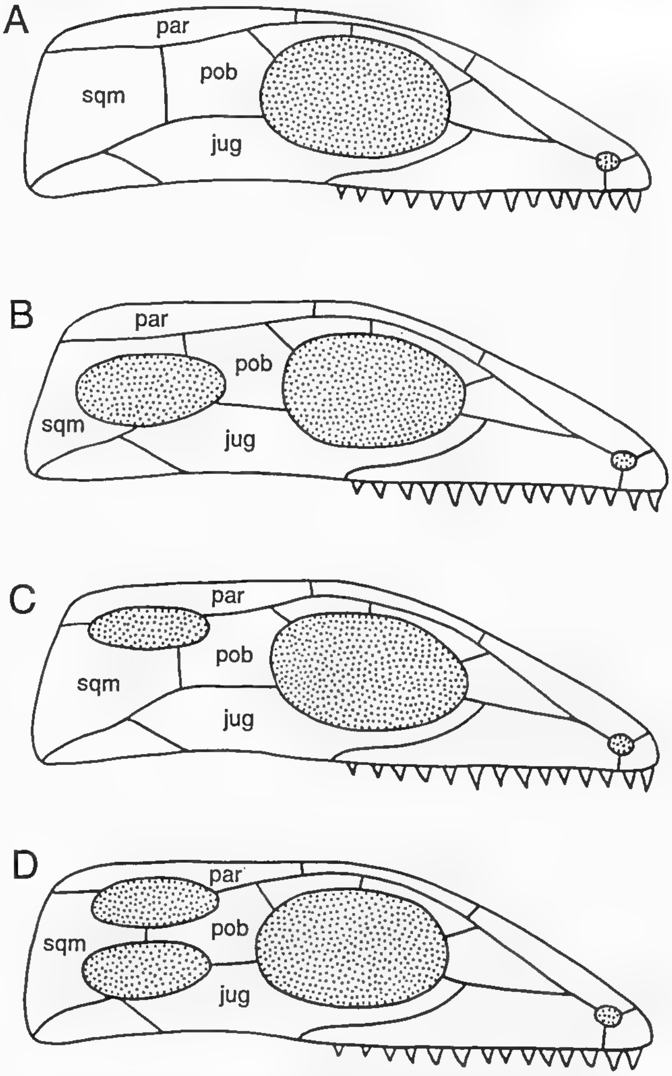

Figure 12.2 The arrangement of the temporal openings in four reptilian subclasses. **A**, Anapsida; **B**, Parapsida; **C**, Synapsida; **D**, Diapsida. **jug**, jugal; **par**, parietal; **pob**, postorbital; **sqm**, squamosal. (After Romer 1945)
[D. Wahl]

sphenodontid tuataras of New Zealand. The latter have had a chequered classificatory history, being long regarded as members of the lepidosaurian order (or sometimes superorder) Rhynchocephalia, from which they were removed (Carroll 1977a), but to which they have been returned recently (Gauthier *et al.* 1988).

Key to the orders of Australian reptiles

1 (a) Head/neck and limbs protruding from a hard, bony shell to which the underlying vertebrae and ribs are fused; no teeth, the jaws covered by a horny sheath; anapsid skull, without any temporal opening; single copulatory organ .... Chelonia

(b) No bony shell, the neck and limbs attached to a scaly body with a flexible vertebral column; jaws with teeth; diapsid skull, usually with two temporal openings on each side; single or paired copulatory organs 2

2 (a) Thecodont teeth; a fully developed secondary palate; well-developed gastralia present; cloacal opening longitudinal .... Crocodylia

(b) Acrodont or pleurodont teeth; no fully-developed secondary palate; gastralia absent; cloacal opening transverse .... Squamata

The brief diagnoses in this key are extended in the individual chapters on each of these orders. In summary, modern reptiles (Class Reptilia) may be characterised by a combination of general features, though the adaptations of individual groups or species have led to full or partial loss of limbs, viviparous modes of reproduction and so forth. The bony skeleton is well-ossified. The well-developed limbs articulate with the large pectoral and pelvic girdles. The skin is dry and scaly, and its outer horny layer is periodically shed (sloughed). Skin glands are generally absent, and the vomero-nasal (Jacobson's) organ is well-developed, though not in adult crocodilians. Osteoderms are often present under the skin. The egg is cleidoic. The skull moves freely on a single condyle, and the first two vertebrae are modified to form an atlas and axis.

13. HISTORY OF DISCOVERY OF THE REPTILIA

Harold G. Cogger

FIRST ENCOUNTERS

When Australia was first encountered by Asian and European seafarers, the entire continent, together with Tasmania, was occupied by indigenous peoples who had an intimate knowledge of the country's reptiles and their habits. Reptiles then and now figure large in Aboriginal culture, including art and religion. It is ironic that herpetologists (Cogger 1970) first formally recorded the pig-nosed turtle (*Carettochelys insculpta*) from Australia in 1970, only to find later that this species had long ago been recorded for posterity by Aboriginal artists in the caves of western Arnhem Land (Fig. 13.1). The large Oenpelli python, *Morelia oenpelliensis*, was not known to science until 1975 (Gow 1977), but is also recorded in the early rock art of Arnhem Land.

Before the discovery of the eastern coast of Australia by Captain James Cook in 1770, and the subsequent establishment of the first European settlement in Australia — the British penal settlement at Sydney (Port Jackson) in 1788 — Australia had been visited, though not always intentionally, by a number of European seafarers and explorers (Whitley 1970). Few records (and apparently no specimens) derived from these early encounters with the Australian fauna exist. Whitley (1970) recorded that no reptiles were among the few Australian animals recorded, apart from crocodiles and marine turtles noted from the southern coastal waters of New Guinea by the Spaniard Luis Vaez de Torres, who in 1606 passed through the Strait subsequently named in his honour. Nor did Abel Janszoon Tasman record any when he landed in Van Diemens Land, later to become known as Tasmania, in November 1642. Nevertheless the first Australian reptilian record goes to Tasman who, in 1644, recorded crocodiles (undoubtedly *Crocodylus porosus*) from Crocodile Island, west of the Wessell Islands, during an expedition to the Gulf of Carpentaria (Whitley 1970).

Figure 13.1 Aboriginal rock art illustrating *Carettochelys insculpta*, in which the position and extent of the limb musculature are shown clearly.
[Photo by A. Georges]

The English buccaneer William Dampier described the plentiful, edible turtles, presumably the Green Turtle, *Chelonia mydas*, when he visited the Kimberley coast in 1688. Dampier again visited the Western Australian coast at Shark Bay in 1699, and on 6 August described the first endemic Australian reptile — the scincid shingleback lizard, *Tiliqua rugosa* (Pl. 6.1). His description is diagnostic. It has already been quoted in an earlier volume in this series (Stanbury 1987), but part of it bears repeating in a herpetological volume: '...at the Rump, instead of the Tail there, they had a Stump of a Tail, which appeared like another Head; but not really such, being without Mouth or Eyes: Yet this Creature seem'd by this Means to have a Head at each End;...the Legs also seem'd all 4 of them to be Fore-legs, being all alike in Shape and Length, and seeming by the Joints and Bending to be made as if they were to go indifferently either Head or Tail foremost. They were speckled black and yellow like toads, and had Scales or Knobs on their Backs like those of Crocodiles, plated on to the Skin, or stuck into it, as part of the Skin. They are very slow in Motion; and when a Man comes nigh them they will stand still and hiss, not endeavouring to get away.' (Dampier 1703). Dampier regarded their odour when opened up as so offensive as to make them inedible — an outcome of their omnivorous habits, including coprophagy.

Dampier also recorded other lizards and a '...small speckled Snake', sea turtles and sea snakes during his visit to Shark Bay, but their specific identity is uncertain, despite Whitley's (1970) identification of the sea snakes as *Pelamis platurus* (possible, but unlikely from the descriptions) and *Laticauda laticaudata* (unknown from this region).

'...RARE AND CURIOUS SPECIMENS'

Initially, scientific knowledge of the native reptiles of Australia was confined to those species found in the vicinity of the first settlement at Port Jackson, or to coastal localities around the continent and Tasmania which were touched upon in the course of maritime explorations and surveys.

The first formal scientific descriptions of endemic species of Australian reptiles appeared in 1790 (White 1790). These had been collected in the early days of the Port Jackson settlement by or for John White, the settlement's Surgeon General. While the descriptions have long been attributed to White, they were almost certainly prepared for White's 'Journal of a Voyage to New South Wales' (1790) by Dr George Shaw in London. Shaw was an ordained clergyman who later qualified in medicine, became a keeper in the British Museum and published, with the artist Frederic Nodder, many early descriptions of animals from New Holland.

White provided illustrations of 12 reptiles, only five of which were formally named: the jacky lizard (*Amphibolurus muricatus*), the copper-tailed skink (*Ctenotus taeniolatus*), the southern leaf-tailed gecko (*Phyllurus platurus*), the eastern blue-tongue lizard (*Tiliqua scincoides*) and the lace monitor (*Varanus varius*). Other species illustrated but not named scientifically in the same work were the eastern water dragon (*Physignathus lesueurii*) (Pl. 5.3), named as a variety of *A. muricatus*, the eggs and adults

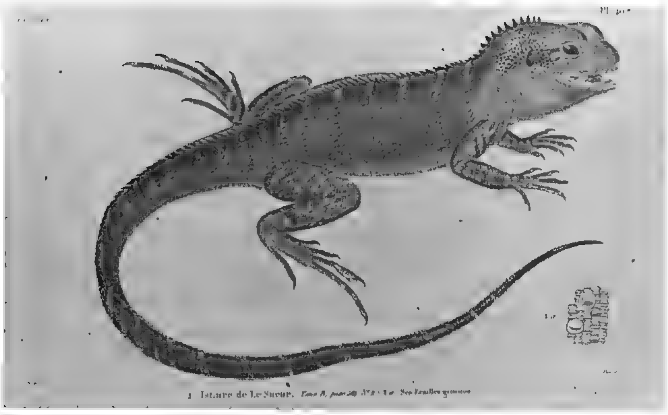

Figure 13.2 *Physignathus lesueurii*, illustrated by Duméril, Bibron & Duméril (1954). [Photo by Australian Museum]

of a garden skink (*Lampropholis* sp., described as the eggs and young of the viviparous blue-tongue lizard!) and six snakes — the young and adult of the diamond python, *Morelia s. spilotes*, the bandy bandy, *Vermicella annulata*, (Pl. 8.4) and a juvenile eastern brown snake, *Pseudonaja textilis*). As various artists' renditions of the colours of the remaining two snakes are different in various editions of White's work, their identity is uncertain; they are probably the green and the brown tree snakes, *Dendrelaphis punctulata* and *Boiga irregularis*, both still common in suburban Sydney.

While the British were busy cataloguing and describing the fauna of the penal settlement of Port Jackson and its environs, a new age of scientific enlightenment was burgeoning in republican France. Of special significance to Australia and Australian herpetology was Napoleon's support of Nicolas Baudin's expedition to the south seas in the vessels *Geographe* (under the command of Baudin) and *Naturaliste* (under the command of Jacques F.E. Hamelin des Essarts). Included among their crews were the naturalists Francois Péron and Antoine Guichenot, and the artist Charles-Alexandre Lesueur — all names enshrined in latinised patronyms later assigned to species of Australian reptiles and frogs.

Baudin's expedition reached the coast of Western Australia in May 1801 (Whitley 1975), first travelling north to Timor, then returning to sail along the western and southern coastline of Australia to Tasmania, where their ships were separated until they both met up in Port Jackson in July 1802, where they stayed for six months. Their intentions, though almost certainly strictly scientific, were deeply distrusted by the colony, believing England and France still to be war. Their naming of part of southern Australia as 'Terre Napoleon' did little to assuage British suspicion as to their territorial objectives. In Port Jackson their ships anchored in Neutral Bay — so named to provide a small neutral territory in which foreign vessels far from home might anchor to obtain fresh food and water. The French naturalists were apparently allowed to travel within the colony, but they were treated with suspicion, Péron was regarded as a spy (Whitley 1975), and collecting was restricted. Nevertheless, they collected marine animals from their anchorage, and took the opportunity to go ashore with the sailors to collect water from the stream running into Neutral Bay. There they collected specimens of the eastern water skink, *Eulamprus quoyii*, which still reside in the Muséum National d'Histoire Naturelle in Paris.

During Baudin's expedition many remote Australian localities were visited, where many animals and plants were collected for the first time. These localities included Shark Bay and King George Sound in what is now Western Australia, Kangaroo Island, Gulf St Vincent and Spencer Gulf in what is now South Australia, and King Island in Bass Strait.

The specimens collected on these expeditions were lodged in the MuséumNational d'Histoire Naturelle in Paris, where they were utilised by the French herpetologists G. Bibron, A. Duméril and A.M.C. Duméril, in their catalogue series on the world's herpetofauna (Fig. 13.2). Many of the Australian species catalogued and newly named by Gray at the British Museum were also catalogued and newly named by the Dumérils and Bibron, often almost concurrently.

Until recently, very few of the numerous illustrations made of these specimens during the voyage by Charles-Alexandre Lesueur and Nicolas-Martin Petit had been published (Bonnemains, Forsyth & Smith 1988). The fine study of the longnecked turtle *Chelodina longicollis* (Fig. 13.3) is one of the earliest illustrations of the species.

19TH CENTURY EXPLORATION OF THE CONTINENT

Some of the most productive and exciting reptile discoveries came not directly through the efforts of individual naturalists, but from broad geographic and natural history explorations of unknown or poorly known parts of the continent as part of the colonising

Figure 13.3 One of the earliest illustrations of longnecked turtles, *Chelodina longicollis*, painted by Charles-Alexandre Lesueur during Baudin's expedition 1800–1804. [Photo by Muséum d'Histoire Naturelle, Le Havre; no. 78086]

Figure 13.4 This illustration of *Varanus giganteus*, published in the *Zoology of the HMS Erebus and Terror* (Günther 1875), is an example of the fine lithographic illustrations reproduced in European jounals in the mid- to late 19th Century. (From Günther 1875) [Photo by Australian Museum]

process. Unfortunately, specimens seen on these expeditions were rarely collected. Heavy preservative and bulky preserved specimens were generally assigned a low priority by explorers preoccupied with carrying adequate food and water. We know from both published and unpublished diaries that occasional specimens were collected on these early expeditions, but few survive today.

In eastern Australia, exploration of the interior began with the successful crossing of the Great Dividing Range immediately to the west of Sydney by a group guided by John Wilson in 1813. Until that time, knowledge of the reptiles beyond Sydney came from maritime excursions which landed at random points along the eastern coast.

Lacking staff trained in taxonomic zoology, and effectively cut off from the critical collections and literature housed in the great museums and universities of Europe, the only reptilian curiosities maintained by Australian institutions were those used for public display and edification, and not for comparative research. Consequently, new discoveries were rushed to the European centres for identification and description, with the result that virtually all of the type specimens of Australian reptile species described before the 1860s, if they still exist, are to be found in European collections.

In 1836 Surveyor-General Thomas Mitchell set out to explore the interior of New South Wales, with a view to discovering the anticipated 'inland sea,' which was thought to be the destination of the rivers flowing west of the Great Dividing Range. As collector, Mitchell took with him John Roach, a convict employed by the Australian Museum, and returned with a handful of reptiles virtually all of which were new to science (Cogger 1979). These were apparently lodged in the Museum on his return, but have since been lost, possibly in the Garden Palace fire of 1882 during which many of the Museum's most valuable specimens were destroyed.

The specimens collected by Edward John Eyre on his 1839–41 explorations in South Australia and south-western Australia were sent to the British Museum in London (now the Natural History Museum), where they still reside. Similarly, specimens collected by Sir George Grey during his 1837–39 expeditions to north-western Australia to find a suitable site for a settlement, were taken to the British Museum.

The diversity of reptiles in northern Australia first became known as the result of opportunistic collecting by ship-based surveying expeditions. The early published catalogues of the Natural History Museum in London (Gray 1845, 1849; Günther, 1858) contain numerous new species and new geographic records attributable to the collecting activities of the crews of the *Beagle*, the *Fly* and the *Rattlesnake*.

Not until 1838, with the establishment of the settlement at Port Essington on Cobourg Peninsula (after unsuccessful attempts to establish settlements at Fort Dundas on Melville Island and at Fort Wellington on Raffles Bay) did systematic collecting result in the discovery of a whole suite of taxa now known to be widespread throughout much of northern Australia. These include *Morelia spilota variegata, Lophognathus temporalis, Oedura marmorata, Diporiphora bilineata* and *Lophognathus gilberti*.

Port Essington was also the destination of Ludwig Leichhardt's 1845 expedition. He was accompanied on the journey by the naturalist John Gilbert, who died on the trip after being speared by Aborigines. Collections made on Leichhardt's forward journey were taken to England from Port Essington, and his specimens are still lodged in the Natural History Museum in London. A full account of the collectors and collections associated with the settlement at Port Essington is to be found in Calaby (1974).

Between 1836 and 1875, the aridity of most of the interior of continental Australia became known through a series of small geographic expeditions, many of them involving tales of amazing fortitude and privation, and often involving heavy loss of life through thirst, starvation and conflict with the indigenous people. Despite encounters with Australia's rich arid-zone herpetofauna, few of these explorations led to significant new knowledge of this fauna.

However, as the essentially arid climatic and geographic features of the interior were defined, so its scientific exploration became more systematic. Naturalist collectors were now an essential component of any well-mounted expedition. Several of these expeditions stand out for their contribution to knowledge of the Australian herpetofauna, although this was not necessarily reflected in the publications of the time.

THE GROWTH OF INDIGENOUS HERPETOLOGY

By the second half of the 19th century there had developed in Australia a strong group of resident natural scientists and strong popular support for scientific exploration. One of the most publicised, well-supported and ill-fated exploring expeditions during this period was that of R.O'H. Burke and W.J. Wills in 1860–61, both of whom ultimately died on the expedition after extraordinary privations. They set out from Melbourne to travel inland to the Gulf of Carpentaria and back. They were initially accompanied by a team which included the 52-year-old German naturalist Dr Ludwig Becker, who died just south of Cooper Creek in the early stages of the expedition, after making exquisite drawings and detailed descriptions of the reptiles which he encountered. Only recently were these drawings published for the first time (Tipping 1979) and showed species which were not subsequently described formally until the latter half of the following century! For example, his diagnostic illustration of the little python *Liasis stimsoni* from Lake Menindee on the Darling River was the only record of this species complex from New South Wales until it was rediscovered in the same area more than a century later. It was not actually named until 1985 (Smith 1985).

In 1875, Sir William John Macleay (1820–1891) funded a private biological and anthropological expedition to the south coast of New Guinea on the MV *Chevert*. Macleay was a wealthy Sydney politician, philanthropist and natural history collector. He was a keen entomologist, having inherited the extensive insect collections of his uncle, Alexander Macleay, and his cousin, William Sharp Macleay. He was a benefactor of the Linnean Society of NSW and a Trustee of the Australian Museum. The expedition suffered from dissension, disease and bad weather, and did not accomplish its primary objectives. However, it provided the first significant records of the herpetofauna of the islands of Torres Strait, an area regarded until recently as of great significance in understanding the role of Quaternary land bridges between Australia and New Guinea.

Another major expedition which led to more formal descriptions of Australia's arid-zone fauna was organised by William Austin Horn, a wealthy South Australian politician who made his fortune in mining. In 1894 he organised an expedition to the area between the MacDonnell Ranges in the Northern Territory and Oodnadatta in South Australia (Spencer 1896). Among his scientific team was Walter Baldwin Spencer, who in 1887 had been appointed to the Chair of Biology at Melbourne University. Spencer collected numerous reptiles in the course of the expedition, and prepared many drawings of them from life. These were polished and published in the Expedition's report on the reptiles (Lucas & Frost 1896), providing one of the first general overviews of the rich reptilian fauna of central Australia.

THE GREAT MUSEUMS OF EUROPE: THE AGE OF THE CATALOGUERS

Few of the early describers of Australia's reptiles had ever actually seen their species alive. Specimens simply arrived on their desk preserved in alcohol or formalin. Some specimens were accompanied by brief notes on colours in life, habits or provenance, but most were not.

In part as a consequence of the great exploring and colonising successes of the major European powers in the late 18th and early 19th centuries — especially those of Britain, France and Holland — and in part as a result of the growth of the European scientific tradition, great institutions were set up in Europe to house, describe and exhibit the products of these successes. In biology, the widespread adoption of the Linnaean system of classification gave new impetus to the task of cataloguing the world's animals and plants. As a result, the growth of museum and university collections was rapid and highly competitive. The British Museum in England, the Museum d'Histoire Naturelle in Paris, the Rijksmuseum in Leiden, the Zoological Museum of Humboldt University in Berlin, as well as smaller museums in most of the other capitals of Europe, gathered and catalogued their collections. These published catalogues provided the major source of information about the kinds of reptiles recorded from Australia, and their distribution within Australia.

In England, the description of our fauna was largely in the hands of the British Museum's John Edward Gray (1800–1875) and, from 1857, his assistant and later successor, Albert Günther (1830–1914; Fig. 13.4). The work of G. Bibron, and A.M.C and A. Duméril in Paris has already been mentioned. Other natural history museums in the capitals of Europe, especially that at Humboldt University in Berlin, obtained small collections of Australian reptiles which were later formally described, but their impact on knowledge of our fauna did not match that of the English and French.

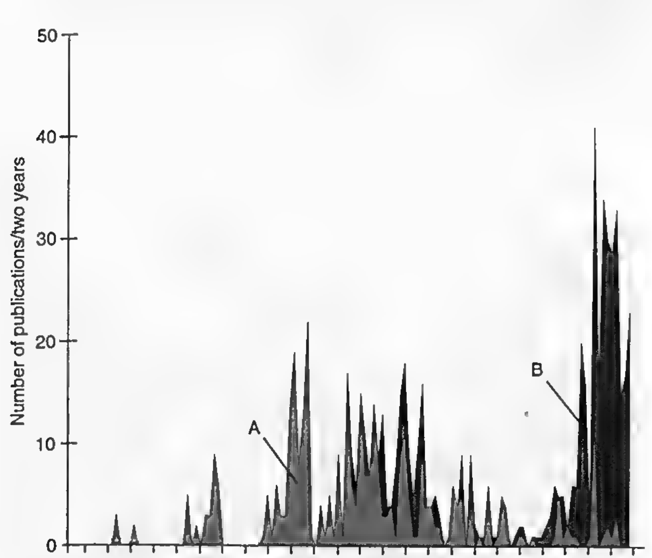

Figure 13.5 The sequence of description of currently valid Australian species, grouped by two-year increments, from 1750 to 1990. **A**, descriptions by taxonomists based outside Australia, primarily in Europe; **B**, descriptions by Australian taxonomists. [D. Wahl]

Figure 13.6 An imaginative and fine illustration of the black-headed python, *Aspidites melanocephalus*. (From Krefft's *Snakes of Australia* 1869). [Photo by Australian Museum]

In the history of the discovery and description of Australia's reptile fauna, one individual stands out. George Albert Boulenger was a Belgian appointed to the British Museum (Natural History) in 1883, after he had published amphibian catalogues based on the Museum's collections in 1882. Boulenger systematically set out to update the reptile and amphibian catalogues of his predecessors, and published between 1882 and 1896 some nine catalogues, containing more than 4000 pages, on the herpetological holdings of the Museum. In the course of this descriptive work, he named and described many new species and genera of Australian reptiles. By providing systematic keys to the reptiles of the world, for the first time he enabled herpetologists in Australia to gain an overview of their entire herpetofauna in both a regional and global context. He provided also the means to identify the specimens which were encountered in growing numbers and variety. While Boulenger's catalogues were soon overtaken by home-grown research in other countries, in Australia his catalogues remained an essential desk-top reference until the middle of the 20th century.

THE SCIENTIFIC DESCRIPTION OF OUR REPTILIAN FAUNA

Australia's reptile fauna currently stands at about 750 species. Of these, some 175 were described by European-based herpetologists before any was formally described by an Australian-based naturalist (Fig. 13.5). But systematic natural history collecting of the kind carried out by the European expeditions of the late 18th and early 19th centuries was not undertaken by Australians themselves until the middle of the 1800s. Indeed, the first description of an Australian species by an Australian-based scientist was published in 1863.

G. Krefft. naturalist

Figure 13.7 Gerard Krefft, Australian Museum.
[Photo by Australian Museum]

In the early days of colonial Australia, interest in our reptilian fauna tended to be general, rather than scientific, and concentrated either on the edible or the venomous. While it was early recognised that Australian reptiles were mostly different at the species level from those of other parts of the world, with a few exceptions (such as the thorny devil, *Moloch horridus*) they were not sufficiently distinctive in form or habits to warrant special attention. The attention of both the public and the early naturalists tended to be drawn to the unique, and often edible, monotremes and marsupials, or the distinctive bird fauna. However, it soon became apparent to the early colonists that a high proportion of our snakes are venomous. People and domestic animals infrequently but regularly died from snake bite, and the early records of life in the colonies are dotted with accounts of these first encounters. Early public displays of reptilian curiosities tended to emphasise our snake fauna. Consequently, it is not surprising that the first nine species described by an Australian-based herpetologist were snakes, and the tenth a crocodile! This preoccupation with snakes is also reflected in the popular literature. The first popular book devoted to a national treatment of Australian reptiles dealt only with snakes (Krefft 1869; Fig. 13.6), as did the second and third (Waite 1898; Kinghorn 1929). The first book to treat the entire Australian reptile fauna did not appear for 175 years (Worrell 1963). The first published regional herpetofauna was for Victoria (McCoy 1878), followed by that of South Australia (Waite 1929).

Whereas 70% of our present snake fauna was described by the end of the 19th century, only 35% of our present lizard fauna had been described by this time. The number of formal descriptions of the Australian reptile fauna significantly increased during certain periods (Fig. 13.5). The first peak occurred in the decade centred on 1845. The first peaks in Australian-based species descriptions are attributable to only a handful of individual researchers — Gerard Krefft (Fig. 13.7) in the 1860s and early 1870s, followed by William Macleay in the late 1870s and early 1880s, and Charles de Vis in the 1880s and 1890s (Fig. 13.8).

THE COLLECTIONS OF AUSTRALIAN REPTILES

By the beginning of the 20th century there were natural history museums in every Australian State, but not in the present-day Northern Territory. Their collections of reptiles had been acquired from a variety of sources, such as major expeditions, routine field collecting, and donations from collectors and the general public. The collections were small, ranging from a few hundred to a few thousands of specimens, but most museums were too underfunded to carry out extensive field surveys of their own. At the Australian Museum, Australia's oldest natural history museum founded in 1827, the first motor vehicle was donated in 1932.

In the universities, several zoologists turned their attention to reptiles, either as experimental animals or as subjects for anatomical or behavioural studies. However, with the exception of the William Macleay collection housed in the Macleay Museum of the University of Sydney, significant zoological museums which curated general systematic collections were not established in Australian universities, as they were in Europe and North America.

One of the most distinctive features of Australian natural history has been the failure to establish a national focus, a problem which continues to the present day. A national museum was not established until 1980, and while responsibility for the relatively small Federally-owned biological collections has been mooted for this institution, it has not been achieved. Indeed, these National Collections were mostly accumulated as working research collections of the various Divisions of CSIRO, and remain so. In recent times, there has been a healthy trend towards regarding all biological collections in Australia simply as elements in a national network, but this has not been recognised at a political level.

As a result of this history of collection-building, the description of Australia's reptile fauna between the turn of the century and the Second World War was left to a handful of museum-based taxonomists, while knowledge of the basic biology and ecology of our herpetofauna tended to come from scientists within the

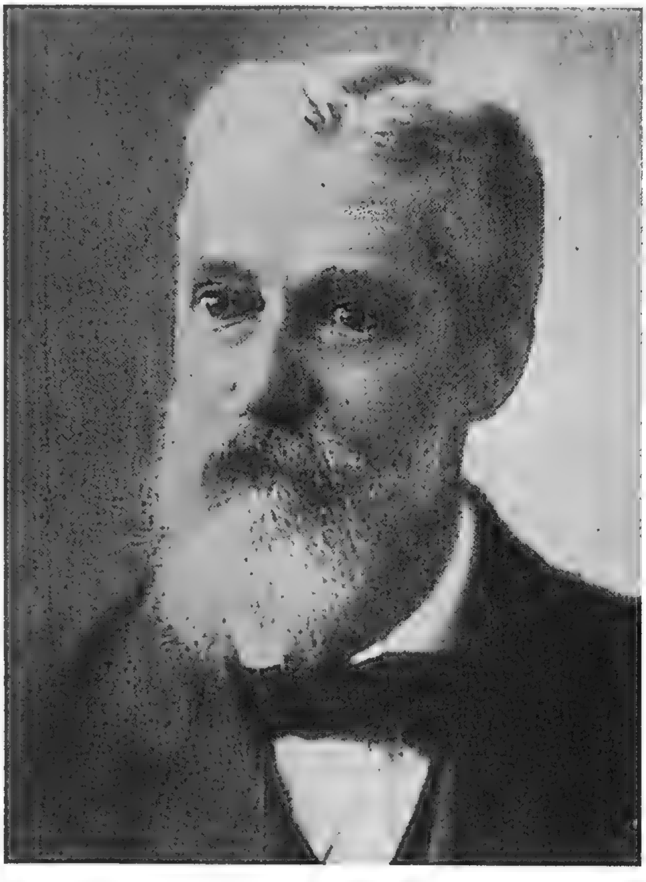

Figure 13.8 Charles de Vis, Queensland Museum.
[Photo by Queensland Museum]

Figure 13.9 Charles Kinghorn, Australian Museum.
[Photo by Australian Museum]

Australian university system. In New South Wales, Dene Fry (killed in France in 1917 at the age of 23) and James Roy Kinghorn (1891–1983; Fig. 13.9) at the Australian Museum dominated systematic herpetology. In Queensland it was Heber Longman at the Queensland Museum, in Victoria Charles Brazenor, and in Western Australia the Director of the Western Australian Museum, Ludwig Glauert. In South Australia Edgar Waite, who moved to the South Australian Museum from Sydney to take up the Directorship of that institution in 1914, made major contributions to systematic herpetology. His review of the Australian blind (typhlopid) snakes (Waite 1918) remains a seminal paper for students of this group, and his superb overview of the State's herpetofauna (Waite 1929) has been alluded to earlier in this chapter and has recently been reprinted by the American Society for the Study of Amphibians and Reptiles as a classic work in herpetology.

Incidentally, this same Society produced for the First World Congress of Herpetology in 1989 a book containing biographies of most of the world's past herpetologists (Adler 1989), including most of those mentioned in this Chapter.

Overseas, the taxonomic decisions of Arthur Loveridge, expressed in his catalogues of Australian and New Guinean reptiles and amphibians in the Museum of Comparative Zoology at Harvard University (Loveridge 1933, 1934, 1948), gave impetus to new studies of the Australian herpetofauna.

THE UNUSUAL STILL AWAITS

Following the Second World War, Australia entered a new era of prosperity accompanied by an influx of migrants from war-torn Europe. The combination of economic growth, the expansion of educational opportunities and the injection of new ideas, a new nationalism, and new technology in transport and communications, brought a renaissance of interest in the composition, ecology and conservation of our native wildlife. In herpetology, this has been reflected in a veritable explosion of newly described taxa (Fig. 13.5) beginning in the 1960s. An early contributor to this knowledge explosion was Eric Worrell, based at the Australian Reptile Park at Gosford.

Without doubt the most prominent contributor to this process was Glen Storr (Fig. 13.10). Based at the Western Australian Museum, he began a systematic taxonomic treatment of a region which had yet to be recognisd as one of the richest herpetofaunas in the world. For 30 years until his death in 1990, Storr described more than 170 new taxa of Australian reptiles, and was a major contributor to the approximately 40% increase in the number of described species of Australian reptiles between 1975 and 1990.

The second half of the 20th century has also been accompanied by a parallel explosion in our knowledge of the ecology and phylogeny of Australian reptiles. Studies of chromosomes, isozymes and DNA have led to a refinement of our knowledge of genetic relationships. Detailed ecological studies of Australian reptiles remain relatively rare (see Bradshaw 1986 and Pianka 1986 for reviews), which impacts significantly on our ability to develop appropriate strategies to conserve our native reptiles.

To date, no Australian reptile is known to have become extinct (Cogger *et al.* 1993). While it is often contended that taxonomic knowledge of Australia's vertebrate fauna is refined and nearly complete, several recent experiences suggest otherwise. Australia's second largest species of python, *Morelia oenpelliensis* was not known to science until 1975 (Gow 1977). Nor was another large python, the carinated python (*Morelia carinata*) found until 1973 (Smith 1981), since when only three specimens have been seen of this Kimberley endemic. In 1992, a distinctive, new, large scincid lizard was found in south-eastern Queensland, less than 200 km from Brisbane, by a wildlife ranger. Still undescribed (Covacevich *et al.* in press), it typifies the need for continuing research into the distribution and taxonomy of Australia's rich herpetofauna.

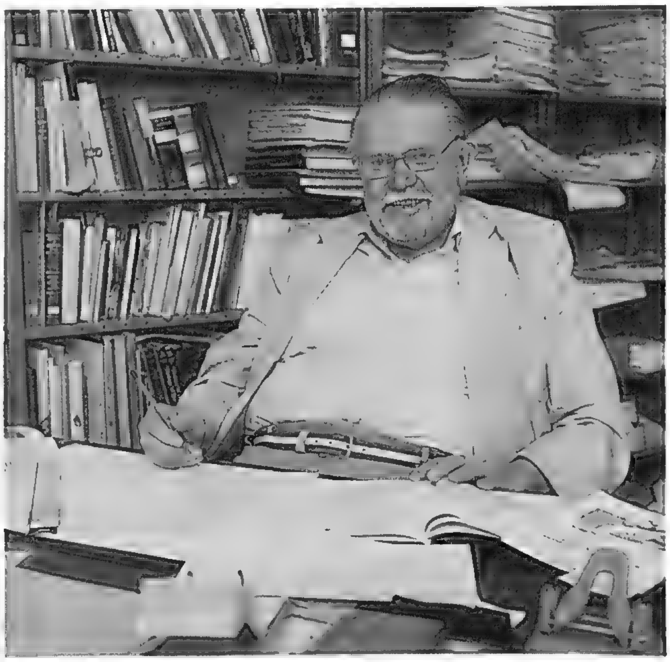

Figure 13.10 Glen Storr, Western Australian Museum.
[Photo by Western Australian Museum]

14. COLLECTION AND PRESERVATION OF THE REPTILIA

Terry D. Schwaner & Chris B. Banks

One of the most important aspects to consider before undertaking any collection is to obtain the requisite permits from the relevant authorities. In terms of the Constitution, control of the collection of Australian fauna is the reponsibility of the six States and two mainland Territories which comprise The Commonwealth of Australia. There are a number of administering authorities in each State or Territory and it is essential to obtain the permission of each relevant authority before collecting begins. Permission to enter any land is a separate issue which collectors should clarify with landowners before collecting. This applies especially to Aboriginal lands and heritage areas.

To assist researchers, a detailed guide to requirements for collecting Australian plants and animals is available (ABRS 1993). The guide provides the contact personnel and addresses of State and Commonwealth authorities responsible for issuing collection permits and licenses. Copies of this guide may be obtained from the Australian Biological Resources Study, GPO Box 636, CANBERRA ACT 2601; telephone (06) 250 9440 or 250 9443, facsimile (06) 250 9448.

Import and export of legally collected material from Australia requires strict observance of international conventions, such as the Convention on International Trade in Endangered Species (CITES). Further information may be obtained from the Chief Executive Officer, Australian Nature Conservation Agency, GPO Box 636, CANBERRA ACT 2601; telephone (06) 250 0200 within Australia, or +61 6 250 0200 from overseas.

Collectors of reptiles in Australia should coordinate their collecting activities with curators of the State collections in their respective areas. These collections are now computerised to provide a quick response to requests for species identifications and distributions. Most State museums now have modern facilities and equipment that may be loaned to assist others in their collecting and preservation efforts.

The frustrating and potentially dangerous nature of collecting reptiles emphasises a need for clear objectives and proper planning when taking reptiles from the wild. Knowledge of the animals' habitats, climatic preferences, and lifestyles will enhance success. Crocodiles and turtles tend to be diurnal, active animals, although the former are most often encountered at night. The saltwater crocodile (*Crocodylus porosus*) is the most aggressive Australian species and great care is needed when dealing with individuals in excess of 3 m in length. Subtropical and tropical reptiles are active year round, whilst species from more temperate southern areas become dormant (or at least restricted in activity) over the colder winter months.

Slowly driving or walking through potential collecting areas is advisable, especially when snakes and lizards are likely to be active. Diurnal species are usually active in the early morning (0630 to 1000 hours) or late afternoon (1600 to 1800 hours) in warmer seasons. However, many lizards will be active throughout the day, and activity times will vary considerably seasonally (for example, Schwaner 1989), geographically, or between local habitats (for example, with light or dark coloured soils; Heatwole 1976). Nocturnal species, particularly some lizards and snakes, are especially active on warm nights following rains.

The exact location, date and collector of each specimen are as important as the specimens themselves. No collector should attempt to take reptiles without being able to locate the animals' capture sites on a map. Where established roads or trails are lacking, distances (in km) from various topographic features, grid coordinates or latitude and longitude must be recorded. Readings from the recently developed Global Positioning System are ideal. Features of the environment and the behaviour of each specimen should also be recorded. Simmons (1987) and Garrett (1989) discuss the types of information required for collected specimens.

Housing and feeding of reptiles in captivity are beyond the scope of this chapter. However, an overview of the topic is given by Cogger (1992; see also references therein).

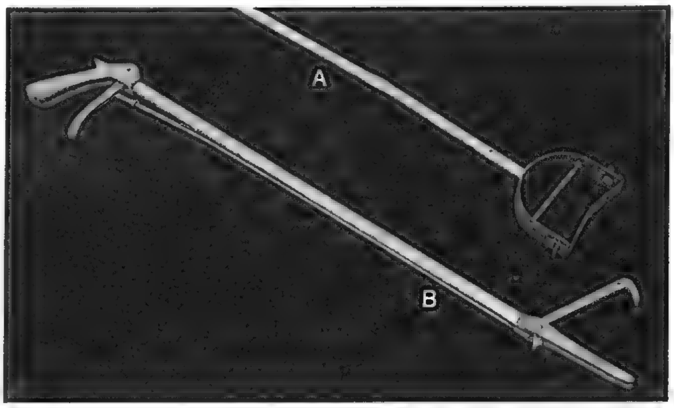

Figure 14.1 Implements used to capture snakes. **A**, head pinning device, showing the leather strap stretched across the fork of the base; **B**, a grab-stick, which can be closed on the snake remotely, by squeezing the handle.
[Photo by C. Glasby]

CAPTURE

Hand capture

Freshwater turtles can be collected occasionally by hand from shallow, clear, still or slowly moving water. When disturbed, they usually dive to the bottom or hide under overhanging banks and aquatic vegetation. Some turtles habitually sit on the bottom, directly below where they entered the water, and, if the water is especially deep or dirty, they can be captured by skin diving or with SCUBA equipment (Cann 1978). Freshwater turtles are less apt to flee if approached indirectly under water. Marine turtles are best caught when they come ashore to lay eggs at night. They can be captured at sea also, by jumping onto them while they rest at the surface, a technique termed 'rodeoing'.

Freshwater and saltwater crocodiles, *C. johnstoni*, and *C. porosus*, up to 1.2 m in length, can be caught by hand from a boat or an airboat (Walsh 1987). However, for larger individuals, collecting equipment should be used to avoid serious injury to all concerned.

All lizards can be captured by hand, but large monitor lizards can inflict painful bites and geckos are subject to damage by rough handling. Hand collecting during cooler hours of the day will be more productive for diurnal lizards with preferred high body temperatures, particularly if the species hides among stones or rock slabs. Small specimens can be coaxed out of rock crevices or tree hollows by gentle prodding with a length of wire. A crowbar can be useful for lifting large rocks (Swanson 1976).

Importantly, habitat disturbance must be kept to a minimum when searching for lizards and snakes. The combination of many physical, chemical and biological processes results in the micro-community which supports the reptile or its prey. Replace

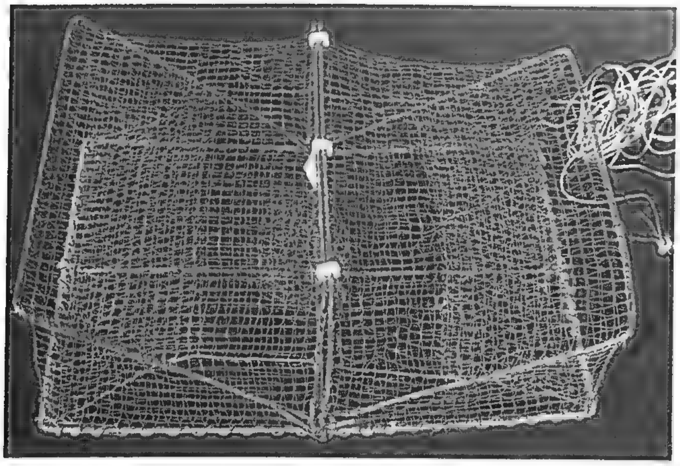

Figure 14.2 A wire netting trap for freshwater turtles. A horizontal, wedge-shaped entry funnel leads inwards from each end; the bait pocket is visible beneath the central bars. [Photo by C. Glasby]

logs, rocks and even man-made debris in their original positions, and avoid damage to living or dead vegetation.

Trenches associated with construction sites and shallow, abandoned wells, are usually worth checking for lizards and snakes that may have fallen in overnight. Inexperienced collectors are warned, however, that venomous snakes may present a particular hazard in such confined situations.

Non-venomous file snakes, *Acrochordus arafurae*, may be caught by feeling amongst submerged vegetation (Shine & Lambeck 1986), and pythons should be grasped quickly behind the head or gently around the body (for less aggressive individuals). However, venomous snakes should not be caught by hand. Though some elapids can be picked up by the tail and deposited in bags or bins, the technique is not recommended, even for experienced snake handlers. A snake stick, also known as a pinning stick, jigger or Head Pinning Device (Ehmann 1975) provides the safest method of catching venomous snakes. Essentially, this is a 1 to 2 m length of metal tubing (about 20 mm in diameter) with a wide fork, or a wooden stick (25 mm in diameter) with a T-shaped section, at one end. A leather strap stretched tightly between the forks, or a piece of foam rubber glued to the T-shaped section, allows the snake's head or neck to be firmly pinned from above, without injury (Fig. 14.1A).

Other methods, including a simple L-shaped jigger, may be used to pin, hook and lift the snake, and, if strong enough, can also be used to pry under bark or small stones. Grab-sticks can be useful for large, swift, venomous snakes. This implement is a 1 to 1.2 m length of aluminium tubing with padded jaws at one end and a hand operated lever mechanism on the other end to close the jaws quickly on the moving snake (Fig. 14.1B).

Once the head or neck is secured, the snake is then quickly, but carefully, grasped behind the pinning stick with the thumb and first two fingers of one hand. The snake is gently pulled until the thumb and fingers reach and feel the angle of the jaw bones (or quadrate area). Once the snake is held firmly, the stick can be removed and the snake lifted from the ground or surface. As many snakes will remain quiet until the pinner is removed and then attempt to jerk free, it is best to grasp the snake's body with a free hand when lifting it, while maintaining the hold on the head and a cautious watch on the snake. A second person should be available to assist at all times when handling and examining a venomous snake.

Two methods are recommended for placing a venomous snake in a bag by hand. The first should be considered for snakes that are small relative to the bag size. An assistant holds the bag open and above the ground while the snake handler lowers the U-shaped body into the bag, using both hands to hold the head and tail. On an agreed signal, the handler quickly drops the snake into the bag and, simultaneously, grabs the top of the bag from the assistant (with either free hand), swirling the bag vigorously, both to drive the snake to the bottom and to twist the top of the bag down on the snake. Lowering the bag to the ground prevents it from unwinding and a stick placed over (at right angles to) the twisted portion can be held in place with a foot while the bag is tied. The hoop bag method (Gow 1989) is safer because the bag is large (1.2 to 1.5 m deep) and the assistant initiates twisting. The snake's body and then the head are lowered into the bag and the head is then carefully grasped with a free hand from outside the bag. The initial hold is released, that hand withdrawn from the bag, and the bag secured with ties before the second hold is released (quickly).

Snakes are best carried in strong calico or linen bags that have been double-seamed along the bottom and sides, and across the bottom corners. Two tying tapes should be sewn below the bag's opening and bags with specimens should always be handled above the tied area — snakes can inflict a bite through the bag. Other bag designs incorporate zippers for quick removal, or use sheer material so that the snake's position can be seen at all times (Weigel pers. comm.). When transporting snakes in bags, consider the need to protect them from injury, or extreme heat and cold.

Trapping

Simple wire drum nets, supported by a strong wire frame or internal cross-supports and with a capacity of about 200 litres, work well for freshwater turtles. A funnel-shaped entry hole, facing inwards, allows the turtle entry but prevents its escape. Bait may be tied to an internal wire or placed in a smaller internal cage. The trap can be tied to the bank, suspended on poles in the water, or from an overhanging branch, and the top 50 to 100 mm of the trap must protrude above the water to allow the trapped animals to breathe. A smaller version which operates on the same principle is shown in Figure 14.2. Other techniques include a plank fixed across the mouth of a large floating barrel, in which a few holes have been bored (Pritchard 1967), or a floating platform encircling a central wire-netting cage (Cann 1978), are alternative designs.

Traps are used for first-time collecting of large crocodiles in habitats that prevent the use of other methods, and for mark-release-recapture studies of growth and movement. An

Figure 14.3 Routine check of pit-traps, in use with a drift fence. The white container buried in the foreground will trap animals, which fall in after wandering along the fence. [Photo by Lesley Muirhead]

easily constructed, portable, cylindrical trap of steel mesh sections was designed by the Conservation Commission of the Northern Territory (Walsh 1987) to capture crocodiles up to 4.5 m total length. Attachable floats allow its use in tidal areas.

Rope traps can be used for crocodiles longer than 5 m in length, to avoid injury in steel traps. These traps take considerable time to construct and require a heavy counterweight, such as a large tree, close to the mouth of the trap when the bait is pulled. The trap can be left alone until it is sprung if a radio alarm, currently available with a range of 30 to 40 km, is used (Webb & Messell 1977).

Pit-traps are effective for collecting small to medium-sized lizards, wandering freshwater turtles and some small snakes (Braithwaite 1983; Mather 1979). A variety of plastic and metal buckets, ice cream containers, steel tubs and PVC piping have been used. The lip of the trap should be flush with the ground surface and great care should be taken to ensure that the surfaces leading to the trap edges are similar to those of the surrounding habitat. Metal sheets, bark strips or large flat rocks, elevated by small stones or sticks to allow animals to crawl under them and into the trap, will also protect trapped animals from sunlight. The efficiency of pit-traps is greatly increased when a drift fence is used (Morton, Gillam, Jones & Fleming 1988) (Fig. 14.3).

Live mammal traps, such as metal Sherman traps will catch small diurnal and nocturnal, terrestrial skinks, and the larger 'bandicoot' traps are effective for large monitor lizards (Cogger 1992). Shine (1977a) used wire funnel traps successfully to catch elapids in eastern Australia — a method often used in other countries for terrestrial snakes (for example, Seigel 1986; Fitch 1987). Similarly, an aerial 'drift fence', consisting of a 15 m × 1 m diameter tube of fine wire mesh, with funnels at either end, and supported 3 to 15 m above ground in tropical forest, has been successful for catching small Central American iguanids and colubrids (Vogt 1987).

All traps should be monitored at least daily. When not monitored, traps should be covered with tight-fitting lids to prevent the needless death of a wandering animal. If lids are not available, pieces of board, sticks or rocks can be placed in the trap to allow a trapped animal to escape. In well-drained areas, small holes in the bottom of pit-traps will prevent water accumulation and subsequent drowning of trapped individuals.

Harpooning

Webb & Messell (1977) used a small harpoon head on a sturdy pole attached to about 50 m of line to capture *Crocodylus porosus*. Crocodiles are approached at night with a spotlight and the harpoon head is jabbed into the soft skin of the neck or the tail of small or wary specimens. Skill is required to make a small wound only, and to avoid the impenetrable osteoderms on the crocodile's back (Walsh 1987).

Netting

Floating nets with a 60 to 80 mm stretched mesh size and cord diameter less than 1 mm have proved successful for catching *C. johnstoni* (Webb, Manolis & Buckworth 1983). Such nets must be checked regularly. Heavy duty commercial fishing nets have also been used to catch *C. porosus*, but are not often effective (Webb & Messell 1977). Freshwater turtles can be caught with gill nets, drag-nets and seine nets with reasonable success, but care must be taken to avoid drowning the turtles, and these methods have potentially disruptive effects on aquatic vegetation and other species. Freshwater turtles can swim under these nets if they are not set close to the bottom, or the animals may bury in the mud to escape capture.

Noosing

Quick-moving dragon and monitor lizards can be caught effectively using a long, light bamboo, aluminium or fibreglass pole, with a slip noose attached securely to one end (Swanson 1976; Madsen & Loman 1987). Portable models have interlocking segments for quick assembly and disassembly in the field.

Snares have been used successfully for *Alligator mississippiensis* and for wary *Crocodylus acutus* (Mazzotti & Brandt 1988; Webb pers. comm.). These techniques have not been applied to Australian species.

Another device, the noose-tube, consists of an aluminium tube (for strength) inside a hollow plastic tube (0.46 to 0.60 m long and 50 mm diameter), and a length of nylon cord affixed and looped at one end, with the other extending through and to the opposite end of the tube. The loop is placed over the head of a lizard or snake and the free end pulled to pin the animal's neck against the end of the pole. Grab sticks and noose-tubes are available commercially and widely used for capturing venomous pit-vipers in the United States (King & Duvall 1984), but home-made versions have been used successfully in Australia (Hutchinson pers. comm.).

Other Live-capture Methods

Stout rubber bands when stretched and fired from between the thumb of one hand and the thumb and forefinger of the other, can stun (or kill) small reptiles (especially lizards). This method is very effective at a distance of 3 to 4 m (or closer), and usually requires that the animal be positioned against a hard surface for maximal impact of the band. Skill is required to prevent killing the animal or breaking its tail. Eye protection should be worn to prevent injury as a result of backfire.

Tinkle & Lawrence (1956) successfully used a 1.2 to 1.5 m length of 16 mm bore aluminium tubing and a close fitting cork (painted with nail polish to increase its visibility and retrieval) as a blow pipe to stun small teiids and iguanids. More lethal versions use a carpet needle inserted into the narrow end of the cork. A water pistol, loaded with water, can be used to knock geckos from walls and rock-faces (Branch 1988).

Though apparently popular in other countries, jaw snares, Pitman snares and stockades (Hutton, Loveridge & Blake 1987) have had minimal success for catching crocodiles in Australia.

Baited hooks can be used to catch turtles, but this can injure animals and the hooks should not be left unattended. A slower and more humane method is to use a line and baited handnet, without a hook, to slowly drag the turtle into grasping range.

Kill-capture

Methods designed to kill-capture reptiles are not recommended unless a small sample is required. Animals killed in this way quickly deteriorate and must be processed to preserve viable tissues, gut contents, internal organs, whole specimens or even skeletal materials. A more effective method for collecting lizards and snakes is to shoot them with .22 dust shot (or 'rat shot'), fired from a pistol or rifle. Cogger (1992) preferred a pistol for animals at close distances to prevent excessive mutilation, and recommended the use of solid .22 bullets for large lizards or arboreal snakes. Small, mouse- or rat-traps, baited with large insects, have been used to catch iguanid lizards in the tropics of Central and South America (Heatwole, Maldonado & Ojasti 1961).

PRESERVATION & STORAGE

Traditional methods of preservation include wet specimen preparation and skeletal collections. These are essential for long term preservation and storage of type specimens, and for vouchers and samples that document geographic ranges, variation in anatomical characters (for example, colour, pattern, scutellation, internal organs, teeth and bones), reproductive condition, and habits (for example, prey in stomach contents). Several excellent references (for example, Hall 1962; Pisani 1973; Simmons 1987,

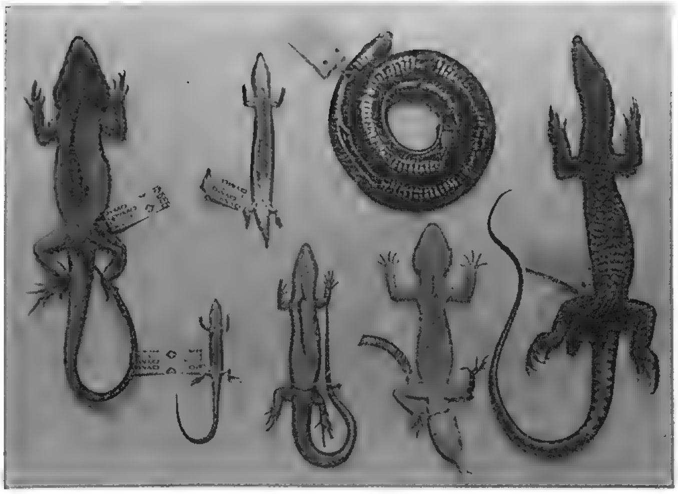

Figure 14.4 A tray of preserved specimens, illustrating appropriate positions for fixation. Note incisions to promote penetration of fixative and the space-saving which results from coiling the body or flexing the tail.
[Photo by T.D. Schwaner]

Cogger 1992; and references therein) provide guidelines and detailed directions for traditional preparation of reptile specimens.

Non-traditional methods are used to preserve viable tissues for cellular, chromosomal and molecular studies. These methods allow a greater range of potential characters for systematic analysis, and thereby extend the usefulness of classically preserved materials. Viable tissue collections, first established in Australia in 1980 by the Herpetological Section of the South Australian Museum (Schwaner 1982), are now present in the Australian Museum, Sydney, and the Western Australian Museum, Perth. Richardson, Baverstock & Adams (1986) provide more details on the collection and preservation of viable tissues and a comprehensive overview of molecular systematic methods is given by Hillis & Moritz (1990).

Although some morphologists regard tissue collecting as only necessary for an immediate project and some molecular systematists ignore the value of morphological features, we favour a balanced approach in which each specimen is carefully processed for tissues, without destroying internal and external anatomy (Schwaner 1982). What is compromised in this effort is time, simply because it takes longer to process a specimen for tissues, in addition to traditional methods of preservation.

Cooper, Ewbank, Platt & Warwick (1989) have addressed the critical issue (more generally considered by Wake, Zweifel, Dessauer, Nace, Pianka *et al.* 1975) of how to kill captured reptiles prior to preservation. Lethal injection with aqueous sodium pentobarbital, called 'Nembutal' or 'Lethobarb', is universally preferred, because death is painless, and is also accompanied by relaxation of the muscles, which facilitates fixing specimens in prescribed positions. However, this narcotic is highly regulated and generally restricted for public use. Similarly, anaesthetic inhalants (for example, chloroform, succinylcholine chloride, trichloroethylene, and ether) require special handling and care as all are volatile and highly flammable. Drowning small specimens in warm water or freezing them are less satisfactory, because they take longer and involve a degree of discomfort to the animal. However, these methods are effective, less painful than pithing, and do not damage the specimen. The proper use of firearms to dispatch large reptiles is quick and effective (see Cooper *et al.* 1989), but this method obviously causes damage to specimens.

Wet Preparation

Dead reptiles (kill-captured or otherwise) deteriorate rapidly in even moderate ambient temperatures. Although the onset of putrification can be slowed by chilling, our experience is that all but the freshest road-killed specimens will soon become infested with maggots. The onset of *rigor mortis*, the appearance of a deep green patch on the belly (indicating a ruptured gall bladder) and a tell-tale odour are good signs that a dead individual has begun to rot. To retard this process, the tissues must be perfused with a preservative that kills bacteria, inactivates digestive enzymes and hardens soft parts.

A 10% solution of formalin — one part of a 40% saturated, or concentrated, solution of formaldehyde gas in water, and nine parts water — is routinely used to fix (or harden) tissue. Formaldehyde (regularly used as human embalming fluid) is a dangerous chemical and should not be inhaled or allowed to come in contact with human skin. Because formalin is acidic (about pH 5), prolonged immersion of specimens can cause long-term deterioration, such as decalcification of bones. Methods to buffer the acidity of formalin with borax have recently come into question (Hughes & Cosgrove 1990), because these solutions lose their buffering capacity over time. Fortunately, this is only a serious problem for specimens fixed and preserved continuously in formalin. Formaldehyde gas can be soaked out of hardened specimens easily and replaced with less toxic ethanol or isopropanol (usually a 70% by volume solution) for long-term storage. In addition to preventing the subsequent growth of bacteria and fungi, these alcohols allow relatively safe handling and examination of specimens. Preservation in consumable spirits can be effective in an emergency.

Reptile skin retards penetration of formalin, and large specimens must be either cut open and immersed in, or injected with, preservatives. Injection of formalin with syringes and hypodermic needles is most effective, but also hazardous. Insulin syringes with fixed, fine needles are ideal for injecting preservative into the limbs and tails of very small lizards and snakes, and for extracting blood from living specimens (see below). For large animals, with accumulations of fat, it is essential to expose the fatty tissues to formalin without delay, to prevent rapid deterioration. We recommend glass rather than plastic syringes, although they are more expensive. Only Luerlock syringes and needles should be used to prevent the two from separating under pressure of injection. The resulting back-spray almost invariably is directed into the face and eyes of the preparator. Even with Leurlock materials, goggles and rubber gloves are essential.

Whenever possible, specimens should be fixed in positions that facilitate the examination and measurement of body parts (Cogger 1992), particularly where specimens are to be used in studies involving accurate measurements (Fig. 14.4). Consideration must also be given to the size and shape of storage containers available to hold specimens, for example, lizards with long tails may not fit into available bottles, unless the tail is bent into a U-shape during preservation.

Some collectors inject formalin into the base of the tail of male lizards and snakes, to evert one or both hemipenes. The shape and ornamentation of these structures provide additional characters for study. Unless these are tied off at their bases with a piece of thread, they may subsequently retract. Similarly, turtle necks often must be stretched during the hardening process to prevent retraction of the head. A wad of paper or similar material should be placed in the mouths of specimens to preserve the jaws in an open position, for later examination of the teeth and palate.

Skeletal Preparation

The preservation of skeletal materials usually involves three stages of preparation — maceration, the use of dermestid beetles or meal worms (*Tenebrio*), and alizarin staining. Maceration is a slow process in which, initially, the specimen is skinned, gutted and most of the muscle is cut away. The carcass is placed in water until the remaining flesh is softened so the bones can be picked or brushed cleaned. With care, whole, articulated skeletons can be prepared by this method. Beetles and meal worms can eat the remaining bits of flesh on a prepared carcass. So efficient are these insects that the bones require only a degreasing process to remove odour and prevent the attraction of other insects to the stored

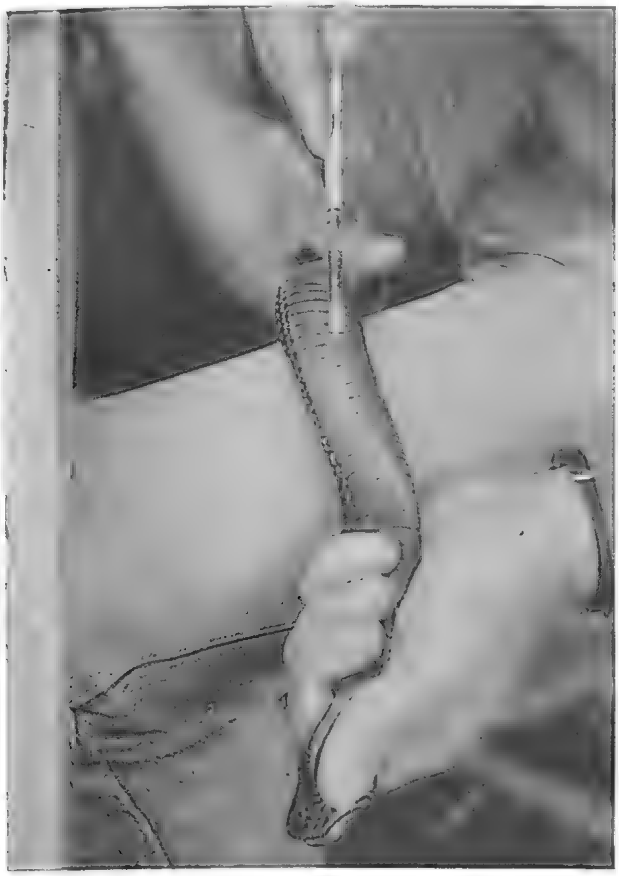

Figure 14.5 Extraction of blood from a live tiger snake *Notechis scutatus* by heart puncture, released and subsequently recaptured, on Kangaroo Island, South Australia. [Photo by M. McKelvey]

collections. However, each specimen must be closely monitored or the efficient beetles will disarticulate the skeletons.

Alizarin staining (for example, Webber 1978; Zug & Crombie 1970) involves a process that clears the muscle tissue of a skinned, eviscerated specimen using solutions of potassium hydroxide and the enzyme, pepsin. Once cleared, the specimen is placed in a bath of the dye alizarin red which has an affinity for bone. More recent preparations also use green or blue stains that are specific for cartilage (Hanken & Wassersug 1981). The final, cleared and stained specimens are stored in glycerin to which a small amount of thymol has been added to retard fungal growth (see Simmons 1987). So specific are these stains that each bone and articulating cartilage of even the smallest specimens is colourfully and vividly displayed when viewed under a dissecting microscope.

Comprehensive skeletal collections require many hours of preparation and every effort should be made to deposit such collections in museums so that they are readily available for comparisons of recent and fossilised bones.

Chromosomes

The number, shape and internal structure of chromosomes are important characters in systematic biology and have been used extensively to determine the status and relationships of Australian reptiles (see King 1985, and references therein). Chromosome preparations can be obtained from various somatic and reproductive tissues, or from cultured reptilian blood cells (particularly white cells) treated with colchicine to inhibit the formation of a mitotic spindle. Freshly treated cells are then fixed with an ice-cold mixture of three parts ethanol or methanol and one part glacial acetic acid, for long-term storage and handling (see Sessions 1990). Sessions (1990) provides an exhaustive discussion of chromosome preparations including protocols for preparing chromosomal materials in the field. Baker, Bull & Mengden (1971) offer alternative suggestions.

Viable Proteins

Immuno-electrophoresis, immunodiffusion on trefoil ouchterlony plates and microcomplement fixation (MC'F) are techniques that have been used to test the relationships of groups of Australian reptile species using antigen-antibody reactions (Baverstock & Schwaner 1985). These methods require purified albumin or transferrin proteins in blood serum. Adequate amounts of these proteins can be obtained from 1 to 2 ml of whole blood, although larger amounts enable samples to be taken. We have found that blood can be drawn quickly from the heart of a medium to large lizard or snake, using an insulin syringe with a fixed needle (Fig. 14.5). The head of a snake is grasped as described above and held with the back of its neck and upper body resting belly-up on the inner forearm of the holder. The rest of the snake's body is held firmly by an assistant. Careful observation will reveal the position of the beating heart. A needle is inserted quickly under (not through) a ventral plate, two or three scutes below the heart. If the tip of the ventricle is punctured, blood should flow freely into the syringe with gentle retraction of the plunger.

In large lizards the needle is inserted through the arm pit, transversely to the plane of the body, to reach the pericardial sac. Some workers are critical of these methods, although we have used them on hundreds of live snakes and lizards without causing the death of a single individual. Nevertheless, alternative methods, such as drawing blood from the caudal sinus, can be used, but this definitely causes discomfort to the animal and care must be taken to hold firmly onto the tail and body during the procedure.

Samples of various tissues (for example, blood, heart, liver, stomach, intestine, kidney and muscle) are essential for genetic studies using electrophoresis of proteins. These tissues must be frozen immediately and maintained at very low temperatures (<-60°C), to preserve proteins for both short-term analysis and long-term storage (Figs 14.6, 14.7). In the field, tissues may be frozen using either 'dry ice' (*i.e.* frozen CO_2 at about -60°C), or liquid nitrogen (at about -196°C). Special containers are necessary

Figure 14.6 Blood samples can be separated into plasma and the cellular fraction by centrifugation. Robust, hand-operated devices can be very effective in field conditions. [Photo by T.D. Schwaner]

for transporting liquid nitrogen. Those that hold spillable liquids are not usually allowed on commercial aircraft. However, Taylor-Wharton Company (Indianapolis Indiana, United States of America) manufactures a 'dry shipper', in 3 or 5 litre sizes, that absorbs liquid nitrogen into a special material located between the chamber and inner shell of the container. Once this material is saturated, excess liquid nitrogen can be poured off. The absorbed liquid keeps samples at ultracold temperatures for days or weeks (depending on the size of the container). These flasks can be carried as baggage on commercial aircraft, but special clearance may be necessary on overseas flights.

Figure 14.7 Storage of tissues in an ultra-cold storage unit at the South Australian Museum. Such units maintain sufficiently low temperatures to preserve proteins for both short-term analysis and long-term storage.
[Photo by Adrienne Edwards]

The relative positions of internal organs are good characters for systematic study. When taking tissues make small, clean incisions. Inflict minimal damage to skin, bone and unwanted organs. Take only portions of organs — for example, the ventricle of the heart, the middle section of the liver (for snakes), stomach or intestines, one kidney, muscle from one hind leg or one side of the body. Consistently dissect the same side of the body for each specimen. Package each tissue separately, but store tissues from the same individual together, or mark each package in such a way as to indicate which specimen each came from (see Dessauer & Hafner 1984).

Nucleic Acids

The number of potential characters for systematic studies of reptiles has been vastly increased by methods that determine the sequence of nucleic acids in their DNA (Werman, Springer & Britten 1990; Dowling, Moritz & Palmer 1990; Hillis, Larson, Davis & Zimmer 1990). In addition, the polymerase chain reaction (PCR) is an exciting new technique for both molecular biologists and curators of traditional museum collections, because fragments of DNA extracted from alcohol or even formalin-fixed specimens can be multiplied (i.e. amplified), overnight, to amounts sufficient for DNA sequencing (Innis, Gelfand, Sninsky & White 1990). These methods finally solve the major drawbacks of previous molecular techniques — namely, the need for large amounts of material from several (often very small) specimens, with the frequent (and increasing) requirement not to kill the animals in the process. As these new methods develop, properly preserved collections of reptiles will become even more valuable than before.

15. GENERAL DESCRIPTION AND DEFINITION OF THE ORDER CHELONIA

John M. Legler

Turtles are members of the order Chelonia (also termed Testudinata). There is general agreement on the monophyly of turtles and their distinction as an order within the Reptilia (Gaffney & Meylan 1988; Romer 1956). At all levels of knowledge the distinction of turtles is unequivocal. Turtles are familiar to humans. There is a word for 'turtle' in most languages and many children can draw a crude, but diagnostic picture of a turtle before they can spell the word. If turtles were known only from fossils, they would be regarded with substantially more awe than they are as familiar animals. The most common English names for chelonians are turtle, tortoise, and terrapin. Each may have special significance in local areas. For example, 'tortoise', as generally used by turtle biologists, refers to the completely terrestrial testudinid chelonians. In Australia, the term is used for any member of the family Chelidae.

Chelonians are toothless, oviparous, quadrupedal, pentadactyl reptiles with a shell and a unique trochlear system for the common tendon of the jaw adductor muscles. The principal and unequivocal diagnostic features of the Chelonia are the shell and the changes in related anatomy that accompany it. The carapace (upper shell) consists of costal bones fused to ribs, neural bones fused to vertebrae, and peripheral bones. The interclavical, clavicals and plates of dermal bone on the belly are incorporated in the plastron. The carapace and plastron articulate laterally and enclose the limb girdles. The limb girdles therefore are surrounded by the axial skeleton, unlike all other amniotes. The evolution of the chelonian shell was a major early modification of the basic amniote body plan (Fig. 15.1). It has served the chelonians well as they have survived and prospered with a minimum of modification, while most of the major events in reptilian evolution went on around them (see Carr 1952 for a delightful account).

There have been a few other reptilian experiments with a 'shell'. *Eunotosaurus* of the Permian of South Africa had broadened ribs, and certain placodont reptiles, especially *Henodus* of the Upper Triassic of Europe, had dermal elements fused to the axial skeleton, but none of these is a turtle nor is any involved in turtle ancestry (Carroll 1988). The homologies and the embryonic development of the chelonian carapace are reasonably well known, but the evolution of the carapace is seemingly still an open issue.

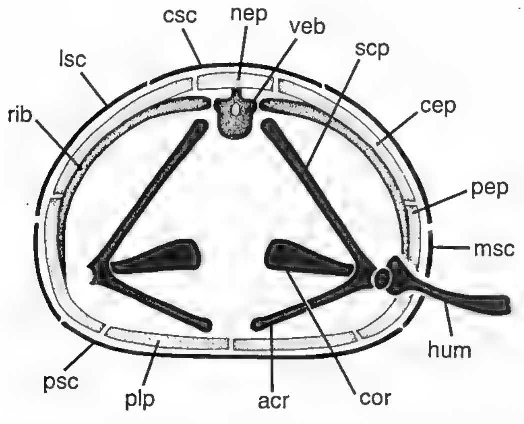

Figure 15.1 Diagrammatic cross-section through middle of a chelonian shell showing relative positions of skeletal and epidermal elements. **acr**, acromion; **cep**, costal plate; **cor**, coracoid; **csc**, central scute; **hum**, humerus; **lsc**, lateral scute; **msc**, marginal scute; **nep**, neural plate; **pep**, peripheral plate; **plp**, plastral plate; **psc**, plastral scute; **rib**, rib; **scp**, scapula; **veb**, vertebra.
[T. Wright]

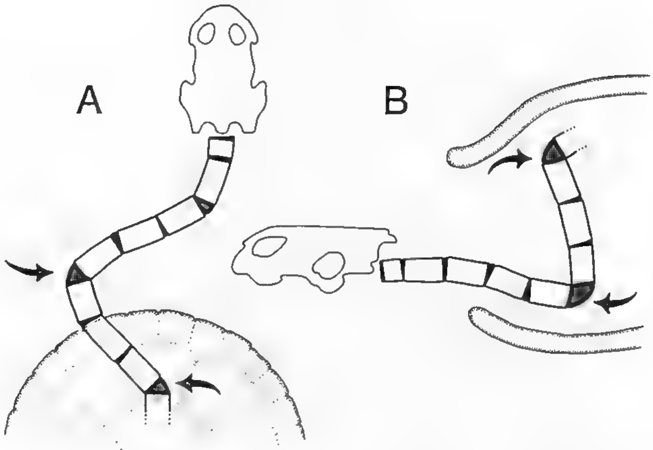

Figure 15.2 Differences in neck flexion and retraction in the two suborders of turtles. **A**, Pleurodira; **B**, Cryptodira. Arrows show points of greatest flexure. (After Williams 1950)
[T. Wright]

Aside from a drastic modification of the skeleton, turtles have remained quite generalised in most other aspects of anatomy, physiology and behaviour. Some adaptive modification has accompanied radiation, over approximately 200 million years, into a wide variety of habitats, ranging from complete terrestrialism in land tortoises (family Testudinidae) to an almost complete adaptation to aquatic life in the marine turtles (families Cheloniidae and Dermochelyidae). Land tortoises have elephantine feet, with short digits and no webbing, and are poor swimmers. Marine turtles are so specialised for swimming that they have difficulty with tetrapodal locomotion on land. However, the changes that occurred during these radiations are relatively small when compared to the initial evolution of the shell.

CLASSIFICATION

The two basic forms of living turtles are grouped in the suborders Cryptodira and Pleurodira. Cryptodires retract the neck straight back, in a sigmoidal curve in the vertical plane. Pleurodires flex the neck laterally, in either direction, in the horizontal plane and tuck it between the carapace and plastron (Fig. 15.2). The pelvis is fused to the plastron in pleurodires but is free in cryptodires. Pleurodires occur only on southern continents and are less diverse than the worldwide cryptodires.

Living turtles comprise 12 or 13 families; recent classifications include about 90 genera and some 260 species. The best checklist is that of Iverson (1992) which includes maps and cladograms, but no drawings. The checklist of Wermuth & Mertens (1961) lacks maps but has useful line drawings of many taxa. King & Burke (1989) also provided a useful checklist. There are two compendia entitled 'Turtles of the World' (Pritchard 1967; Ernst 1989).

There is general agreement on the equal subordinal rank of cryptodires and pleurodires, on extant families, and on suprafamilial groupings. The most recent, most complete, most complex, and probably best classification and phylogeny of turtles is that of Gaffney & Meylan (1988). They included all known fossil and living taxa and invoked many non-traditional taxonomic ranks, such as 'parvorder', 'capaxorder' and 'microorder'. As their work is of great value to a specialist but not a lucid source of general knowledge, I have taken liberties in simplifying their classification. The following classification is based on living taxa, and the present superfamilies differ slightly from those of Gaffney & Meylan.

Suborder Cryptodira

The lateral and posterior emargination of the dermal skull is moderate. There is nearly always a well-defined temporal (zygomatic) arch from the posterior orbital rim to the anterior rim of the tympanic aperture. The trochlear apparatus for the mandibular adductor tendon is formed by the antero-dorsal ridge of the otic capsule, comprising the prootic, the quadrate or both, and is a true synovial joint. The neck flexes in a vertical (sagittal) curve and is usually retractile. The cervical central articulations are well-developed, always broad and are typically double on posterior cervicals. The pelvis is not fused to the plastron. The mesoplastron is never present. The posterior cervical spines are low, and the postzygopophyses are wide apart.

Superfamily Chelydroidea. The North American family Chelydridae includes two monotypic genera of snapping turtles. Inclusion of the big-headed turtles of Asia (family Platysternidae, one monotypic genus) in this superfamily is moot.

Superfamily Chelonioidea. The typical marine turtles occur in all temperate and tropical seas. The family Cheloniidae includes five genera, all of which are present in Australian waters.

Superfamily Dermocheloidea. The family Dermochelyidae includes only the monotypic genus *Dermochelys*. The leatherback turtle, *Dermochelys coriacea*, has a cosmopolitan distribution in arctic, temperate and tropical seas.

Superfamily Trionychoidea. The softshelled turtles of North America, Asia and Africa are placed in the family Trionychidae. Seven genera are recognised. The pig-nosed turtle *Carettochelys insculpta*, sole member of the family Carettochelyidae, is the only freshwater cryptodire in Australia. It occurs also in New Guinea.

Superfamily Kinosternoidea. One species, the River Turtle, *Dermatemys marwi*, is placed in the Family Dermatemydidae, of central America. Four genera of the related musk turtles, family Kinosternidae, occur in North, Central and South America.

Superfamily Testudinoidea. Most of the pond turtles of the family Emydidae are partly aquatic. Nine of the 10 genera occur in North America, and *Emys* occurs in Europe. The closely related batagurid pond turtles, family Bataguridae, are mostly Oriental (22 genera), but *Rhinoclemys* occurs in central and adjacent South America. Australia is the only continent lacking any land tortoises of the widespread family Testudinidae. This family comprises 11 genera, five of which occur only in Africa.

Suborder Pleurodira

The lateral emargination of the dermal skull roof is usually extreme, and the posterior emargination is absent or slight. The temporal arch is variable, absent or posteriorly displaced in most chelids. The trochlear apparatus for the mandibular adductor tendon is formed by the lateral pterygoid process; the lubricatory capsule is an evagination of the buccal mucosa and not truly synovial. The neck flexes laterally to either side and is tucked under the anterior edge of the carapace, but is not truly retractile. The cervical central articulations are well-developed, but are never double. The pelvis is always fused to the plastron. Mesoplastra may be present or not. The posterior cervical spines are relatively high, and the postzygapophyses are closely approximated or fused.

Members of the family Pelomedusidae lack nasal bones, and the vomer is absent in extant forms. The lateral temporal arch includes the jugal and quadratojugal bones. The second cervical centrum is biconvex, and the remainder are procoelous or have saddle articulations. A mesoplastron is present in some taxa. The normal number of chromosomes is 2n = 26 to 36 (by virtue of microchromosomal reduction) (Bull & Legler 1980). There are seven species in two genera in South America, two genera and 16 species in Africa, and one monotypic genus in Madagascar.

In the family Chelidae, nasal bones are present in all genera but *Chelus*, and the vomer is present. A posterior parietosquamosal arch is present (absent in *Chelodina*), and the quadratojugal is absent. The centra of the fifth and eighth cervical vertebrae are biconvex, and saddle joints are never present. A mesoplastron is absent. The normal chromosome number is 2n = 50 to 64 (96 in triploid *Platemys*), 2n = 50 in Australian shortnecks and 2n = 54 in Australian longnecks (Bull & Legler 1980). The family occurs in South America, Australia, New Guinea and Roti (Lesser Sunda Islands). There are eight genera and approximately 29 species in Australia; four of these genera and six endemic species are present in New Guinea. Five genera and approximately 20 species occur in South America.

KEY TO THE GENERA OF AUSTRALIAN TURTLES

Keys can consist of characters that diagnose the taxa or simply of characters which identify a taxon within geographic limits. Diagnostic characters of Chelonia are often internal. The following key is utilitarian and uses characters that may have significance only within Australia. Internal characters, when used, are coupled with external characters. Three of the eight genera of freshwater chelids recognised in Australia are undescribed (Legler in press); two are provisionally referred to as 'groups', and one is termed the 'shortnecked alpha'.

Key to the genera of Australian turtles

1 (a) Forelimbs flipperlike (Fig. 15.3A); claws reduced and atypical; neck retracted vertically; pelvis not fused to plastron. Cryptodira 2

(b) Forelimb bearing a webbed hand with four or five claws (Fig. 15.3B), not flipperlike; neck retracted laterally; pelvis fused to plastron. Pleurodira: Chelidae 8

2 (a) Shell bearing discrete, regular, enlarged cornified scutes (Fig. 15.3C). Cheloniidae 4

(b) Shell lacking discrete scutes (Fig. 15.3D) or covered with numerous small, pebblelike osteoderms (Fig. 15.3E), not discrete enlarged scutes 3

3 (a) Nostrils at tip of fleshy pig-like proboscis; entire shell covered by undivided soft skin; no discrete scales on top of head (Fig. 15.3D); freshwater and estuarine habitats of north-western Australia and New Guinea. Carettochelyidae .... *Carettochelys insculpta* (Pl. 3.9)

(b) Nostrils flush with surface of snout; no proboscis; head bearing discrete enlarged scales; shell covered with many small osteodermal scales (Fig. 15.3E); northern Australia (Dermochelyidae) .... *Dermochelys coriacea* (Pls 3.7, 3.8)

4 (a) Four lateral scutes on each side of carapace (Fig. 15.3C) 5

(b) More than four lateral scutes on each side of carapace (Fig. 15.3F) 7

5 (a) Anterior part of head narrow, attenuated and beak-like in profile; two pairs of prefrontal scales (Fig. 15.3G) .... *Eretmochelys* (Pl. 3.2)

(b) Anterior part of head rounded and blunt in profile; one pair of prefrontal scales (Fig. 15.3H) 6

6 (a) Four or more postocular scales; large scales on eyelid; anterior surface of antebrachium covered by medium to large scales (no broad central band of minute scales) (Fig. 15.3I) .... *Chelonia* (Pl. 3.5)

(b) Three postocular scales; many small scales on eyelid; anterior antebrachium with a perimeter of large scales surrounding a broad median area of minute scales or wrinkled skin (Fig. 15.3J) ..... *Natator* (Pl. 3.4)

7 (a) Four enlarged inframarginal scales on each bridge, each usually bearing a pore near posterior border (Fig. 15.4A); six or more lateral scutes on each side; mandibular rami bow outward; maxillary bones separated by vomer; predominantly greyish (young almost black) .... *Lepidochelys* (Pl. 3.6)

(b) Three enlarged inframarginals on each bridge, never with pores (Fig. 15.4B); less than six lateral scutes on each side; mandibular rami straight or bowed inward slightly; maxillary bones in contact; dorsal colouration predominantly reddish brown .... *Caretta* (Pl. 3.1)

8 (a) Manus with four claws; gulars in contact; intergular not on anterior edge of plastron (Fig. 15.4C) (longnecked chelids) 9

(b) Manus with five claws; gulars not in contact, intergular on anterior edge of plastron (Fig. 15.4D) (shortnecked chelids) 10

9 (a) Plastron extensive, almost covering the anterior orifice of shell (or retracted soft parts) in ventral view (Fig. 15.4E); neck shorter in comparison to shell; dorsum of neck with many blunt conical tubercles; musk secretion copious and strongly odoriferous .... *Chelodina longicollis* group (Pl. 3.11)

(b) Plastron less extensive, covering only about half of anterior orifice of shell (or retracted soft parts) in ventral view (Fig. 15.4F); neck longer in comparison to carapace; skin of neck lacking obvious tubercles; musk secretion slight, odour noticeable, but not strong .... *Chelodina expansa* group

10 (a) Intergular excludes both gulars and humerals from midline contact; temporal roofing of skull extensive; head shield covers most of head .... *Pseudemydura* (Pl. 3.13)

(b) Intergular separates only gulars, humerals in contact; temporal roofing of skull substantially emarginate from below; head shield variable but never covering most of head 11

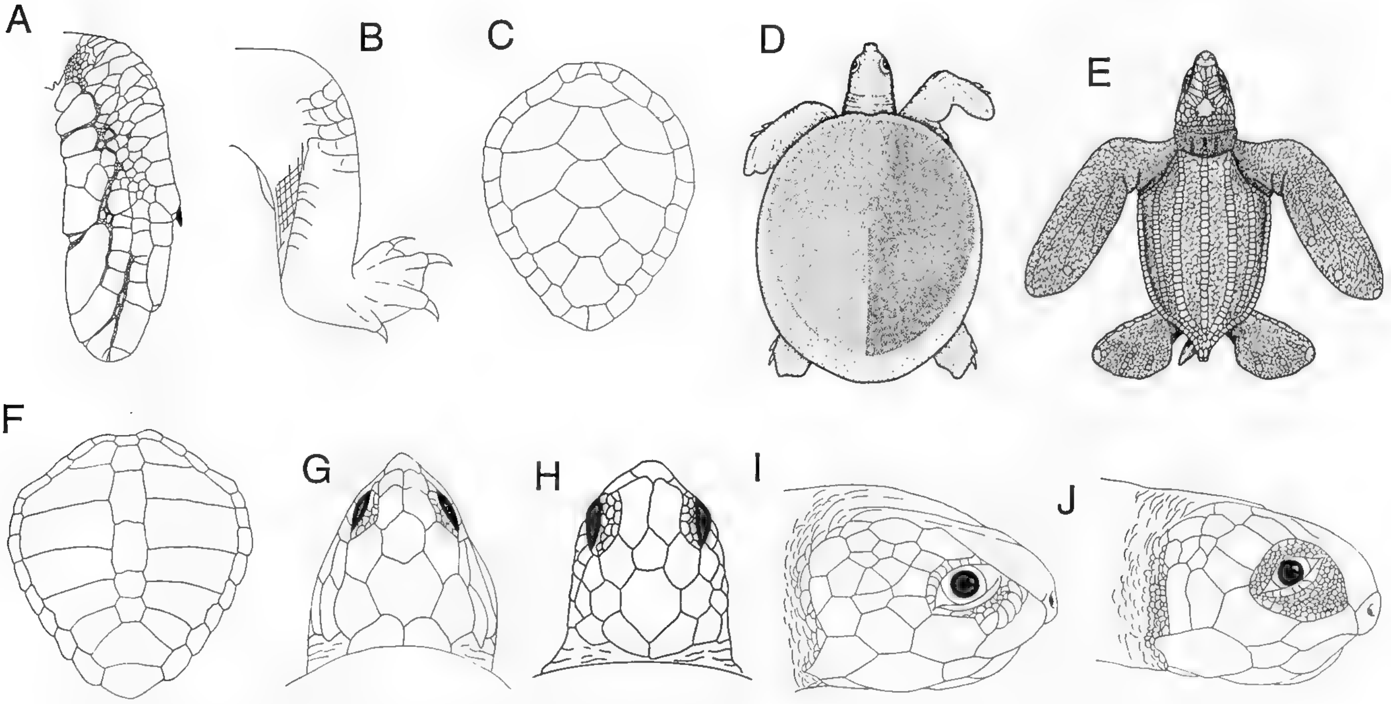

Figure 15.3 Key characters for chelonians. Pertinent features of elements A–J are noted in the key above and on the previous page.
[A-C, F, G, I, J, H.G. Cogger; D, E, H, D. Wahl]

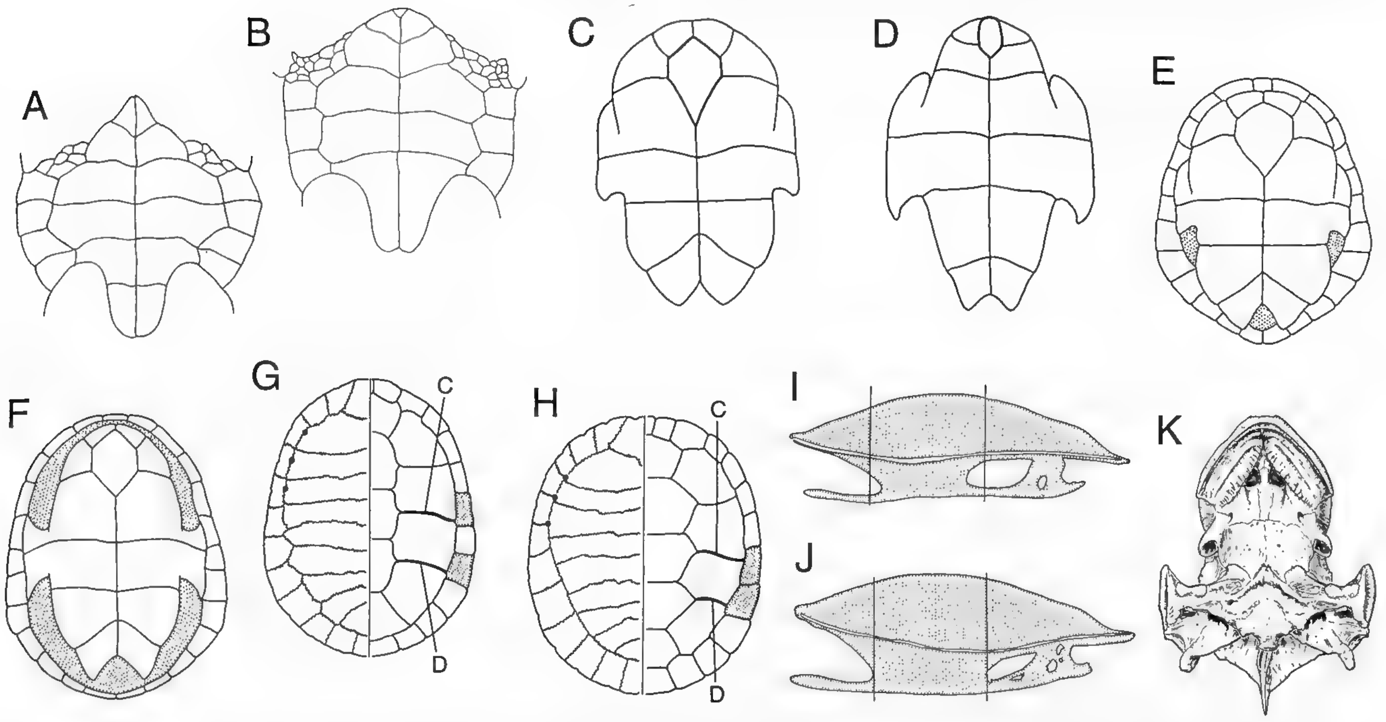

Figure 15.4 Key characters for chelonians. Pertinent features of elements A–K are noted in the key adjacent and below. Black dots on the marginal/costal sutures of G and H indicate positions of rib tips. [K, L, H.G. Cogger; M-T, T. Wright; U, J. Legler]

11 (a) Interlateral seams C and D contact posterior parts of marginals 6 and 8; rib tips of costals 2 to 4 articulate with gomphoses in centres of peripherals 4 to 6 (Fig. 15.4G); a distinct white, ivory or silver iris at all ages .... *Rheodytes* (Pl. 3.12)

(b) Interlateral seams C and D contact marginals 7 and 8; rib tips of costals 2 to 4 articulate in or near interperipheral sutures (Fig. 15.4H) ; iris variable, if pale then yellowish, not white or ivory 12

12 (a) Shell shallower and/or bridge shorter (Fig. 15.4I); always a pale contrasting iris; never any median ridging on the triturating surfaces of jaw sheaths 13

(b) Shell deep and spacious; bridge long (Fig. 15.4J). Eye dark and lacking contrast at all ages; a well-defined median ridge on the triturating surfaces of the jaw sheaths (Fig. 15.4K) .... *Elseya dentata* group

13 (a) Tail distinctive and large: precloacal length greater than postcloacal length at all ages; tail laterally compressed; cloacal orifice a longitudinal slit; tail length up to 53% of carapace length in adult males .... 'Shortnecked alpha'

(b) Tail normally chelid: precloacal length greater than postcloacal length only in adult males; tail rounded in cross section, not laterally compressed; cloacal orifice round; maximum tail length always less than half carapace 14

14 (a) A well-defined head shield at all ages; dorsum of neck bearing many sharp tubercles; gular barbels always well-defined and longer than wide; rear edge of carapace may be denticulate at any age .... *Elseya latisternum* group

(b) Distinguishable headshield only in the largest adults; neck usually smooth, low rounded tubercles at most; gular barbels absent, never longer than wide; rear edge of carapace never denticulate ... *Emydura* (Pl. 3.10)

16. MORPHOLOGY AND PHYSIOLOGY OF THE CHELONIA

John M. Legler

Turtles are the subject of some of the earliest accounts of vetebrate anatomy, for example Bojanis (1819). Much of the work on turtle anatomy was done in Europe before 1920. The following important anatomical studies include but do not emphasise Australian turtles. Hoffman (1890) commented on the Australian chelid genera *Chelodina* and *Emydura* and several South American chelids, and Siebenrock (1897) discussed the skull of *Chelodina longicollis*. More recently, Schumacher (1973) described the jaw musculature of *Chelodina longicollis* and *Emydura* species and Walther (1922) presented a thorough anatomical study of a single specimen of *Carettochelys insculpta*. Ashley (1955) and Bojanus (1819) described and illustrated typical turtle anatomy (*Pseudemys* and *Emys*), which is applicable to turtles of both suborders. Surveys of anatomy and physiology prepared before the middle of this century are based largely on the common or easily available taxa (for example *Emys*, *Testudo*, *Chrysemys* and *Chelydra*) in Europe, Asia and North America. Australian turtles received attention in direct proportion to their availability in collections outside Australia. The expansion of modern biological studies and especially Australian chelids since the 1950s essentially began with Goode (1967).

Terminology for chelonian shell structures varies. That standardised by Carr (1952) is used here (Figs 16.1, 16.2). Unpublished data and observations, especially for Australian chelids, are drawn from the author's research, and appear in statements which lack citations, unless otherwise indicated.

EXTERNAL CHARACTERISTICS

Turtles range widely in size. Using carapace length as a basis for comparison, the smallest are the North American *Sternotherus* sp. and *Clemmys muhlenbergi*, which mature at lengths of less than 100 mm. *Dermochelys coriacea* (Pl. 3.7, 3.8) is the largest living turtle, with a maximum length of 2.4 m and a maximum weight of 919 kg (Morgan 1989) and ranks with the largest living reptiles. *Chelonia mydas*, largest of the cheloniid marine turtles, can attain a length of 1.2 m (Pl. 3.5). Freshwater turtles are more modest in size, and few attain lengths exceeding 300 mm. Most adults longer than 300 mm considered large. One of these is *Carettochelys*, which grows to about 500 mm in length, and lengths exceeding 400 mm are quite common in Asiatic river batagurids, trionychids and chelydrids. The smallest Australian chelids are *Pseudemydura umbrina* (smallest female 120 mm; Burbidge 1967; Pl. 3.13, 3.14) and male *Emydura* sp. (approximately 100 mm; Cann & Legler 1993). Tortoises attain a moderately large size on islands, such as the Galapagos, but they never reach a size at which they become graviportal.

Adult males of Recent turtles may be smaller or larger than females, or equal in size (Berry & Shine 1980). This range in dimorphism in size is seen in Australian chelids (Chapter 21). In some batagurids and emydids there are some striking sexual differences in colour and pattern, as illustrated by Ernst & Barbour (1989). The sexes of Australian chelids differ mainly in form rather than colour, though the orange head pattern of male *Rheodytes* is characteristic. The shell of females tends to be deeper than that of males, in which the tail is more robust.

BODY WALL

The chelonian shell is an extremely specialised body wall . The shell is *ipso facto* protective, and this must be considered its chief selective advantage. If *Dermochelys* is excluded, the variations

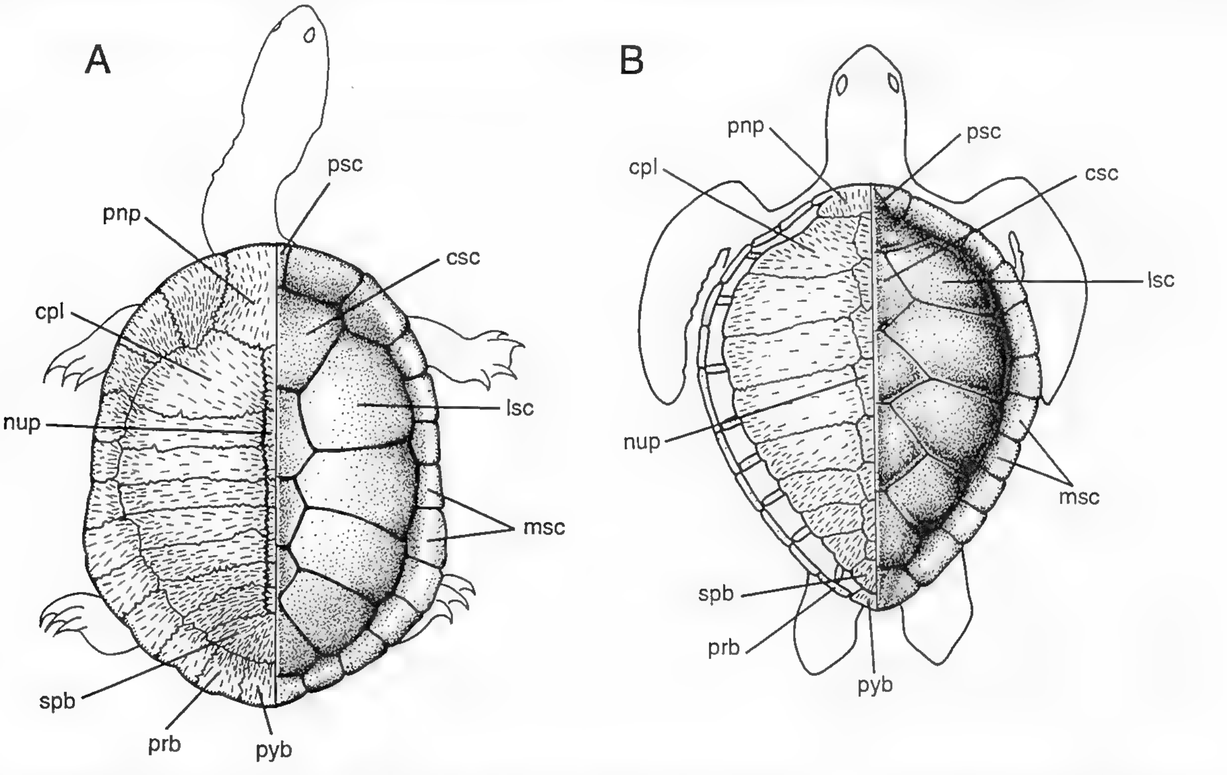

Figure 16.1 Epidermal laminae (right) and bony elements (left) of the carapace. A, *Chelodina longicollis*; B, *Chelonia mydas*. **cpl**, anteriormost of eight costal plates; **csc**, anteriormost of five central scutes; **lsc**, anteriormost of four lateral scutes; **msc**, marginal scutes; **nup**, neural plate; **pnp**, preneural plate; **prb**, posteriormost of 11 peripheral bones; **psc**, precentral scute; **pyb**, pygal bone; **spb**, suprapygal. Interlaminal seams are shown by solid lines and irregular lines indicate sutures. (After Cogger 1992)

[T. Wright]

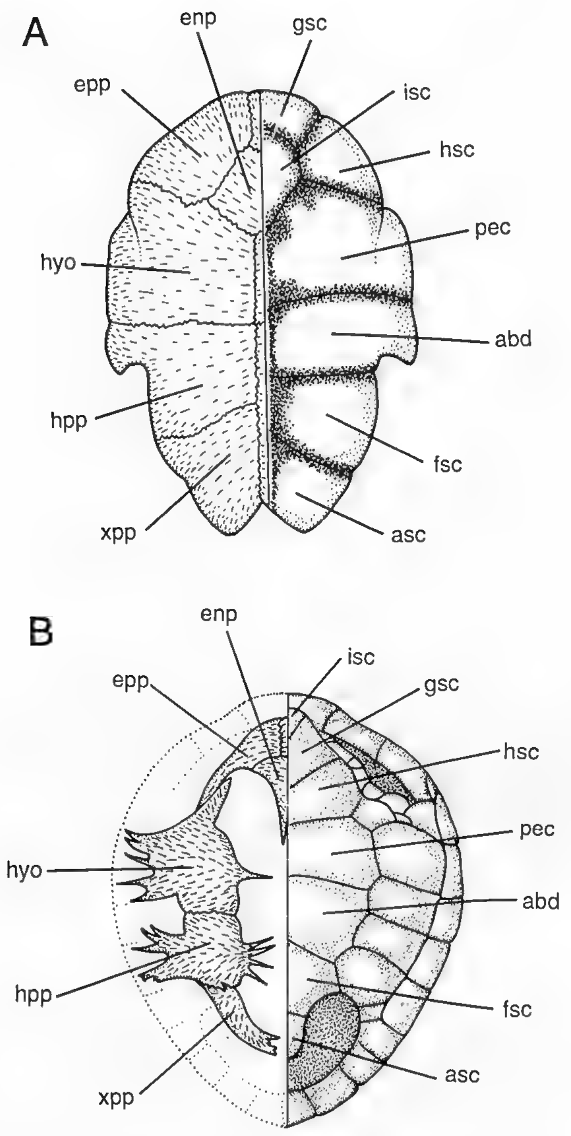

Figure 16.2 Bony elements of the plastron (left) and epidermal laminae (right). **A**, *Chelodina longicollis*; **B**, *Chelonia mydas*. **abd**, abdominal scute; **asc**, anal scute; **enp**, entoplastron; **epp**, epiplastron; **fsc**, femoral scute; **gsc**, gular scute; **hsc**, humeral scute; **hpp**, hypoplastron; **hyo**, hyoplastron; **isc**, intergular; **pec**, pectoral; **xpp**, xiphyplastron. Interlaminal seams are shown by solid lines and sutures by broken lines. (After Cogger 1992) [T. Wright]

seen in fossil and recent turtles are relatively slight and the basic plan and its homologies have not changed. Zangerl (1969) reviewed the structure of the chelonian shell. The shell is a combination of discrete bony and epidermal elements. Some of the former comprise an internal endochondral element fused to an external dermal element. Endochondral elements have cartilaginous precursors, and dermal precursors ossify in the dermis. The epidermal scutes are normally keratinous, thin, and separated from the underlying bony elements by only a thin layer of soft, vascular, germinative tissue.

The bony elements of the carapace consist of a mid-longitudinal series of neural elements flanked on each side by a lateral costal series, all surrounded by a peripheral series (Fig. 16.1A, B). Fusion occurs between the neural plates and the neural arches of the vertebrae, and between the costal plates and the underlying ribs. The peripheral elements have no endoskeletal component. The bony parts of the carapace articulate suturally via their dermal components, and usually do not co-ossify.

There are eight costals on each side. The main shaft of the rib is visible only as a slight bulge on the inside of the element, but the head of the rib, which articulates with the vertebral centrum, and the tip of the rib are clearly visible. The tip articulates with a pit or groove in a peripheral bone or between two peripherals. There are 10 dorsal vertebrae, and 10 pairs of ribs. The first and second ribs are fused to the first costal element. The ninth and tenth ribs are fused with the eighth costal element.

The most anterior and posterior of the five to eight neural elements (Fig. 16.1) are not associated with vertebrae. The nuchal bone is a large keystone for the anterior end of the carapace. The pygal bone, situated posteriorly, is preceded by a variable number of suprapygals. The number of neurals varies but is usually eight in turtles with a full series. Most Australian chelids lack neurals, though vestiges occur in some (Rhodin 1977), and they are present in South American chelids. In the absence of neurals, the costal elements articulate with each other and with the neural arches along the dorsal midline. There are usually 11 pairs of peripheral bones in recent turtles (Fig. 16.1). The number is reduced in kinosternoids and trionychoids, and there are 10 in the genus *Carettochelys* (Fig. 22.1A).

The plastron typically consists of nine bony plates articulated suturally. These are the unpaired anterior entoplastron flanked by the paired epiplastra and the paired hyoplastra, hypoplastra and xiphyplastra (Fig. 16.2). In a few extant pelomedusids and some fossils, a pair of mesoplastra occurs between the hyo- and hypoplastral elements.

The hyoplastral and hypoplastral elements articulate with peripheral bones, usually between the third and seventh, on each side via two vertical or diagonal pillars of bone called the axillary and inguinal plastral buttresses. These buttresses form the bridge, an isthmus of bone between the carapace and plastron. Buttresses are substantial and strong in most Australian chelids. Sutural articulations within the plastron and between the plastron and the buttresses may loosen and become movable joints or hinges that can partly, or completely, close the shell.

The anterior plastral plates incorporate the dermal components of the primitive pectoral girdle. The interclavical fuses to a dermal plate to become the entoplastron, and the clavicles do likewise with the epiplastra. Vestiges of pectoral elements can be seen in the formed plastral elements. The rest of the plastron may be derived from the gastralia, or belly armour.

Superimposed upon the bony shell are epidermal scutes (also termed laminae or shields). These are hardened or cornified layers of the epithelium separated by depressions called seams. Most scutes overlap two or more bony elements and further increase the strength of the shell. The scutes are arranged in series similar to the bones: the median central scutes overlap neurals and costals; the lateral scutes on each side overlap the costals and the peripherals; and a circumferential series of marginal scutes overlaps the peripherals (Fig. 16.1). The precentral is an unpaired anterior scute in the marginal series. Among extant turtles the usual numbers of centrals, laterals and marginals are 5, 4 + 4 and 12 + 12, for a total of 38 carapace scutes, including the precentral. There is often an extra scute between the fourth and fifth central scutes in the *Chelodina expansa* group. Extra lateral scutes occur in some marine turtles. Cryptodires with reduced peripheral bones also have a reduced number of marginal scutes. Trionychids and *Carettochelys* have no defined scutes at all (but see Zangerl 1959), and the entire shell is covered by undivided soft skin (Pl. 3.9).

Chelonians typically have 12 or 13 scutes on the plastron (always 13 in chelids) (Fig. 16.2A): an unpaired intergular plus 6 pairs of large scutes termed the gulars, humerals, pectorals, abdominals, femorals and anals, respectively. Most cryptodires lack an intergular scute (Fig. 16.2B). Most aquatic turtles shed scutes periodically as they grow; scutes can also wear away gradually. Moll & Legler (1971) describe the process of bone and scute growth and scute shedding. The frequency of scute shedding is variable among species of Chelidae (see Chapter 21) and irregular in testudinid land tortoises and terrestrial emydids. In trionychids and *Carettochelys* the epidermal covering of the shell is not divided into discrete scutes and epidermal shedding occurs, presumably by the gradual exfoliation of individual cells.

The skin of turtles is soft, mostly smooth and divided only by shallow grooves. Scales are present on the feet, antebrachium, crus and, to a lesser extent, the tail and head. Many chelids have a well defined, cornified shield on the dorsal surface of the head where soft skin is in direct apposition to the roofing bones of the skull (Pl. 3.14). The head shield is often distinctly coloured and textured.

A variety of integumentary organs occurring in the skin of turtles can be considered in two broad categories: invaginations and evaginations (or integumentary appendages) (Legler & Winokur 1979; Winokur 1982b; Winokur & Legler 1974, 1975).

Integumentary appendages are projections of the body surface which are thought to function as mechanoreceptors. They are used in foraging and perhaps a variety of other tactile ways (see below). Winokur (1982b) recognised three kinds of integumentary appendages in chelonian skin: tubercles, barbels and fimbriae. Each consists of epidermis and a core of dermis and subcutaneum with its blood vessels and nerve twigs, but lacks a glandular, skeletal or muscular component.

Tubercles are usually blunt-tipped, short, conical extensions of the integument (Pl. 3.12, 3.14) that are slightly movable; they may also be cornified and sharp-tipped. Tubercles occur chiefly on the neck and tail and are often arranged in dorso-lateral rows. Gular barbels, also termed mental barbels and chin barbels, are single or paired, usually blunt-ended, elongate cylindrical or conical projections just posterior to the mandibular symphysis. They can be moved easily by contact with a foreign object and probably by water flow. Well-developed barbels occur in the Chelydridae, Kinosternidae, Pelomedusidae and Chelidae and could have evolved independently in these four groups. Murphy & Lamoreaux (1978) described the use of barbels in the mating behaviour of Australian chelids (Fig. 21.8). Fimbriae are elongate extensions of the integument, normally flattened and flexible, and often branched or bearing a complex secondary topography. Fimbriae reach the zenith of their development in the South American chelid, *Chelus fimbriatus*, and in North American Alligator Snapping turtles (*Macroclemys*). In these species the fimbriae play a role in camouflage. Hartline (1967) demonstrated a sensory function for the fimbriae of *Chelus fimbriatus*.

Invaginations of the chelonian integument include mental glands (Winokur & Legler 1975), rostral pores (Winokur & Legler 1974) and follicular tubercles (Legler & Winokur 1979). Rostral pores are invaginations of various depths and complexity in the epidermis of the narrow band of skin between the nostrils. They may be large and melanistic or cryptic. They occur in all families of turtles except the marine turtles and the Carettochelyidae. In longitudinal sections the epidermal invaginations may be simple and cylindrical or highly branched. Dead cells from the stratum corneum tend to fill the lumen of the pore and sometimes form a projecting plug of waxy to keratinous tissue. The dermal papillae associated with rostral pores are highly innervated. Rostral pores may facilitate deep mechanical stimulation of the dermal papillae via the dense core of keratinised tissue. A follicular tubercle is essentially a neck tubercle containing a deep invagination similar to a rostral pore. Follicular tubercles have been observed only in the *Elseya latisternum* group. A follicular tubercle would combine the sensory functions of a barbel and a rostral pore.

Mental glands are paired integumentary glands (or glandular vestiges) on the anterior throat skin. They occur in the Emydidae, Bataguridae, Platysternidae, and Testudinidae. They are highly specialised pheromonal structures in some testudinids, but are usually cryptic and only marginally secretory in the other families. There are no mental glands in chelids. Mental glands and rostral pores may be vestiges of glandular structures in primitive amniotes that have lost their original function but have been re-exploited in groups where the primordia persist.

Musk glands are located within the shell, between the buttresses, in the angle formed by the peripheral bones. They develop from ectodermal invaginations that migrate internally before the shell forms. During ontogeny the ducts develop a *tunica muscularis* of striated muscle and are innervated by the posterior rami of the inner intercostal nerves (Ogushi 1913; Stromsten 1917; Vallén 1944). Their ducts go to orifices near the union of the marginal scutes and the soft skin anterior and posterior to the bridge. The ducts usually pass through osseous foramina or grooves in the buttresses. Musk glands occur in all turtles except the Testudinidae and the *Chrysemys* complex of the Emydidae. The taxonomic occurrence of musk glands suggests that they are primitive structures and that their absence in testudinids and most emydines is a derived condition.

Ten morphological patterns of glands, ducts, and orifices were recognised by Waagen (1972). Chelids have a 'pattern 3' type in which there is a gland at each end of the sternal cavity on each side and ducts pass through osseous canals in the buttresses. Orifices lie between the third and fifth, and eighth and ninth marginal scutes. This pattern also is found in most pelomedusids and in all cheloniids, except *Lepidochelys*. In *Carettochelys* there are three glands: an anterior gland at the third rib tip, with its orifice at the anterior edge of the fourth peripheral bone; a doubled axillary gland at the fourth rib tip, its two ducts anastomosing on a single orifice at the fifth and sixth peripheral bone; and an inguinal orifice at the eighth without any glandular connection (one specimen dissected). Zangerl (1941) described and illustrated musk glands in *Chelydra*.

The formation of musk is probably holocrine. Eisner, Jones, Meinwald & Legler (1978) isolated the following compounds from the musk of *Chelodina longicollis*: oleic acid, linoleic acid, palmitoleic acid, palmitic acid, stearic acid, citronellic acid and beta-ionone. *Chelonia mydas* produces PAS-positive, protein-rich nonacidic musk. In *Sternotherus odoratus*, droplets of free lipid are present in the musk (Ehrenfeld & Ehrenfeld 1973). Studies on the function of the odiferous musk of *Chelodina longicollis* are inconclusive, although it is suspected of being a deterrent to predators (Kool 1981; Dorrain & Ehmann 1988; see Chapter 21).

SKELETAL SYSTEM AND MUSCULATURE

The pectoral girdle is distinctive and tri-radiate. The scapula is L-shaped, and its contribution to the glenoid cavity lies at the angle. One of its rod-like limbs extends dorsally to the inside of

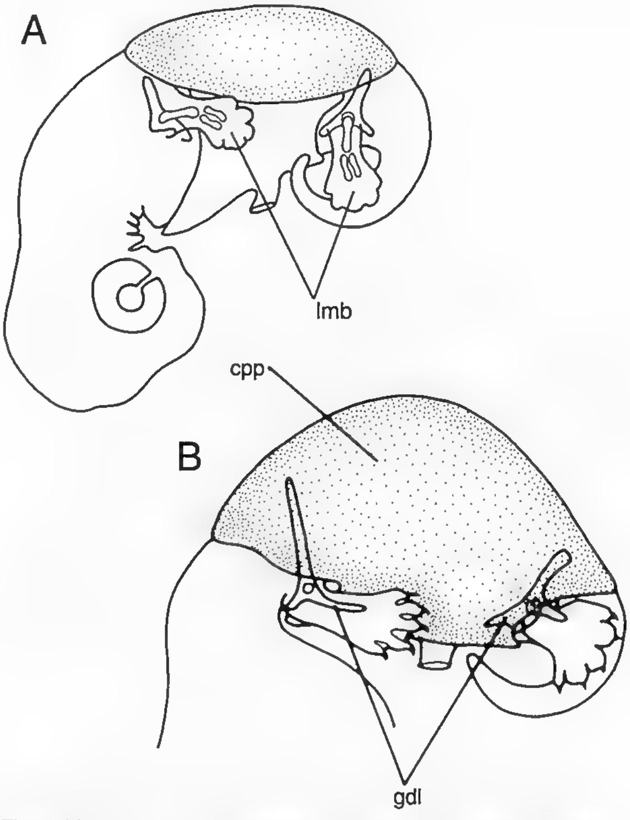

Figure 16.3 Relationship of the carapace primordium to the limbs and girdles in *Chelydra* embryos. A, at 10 mm; B, at 20 to 25 mm. cpp, carapace primordium; gdl, girdle; lmb, limb. (After Ruckes 1929) [T. Wright]

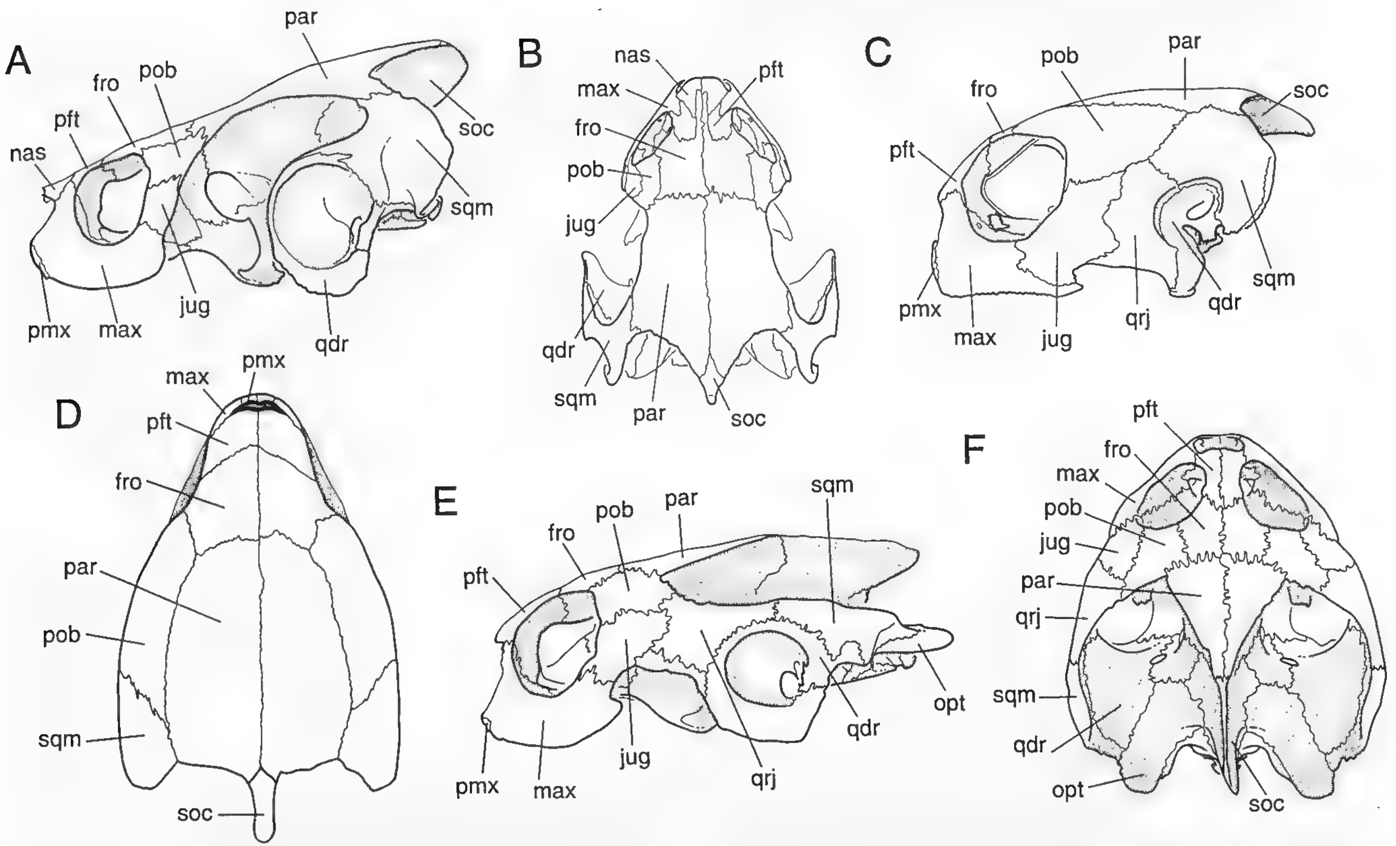

Figure 16.4 The extent of temporal roofing in the turtle skull. **A**, *Emydura macquarii*, in lateral view, showing emargination from below; **B**, *Emydura macquarii* in dorsal view; **C**, *Chelonia mydas*, in lateral view, showing little emargination; **D**, *Chelonia mydas* in dorsal view; **E**, *Podocnemis* sp., in lateral view, showing emargination from behind; **F**, *Podocnemis* sp. in dorsal view. **fro**, frontal; **jug**, jugal; **max**, maxilla; **nas**, nasal; **opt**, opisthotic; **par**, parietal; **pft**, prefrontal; **pmx**, premaxilla; **pob**, postorbital; **qdr**, quadrate; **qrj**, quadratojugal; **soc**, supraoccipital; **sqm**, squamosal. [T. Wright]

the carapace and the other arm, the acromion process, extends antero-medially at right angles. The coracoid bone joins the scapula at its angle and contributes to the glenoid cavity. It extends postero-medially, in the same plane as the acromion. The arms of the pectoral girdle therefore bear a nearly rectilinear relation to one another (as do the three edges in one corner of a box), and the glenoid cavity lies at the outside apex (Fig. 15.1).

The pelvis is mobile and free of direct shell attachments in cryptodires. In pleurodires, the pubis and ischium fuse to the xiphyplastron, and the ilium fuses with the eighth costal element. The top of the ilium in pleurodires is robust and triangular in cross section at the iliocostal interface. The joint contains soft tissue and may be a partially mobile symphysis. The plastropelvic joints are sutural. All the bones of the pelvis contribute to the acetabulum. In turtles the pubis and ischium do not have a substantial lateral exposure (as in other reptiles), but are folded ventro-medially, with most of the lateral face directed ventrally.

The extreme modification of the tetrapod body plan, resulting in the shell and internal position of the girdles, must have been tremendously advantageous; the shell may be reduced but it is never lost. In features other than the shell, turtles have remained remarkably generalised in most skeletal and visceral structures. These generalised traits are primitive and support the idea that turtles could be the closest living relatives of prototypic amniotes.

It was once thought that the limb girdles had migrated to the inside of the rib cage, both ontogenetically and phylogenetically (Wagner 1922; Ewert 1985). This has been disproved by developmental studies. Turtle limb buds appear on a typical, tubular vertebrate embryo. The carapace and plastron primordia then appear as circumferential ridges above and below the limb buds. The carapace primordium is oriented in the frontal plane and the ribs, which appear slightly later, are short, straight and horizontal. The precursors of the limb girdles probably do not move at all as the carapace primordium radiates and overgrows the girdle rudiments before turning ventrally and actually enclosing them. During this process the characteristic widening of the body occurs (Ruckes 1929; Ewert 1985) (Fig. 16.3).

The chelonian skull is anapsid and toothless. Roofing of the temporal region over the mandibular adductor muscles ranges from complete to nil, but there is no true fenestration as there is in other reptiles. The edges of the temporal roof are emarginated from behind, from below or both. Posterior emargination interrupts the parietosquamosal contact and, when coupled with at least slight ventral emargination, creates a lateral temporal arch ('zygomatic' arch) formed by combinations of the quadratojugal, jugal and postorbital (Fig. 16.4E, F). Posterior emargination is typical of most cryptodires and of the pelomedusids among the pleurodires. In some cryptodires the lateral arch has been lost entirely. All chelids show a substantial ventral emargination which eliminates the quadratojugal and leaves no bony bridge between the quadrate and the posterior rim of the orbit (Fig. 16.4A, B). The emargination is least in *Pseudemydura*, leaving a dorsal roofing that is extensive. In other Australian shortnecks the emargination is greater, leaving a posterior temporal arch of moderate width. Ventral emargination is complete in both groups of *Chelodina*, in which parietosquamosal contact has been lost completely. South American chelids retain a thin posterior temporal bar. The two families of marine turtles show little or no emargination (Fig. 16.4C, D) (Boulenger 1889; Gaffney 1979).

In all Recent turtles teeth have been supplanted by horny, epidermal sheaths over the jaw bones. These sheaths have sharp, vertical tomial edges, the lower sheath fitting inside the upper one when the jaws are closed, thereby creating an efficient shearing mechanism. Medial to the tomia there is a horizontal triturating or crushing surface. Upper and lower triturating surfaces occlude and in some turtles are modified for crushing seeds or molluscs. In both suborders there may be one or two median alveolar ridges on the triturating surfaces. These have evolved independently several times, for example, in *Dermatemys*, *Batagur* and the *Elseya dentata* group, and are associated with herbivory (Fig. 15.4U). Both the tomial edge and the triturating surfaces may develop serrations or pustules analogous to teeth.

The jaw musculature of turtles has a unique arrangement (Fig. 16.5). In all amniotes the mandibular adductors insert via a common tendon on, or near, the coronoid process of the mandible.

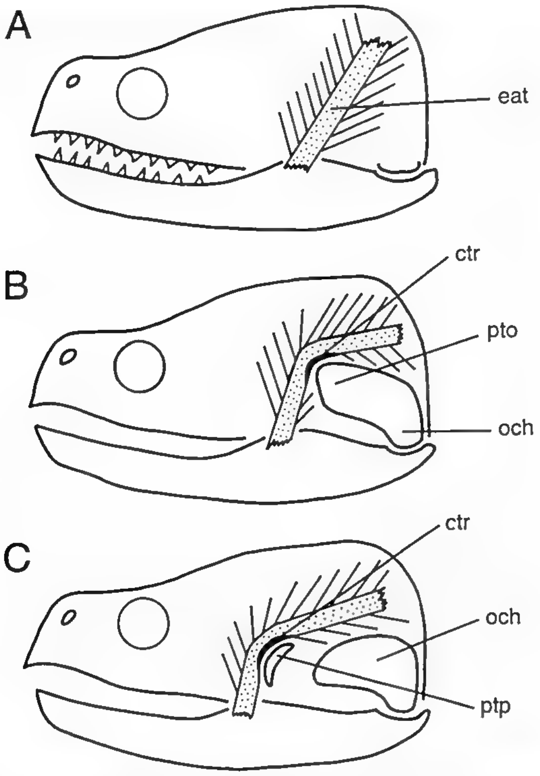

Figure 16.5 The course of the mandibular adductor tendon. **A**, non-chelonian reptiles; **B**, cryptodires; **C**, pleurodires. **eat**, external adductor tendon; **ctr**, cartilago transiliens; **och**, otic chamber; **pto**, processus trochlearis oticum; **ptp**, processus trochlearis ptergyoidei. (After Gaffney 1975) [T. Wright]

In non-chelonians the passage of this tendon to its insertion is direct and uninterrupted. In turtles the attachments remain the same, but the enlarged otic capsule creates an obstruction around which the muscles must pull. Force must be smoothly translated from a horizontal vector to a vertical one. Muscular efficiency is enhanced by using a trochlear (pulley) system and a sesamoid element (cartilage or bone) in the tendon. In cryptodires the trochlea is the antero-dorsal edge of the otic capsule and the lubricated contact with the sesamoid bone is synovial. In pleurodires the trochlea is formed by a lateral process of the pterygoid bone and the lubricated surface is formed by an evagination of the mouth lining (*ductus angularis oris* of the buccal mucosa).

The usual, and probably primitive, phalangeal formula of the manus and pes of turtles is 2,3,3,3,3 (or 2). All Australian chelids have the formula 2,3,3,3,3 for both manus and pes. Modifications in the flippers of marine turtles and *Carettochelys* result from elongation of phalanges (Romer 1956).

Intercostal spaces are filled with dermal bone in turtles, and the intercostal musculature has become obsolete. There is some evidence that striated muscle lies directly on the lung and is homologous to the intercostal muscles of other reptiles (George & Shah 1954). The homologues of the lateral belly muscles, *m. obliquus abdominis* and *m. transversus abdominis*, remain beneath the skin of the inguinal pockets and function in respiration (see Respiration).

LOCOMOTION

Locomotion is constrained in turtles by the rigid vertebral column, by the extent of the bridge and, in pleurodires, by the fusion of the pelvis to the plastron. Trunk movements of any kind are impossible and locomotion is achieved entirely by limb movements. All turtles can move on land and in water to some extent and most, including chelids, are rather efficient at both. Terrestrial and aquatic gaits in turtles have been analysed in substantial detail (Walker 1973, 1979; Zug 1971), but only the latter are described here.

Freshwater turtles swim with alternate movements of the front and hind feet. The forelimb and hindlimb on opposite sides provide propulsive force while their contra-lateral counterparts recover. At times, only the forelimbs are used and the hindlimbs act as balancers or rudders. Marine turtles and *Carettochelys insculpta* each show convergent modification of the front limbs as flippers; they are used simultaneously in a 'flying' motion for forward propulsion (Pl. 3.9). When chased, however, *C. insculpta* swims rapidly by moving the flippers alternately and coordinating them with the hind feet in a trot-type swimming gait.

Freshwater turtles typically escape towards the bottom in a long, curving path which is banked as 'tight' as the turtle can make it at top speed. At the bottom the turtle usually pauses momentarily, turns its body by obtaining purchase on the substrate, and swims off again at speed, usually in the opposite direction. This 'terminal reverse behaviour' has been observed in most freshwater turtles, including all Australian chelid genera except *Pseudemydura*.

Turtles seldom move rapidly in nature; movements are generally slow and deliberate with frequent pauses for rest, circumspection and feeding. Rapid movements are brief, quite obvious, and normally associated with feeding, aggression, or mating. Chelid turtles probably have no reason to swim long distances, unlike marine turtles which require greater precision and economy of energy.

FEEDING AND DIGESTIVE SYSTEM

Knowledge of natural diet of chelonians has accelerated since the development of stomach flushing (Legler 1977; Legler & Sullivan 1979). Most freshwater chelonians are opportunistically omnivorous as discussed in Chapter 17. The typical feeding behaviour of aquatic omnivores is quiet, unhurried prowling near the bottom, grazing on aquatic vegetation, investigating 'windfalls', and opportunistic lunges at small invertebrates.

Freshwater turtles employ two basic feeding techniques. In inertial feeding, the prey is grasped with the jaws, either deliberately or with a fast strike. After the prey is reorientated by repeated regrasping, it is gradually moved backward into the mouth by rapid forward movements of the head and neck. When the prey or food item is too large to swallow, all freshwater turtles will turn the head to one side and use the claws of one forelimb to tear the prey into more manageable fragments.

Suck and gape feeding involves a fast strike at the food object, depressing the hyoid apparatus, opening the mouth, and drawing the object into the mouth and pharynx, together with a substantial volume of water (Fig. 21.6). The hyoid movements rapidly and substantially increase the volume and reduce the relative pressure of the combined mouth and pharynx. *Chelus*, *Hydromedusa*, and the Australian longnecks use gape and suck feeding almost exclusively to ingest live animals small enough to pass into the mouth. In *Chelodina expansa* and *Chelus* the entire strike and initial ingestion phase is much too fast to follow with human vision. The action slows perceptibly when the mouth closes and swallowing begins. *Chelus* is significantly faster than any of the longnecked chelids. Stomach flushings from *Chelodina expansa* suggest that prey is selected on the basis of length. Objects of an appropriate size therefore may pass into the mouth without touching the jaws and they reach the stomach whole, undamaged and occasionally alive.

Some turtles have been observed to gather and swallow particulate matter by moving slowly at the surface with the mouth open. This behaviour (neustophagia) has been observed in *Podiocnemis* (Belkin & Gans 1968) and in *Emydura* (Legler 1976).

Parsons & Cameron (1977) reviewed the general internal topography of the gut and Luppa (1977) the histology and histochemistry. Jacobshagen (1920) presented a substantial study of the gut. The gut consists of a continuous tube connecting the mouth to the cloacal orifice. The internal topography of the gut is seldom simple and smooth. The various folds and ridges of the intestinal mucosa increase the internal surface area for secretion and/or absorption and act as distensive pleats. The major pattern of ridging and folding is usually longitudinal. Less commonly it is transverse or oblique, for example, in trionychids. The longitudinal folds probably allow free passage of food through the lumen whereas food would be impeded by transverse or oblique folds (Parsons & Cameron 1977).

Some mechanical breakdown is accomplished by the tomial edges of the jaw sheaths and any accessory alveolar ridging within the mouth. This usually has more of a crushing than a chopping effect and is of little use for fragmenting muscle tissue. Long blades of vegetation can be ingested whole by scoring them and then folding them repeatedly into masses that can be swallowed (Legler pers. obs.).

The tongue of chelids is smooth and simple and appears to have little function in feeding. Chelids and many other aquatic chelonians cannot, or do not, swallow out of water.

The oesophagus is a distensible tube of transmission from the pharynx to the stomach. Food travels through the oesophagus either whole or in large chunks. The tube has no known digestive function. Its lining consists typically of longitudinal folds. *Lissemys* is unusual in having transverse or oblique folds (Parsons & Cameron 1977). In marine turtles there are long, sharp, keratinised papillae, directed posteriorly. All Australian chelids possess uniquely developed oesophageal glands which are discussed in Chapter 21.

The stomach is sac-like and distinctly larger than adjacent parts of the gut. The *tunica muscularis* imparts thickness and firmness to the gastric wall. Most turtles have many broad, rugose, longitudinal folds in the gastric mucosa. *Lissemys punctata* and *Platemys platycephala* lack any trace of folds. The stomach is a holding vessel that receives, churns and partially digests materials passing into it from the oesophagus (Parsons & Cameron 1977).

The small intestine of all turtles is similar. Longitudinal folds form a zigzag pattern, which probably disappears as the tube is distended. Various smaller oblique and transverse cross-connections form a net-like pattern between the major folds. This pattern is most complex in the duodenum and becomes simpler and lower towards the colon, as the angles on the zigzags change from acute through obtuse angles to simple longitudinal folds near the end of the ilium. Trionychids appear to be an exception; *Lysemys punctata* the lacks folds, and those in *Apalone spiniferus* are low and oblique. All trionychids have a single large fold near the pylorus and smaller transverse folds near the end of the ilium (Parsons & Cameron 1977).

Parsons & Cameron (1977) found little uniformity in colonic structure except for a large lumen, generally reduced internal topography, and thin walls. They attribute some of the variation to different degrees of distension.

CIRCULATORY SYSTEM

The oval, nucleated erythrocytes make up 20 to 30% of blood volume and carry about the same amount of haemoglobin as mammals. Erythrocyte life span is 600 to 800 days in the cryptodire, *Terrapene* (Bellairs 1969; Dessauer 1970). The chelids *Chelodina longicollis* and *Emydura kreffti* have 508 to 583 erythrocytes/mm^3 x 10^{-3}, representing a packed cell volume of 21.0 to 29.5%. Erythrocytes are 17 to 22 µm long and 9.6 to 12.8 µm wide. Freshwater species have larger and fewer erythrocytes than terrestrial ones (Frair 1977). Dessauer (1970) presented a detailed and informative summary of plasma electrolytes, packed cell volume and organic constituents of the blood.

Three main arterial vessels, the 'aortic arches', emanate from the heart, and represent the embryonic fourth and sixth aortic arches. They are, from right to left, the right aortic arch, the left aortic arch and the pulmonary arteries. The right aortic arch gives rise to a massive brachiocephalic trunk which vascularises the forelimbs, head and neck, and some anterior viscera. The left aortic arch has only visceral branches. It vascularises most of the coelomic viscera via two major visceral trunks, the coeliac and mesenteric arteries, before it anastomoses with the right arch to form the dorsal aorta. This vessel gives rise to all other arteries in the posterior half of the body.

The systemic venous system drains into the right atrium via the sinus venosus, and the pulmonary system drains into the left atrium via the pulmonary veins. There is a renal portal system.

White (1976) classified reptilian hearts as crocodilian and non-crocodilian. Non-crocodilian hearts are often referred to as 'imperfectly' divided, or 'imperfectly' four-chambered, because the interventricular septum is structurally incomplete. Recent work shows that the non-crocodilian heart performs a separation of blood flow far more efficiently than its anatomy suggests (Webb 1972; Webb, Heatwole & de Bavay 1971, 1974; White 1976). The 'imperfection' in the ventricular structure actually permits cardiopulmonary options in turtles that would be impossible in the completely divided avian or mammalian heart. This scenario was predicted as early as 1873 by the work of Sabatier (White 1976).

White (1976) referred to the ventricle as a single chamber with three subdivisions: a cavum arteriosum, confluent with the left atrium via an atrioventricular valve, and a cavum venosum, valvularly confluent with the right atrium. These two chambers are incompletely separated by a vertical septum. The hiatus in this incomplete septum, the interventricular canal, is towards the head. The third subdivision is the cavum pulmonale, which is narrowly contiguous with the cavum venosum.

Cardiac flow has been studied in only a few chelonians, including the cryptodires, *Pseudemys scripta* and *Chelydra serpentina.* During normal air breathing, systemic venous blood is returned to the right atrium, then flows through the right atrioventricular valve into the cavum venosum and thence to the cavum pulmonale. From there it passes to the lungs via the pulmonary arteries for oxygenation, it is returned to the left atrium via the pulmonary veins, passes into the cavum arteriosum and then, via the interventricular canal, to the cavum venosum and into the two aortic arches. Some of the blood passing through the left atrioventricular valve is shunted across the interventricular canal and back into the pulmonary circuit during normal breathing. Therefore, under aerobic conditions, blood going to the lungs is more highly oxygenated than that entering the right atrium.

During a dive, when the lungs are not in use, most systemic blood flowing into the cavum venosum by-passes the cavum pulmonale and is routed directly into the aortae. This may be caused by vasoconstriction of the pulmonary arterial branches causing the cavum pulmonale to fill with blood and exert a back pressure.

The heart beats more slowly during a dive. If a turtle remains inactive, energy requirements are less than in air, and glycolysis and other anaerobic pathways then meet vital needs. Turtles store more tissue glycogen than other reptiles (Dessauer 1970). During extended submergence, oxygen tension in *Pseudemys scripta* drops to near zero. Carbon dioxide tension rises to 100 to 150 mm Hg, and reaches a plateau after 24 hours. The pH falls to 6.8, then continues to fall more slowly, and lactate levels increase (up to 50 mEq/l in 24 hours) throughout submersion (Dessauer 1970).

Turtles are remarkably tolerant to anoxia, exceeding that of all other tetrapod vertebrates (Dessauer 1970). Some *Chrysemys picta* have lived for three to four months underwater at 1.5° to 3.5°C. Anoxia tolerance for various turtles studied by Belkin (1963) ranged from 114 to 1980 minutes. The only chelid turtles sampled had values of 360 and 570 minutes. Aquatic turtles can spend the entire winter underwater (Musacchia 1959). *Chelonia mydas* spends the winter underwater at 15°C in the Gulf of California (Felger, Clifton & Regal 1976) and *Caretta caretta* hibernates underwater off Florida (Carr, Ogren & McVea 1980/1981).

Lymphatics occur almost everywhere in living body tissues but are difficult to observe. They begin as blind lymph capillaries in reptiles lack lymph nodes and valves. The confluence of the lymphatic vessels with veins is usually close to the jugular–subclavian vein anastomosis. Reptilian lymphatic systems were first described by Panizza (1833a). Bojanus (1819) provided a reasonably detailed account for *Emys orbicularis.* A pair of macroscopic lymph hearts just internal to the posterior part of the carapace beat at a frequency of 3 to 45 times per minute. Ottaviani & Tazzi (1977) provided a detailed account of lymphatic systems in reptiles which included several cryptodires.

THERMOREGULATION

Temperature of the circulating blood probably is registered in the hypothalamus (Bellairs 1969; Rodbard 1948). Like other reptiles, turtles are ectothermic heliotherms and derive heat chiefly by moving into the sun or into a warmer medium (see Chapter 21). The chelonian shell is probably better insulation than the non-bony dermis of other reptiles.

Turtles can acclimate to a wide variety of environmental temperatures. The preferred temperature range in most turtles is 25° to 33°C (Hutchinson 1979), and critical maxima range from 39° to 42°C (Bellairs 1969). A large *Pseudemys* warmed by basking can maintain a deep-core body temperature above ambient water temperature for several hours after re-entry (Moll & Legler 1971). Activity is reduced but possible at low temperatures. *Terrapene* can copulate at 15°C (Legler 1960b) and North American *Pseudemys* may court under ice.

The optimum water temperature for Australian chelids is between 25° to 28°C. In the Tweed drainage of northern New South Wales, *Emydura* species and *Elseya latisternum* are lethargic at water temperatures of 15° to 17°C but nevertheless will attempt to escape from a diver. *Emydura* sp. in the Macleay drainage, New South Wales, is slow but active throughout the winter at temperatures of 4° to 8°C, and some individuals caught in winter have filamentous algae in the stomach. Under these conditions, aquatic turtles with alternative respiratory mechanisms, such as *Elseya latisternum* (King & Heatwole unpub. data), probably can pass the winter without breathing air.

Dermochelys coriacea feeds as far north as the Arctic Circle and can maintain deep core temperatures of up to 18°C in ambient seawater temperature, by virtue of their large size, use of peripheral tissues as insulation and counter-current exchange in the limbs (Frair, Ackman & Mrosovsky 1972; Greer, Lazell & Wright 1973; Paladino, O'Connor & Spotila 1990; Standora, Spotila, Keinath & Shoop 1984).

RESPIRATION

The lungs of all turtles are functional in pneumatic air breathing. No species is known to have lungs with reduced lung capacity or efficiency, though many aquatic turtles have evolved alternative respiratory structures analogous to gills. The useful comparisons of lung morphology by Gräper (1931), and information on all Australian chelids, except *Pseudemydura* (University of Utah unpub. data) form the basis for this description of lung structure and function.

The basic lung plan found in unspecialised cryptodires and in all chelids examined, consists of eight distinct subdivisions or lobes. Four of these are small, medial and almost cubic in proportions and four are lateral, larger and significantly wider than long.

The pulmonary hilus lies ventro-medially, between the first and second medial lobes. The primary bronchus passes through the hilus and between the median and lateral lobes. The bronchus communicates with the lobes via separate baffled openings. At the hilus, the pulmonary artery bifurcates into a superficial, ventral trunk and a deep trunk, which penetrates the lung and then runs superficially along the dorsal surface. Each trunk has major branches to each of the lobes, forming a collateral arterial supply. A single venous trunk runs parallel to the bronchial passageway ventrally, receives blood from a major vein from each lobe and exits at the hilus. This arrangement represents the 'Grundplan 4' of Wolf (1933). Gräper (1931) showed cross sections through the lungs of several pleurodires, including *Chelodina longicollis.*

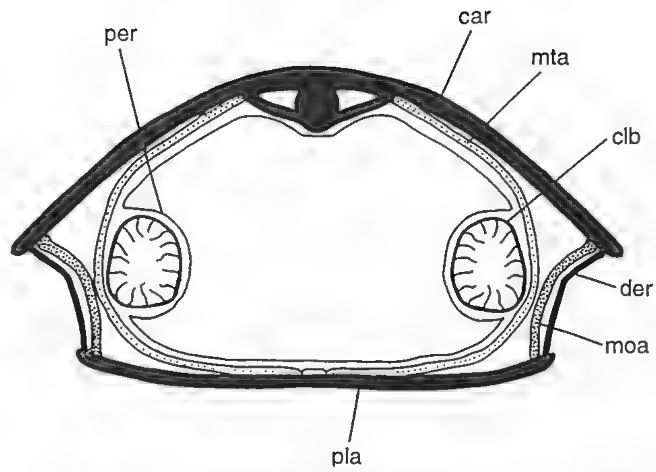

Figure 16.6 Schematic transverse section of a young *Rheodytes leukops* at the level of the inguinal pocket (posterior one-third of body), showing the relative positions of the *m. transversus abdominis* and *m. obliquus abdominis* muscles, the cloacal bursae, and the shell. The *m. obliquus abdominis* lies just below the skin of the inguinal pocket and attaches by its inner surface to the *m. transversus abdominis.* **car**, carapace; **clb**, cloacal bursa; **der**, skin; **moa**, *m. obliquus abdominis*; **mta**, *m. transversus abdominis*; **per**, peritoneum; **pla**, plastron. (Modified from a drawing by Mark T. Nielsen, University of Utah) [T. Wright]

Specialisations of the lung result from subdivision of the eight basic lobes. In marine turtles and trionychids the intermediate septa are complete and the resulting subordinate lobes are ventilated individually. The lobes are divided incompletely in *Carettochelys* and kinosternids. The eight lobes in the large, thin-walled lungs of testudinids have minimal interlobular subdivision. In *Rheodytes leukops* there may be a slight reduction in secondary chambering and total internal surface area but, in comparison to other shortneck species, these differences are slight, and not of the magnitude that one might expect in a gill breather.

In cryptodires the lungs may be attached to the dorsal peritoneum, to some of the anterior respiratory muscles, to the aponeurosis of the *m. transversus abdominis*, or to an extensive connective tissue 'diaphragm' ventral to the lungs (Gans & Hughes 1967; Gaunt & Gans 1969). In Australian chelids examined, the lungs are attached to the peritoneum only by their dorso-medial edges and seem to be free of visceral attachments. They often are completely collapsed in preserved specimens (J. Legler pers. obs.).

The definitive modern works on lung ventilation are based on the testudinid *Testudo graeca* and the aquatic turtle, *Chelydra* (Gans & Hughes 1967; Gaunt & Gans 1969). No detailed studies have been published for chelids but useful extrapolations can be made from information from cryptodires.

The lungs lie just beneath the carapace and are about half the length of the carapace when deflated. They extend between the pectoral and pelvic girdles and occupy the dorsal part of the visceral space. As such, they permit easy surgical approach from the dorsal side of the body and are vulnerable to dorsal puncture wounds.

The coelomic cavity of turtles, like that of most reptiles, is divided into a pericardial cavity around the heart and a common peritoneal cavity for the remaining organs, including the lungs. There is no diaphragm, though partial division of this cavity by a sheet of connective tissue between the lungs and all ventral viscera occurs in some testudinids (Gans & Hughes 1967).

While terrestrial chelonians can breathe at will, except perhaps while burrowing, aquatic turtles must coordinate breathing with times when the nostrils are above water. In deep water, this necessitates swimming to the surface. In shallow water, longnecked chelids may merely extend the neck to reach the surface, and require no limb activity at all.

Turtles can vary intracoelomic pressures and volumes by pulling in the limbs, head and neck. More subtly, this can be achieved by simple rotations of the pectoral girdle and by contractions of the highly modified belly muscles. A dramatic example of this, particularly in cryptodires, is the rapid withdrawal of appendages when a turtle is picked up or startled, accompanied by a hiss of air escaping from the glottis and the expulsion of fluids from the cloaca.

The *m. transversus abdominis* constitutes a contractile sling running beneath the peritoneum and the posterior viscera and attaching to the inner surface of the carapace on each side (Fig. 16.6). When it contracts it lifts and compresses the visceral mass and indirectly exerts pressure on the lungs. The *m. obliquus abdominis* lies beneath the subcutaneus tissue of the inguinal pocket and attaches to the edge of the carapace above and the plastron below. When contracted, it flattens the inguinal depression and decreases intracoelomic pressure. In Australian chelids, these two sheet-like muscles are attached to one another by an aponeurotic patch corresponding to the deepest part of the inguinal pocket. Not only are they antagonistic, but when one contracts it pulls the other with it. The *m. diaphragmaticus* is an anterior analogue of the *m. transversus abdominis* and helps to lift a common aponeurosis in *Chelydra* (Gaunt & Gans 1969a). The *m. transversus abdominis* lifts the 'diaphragm' of tortoises, which achieves further coelomic compression by inward rotation of the pectoral girdles (Gans & Hughes 1967).

At the water surface, lung ventilation in Australian chelids could be satisfactorily explained by operation of only the *m. transversus abdominis*, *m. obliquus abdominis* and hydrostatic pressure. However, observations of captive shortnecked chelids, except *Rheodytes*, show a rapid ventilation of lungs during the first few seconds at the surface. Muscular activity associated with this behaviour has not been analysed, but movements of both inguinal pocket and anterior limbs have been recorded.

The nostrils are at the tip of a long proboscis in *Chelus*, *Carettochelys* (Pl. 3.9) and trionychids, permitting cryptic surface breathing. Erectile tissue and well-defined masses of smooth muscle occur in the snouts of chelids, *Carettochelys* (Winokur 1982a), and in marine turtles (Parsons 1971). In all of these, the two sets of smooth muscles surrounding the nasal canals seem to be nasal dilators. The erectile tissue may act as an antagonistic nasal constrictor, thereby providing a degree of control over water passing in or out of the nostrils. Such control may be important in closing the nostrils during sleep or controlling the flow through the nose for olfactory purposes. An additional mass of smooth muscle, *m. arrector rostri*, controls the angle of the proboscis-like snout in *Carettochelys*, and probably positions it optimally when the animal is buried in bottom silt with only its snout protruding.

Ward (1970) demonstrated experimentally that virtually the entire gut of turtles has the ability to extract oxygen from water. However, the two primary regions involved with accessory, or gill respiration are the buccopharyneal region and the cloacal bursae. The buccopharyneal region accounts for 49% and the cloaca and its bursae for 33% of non-pulmonary oxygen uptake by *Elseya latisternum* at 20°C and 30°C (King & Heatwole unpub. data). Aquatic turtles using gill respiration are vulnerable to fish poisons, derris and rotenone (Bellairs 1969; Rosen pers. comm.).

Cloacal bursae are dorso-lateral diverticula of the cloaca and are unique to some groups of turtles, including the Chelidae. They are absent in the Trionychoidea, Kinosternoidae, Testudinidae, the two families of marine turtles, the African pelomedusids, and in some (usually terrestrial) members of the Emydidae and Bataguridae. The bursae are probably a primitive chelonian character and absence is a derived condition. In general, cloacal bursae are better developed in aquatic than in terrestrial turtles.

Cloacal bursae have been known for more than two centuries and Pickel (1889) reviewed the early literature. Interest in cloacal bursae was renewed with the discovery of *Rheodytes* (Legler & Cann 1980; see Chapter 21). King & Heatwole (in press) examined the cloacal bursae of *Elseya latisternum* and found extensive modification consistent with a respiratory function.

Smith & Nickon (1961) suggested that bursae only have a respiratory function in cold, inactive turtles surviving under water. The contrary is true, however, in *Rheodytes* and *Elseya dentata*. These animals swim at top speed in water of 25°C or warmer with the cloacal orifice widely dilated. Chelids have not been observed surfacing to breathe when chased, in contrast to *Apalone* species and *Chelydra*, which can be forced to breathe under such circumstances.

The cloacal bursae probably assist in buoyancy control, as air can be expelled from the lungs without placing the animal in respiratory jeopardy. Before an escape dive, many Australian chelids, particularly shortnecks, expel air from the mouth. This air presumably originates from the lungs. Captive *Rheodytes* are always negatively buoyant. They walk on the bottom with ease, and regularly release large bubbles of air from the mouth. This suggests a release of accumulated gas from the lungs and may be a factor in maintaining negative buoyancy.

The cloacal bursae are retroperitoneal and lie internal to the inguinal pocket. Two layers of striated muscle lie lateral to the bursae at this level. The *m. transversus abdominis* muscle girdles most of the peritoneal cavity, and the *m. obliquus abdominis* muscle lies immediately below the subcutaneous tissue of the inguinal pocket. These sheets of muscle curve away from each other and are joined by a broad aponeurosis, corresponding to the centre of the inguinal concavity. The bursal wall also is attached to the *m. transversus abdominis*. These muscles are antagonistic, whereby the *m. transversus abdominis* decreases intracoelomic volume and increases pressure to constrict the bursal sac, and the *m. obliquus abdominis* does the converse. The two muscles produce the pumping movements that can be observed in the inguinal pockets of all Australian chelids, in or out of the water (Fig. 16.6). The intrinsic smooth musculature of the bursal wall may assist in emptying the bursae or may maintain muscular tonus in the bursal wall during rapid filling. The circulatory modifications, if any, necessary to serve the cloacal bursae of *Rheodytes* and other chelids have not been investigated.

During buccopharyngeal respiration the hyoid apparatus is lowered, thereby increasing the volume and reducing the pressure in the mouth and pharynx. Water is drawn into the cavity through the nostrils and/or the mouth and then forced out through either or both of these passages. Exchanges of O_2 and CO_2 occur at the surface of the vascular buccal mucosa, especially the roof of the mouth (Ward 1970). Water passed through the nose and mouth probably also serves gustatory and olfactory functions. All aquatic turtles appear to practice buccopharyngeal respiration to some degree. *Carettochelys insculpta* has a buccopharyngeal gill consisting of branched vascular papillae in the mouth and pharynx (Winokur 1988).

No turtle has both cloacal bursae and specialised structures for buccopharyngeal respiration. However, of the four families of freshwater turtles that lack bursae, all have developed at least some papillose specialisation of the mouth, and three of these families can be termed buccopharyngeal gill breathers (Dermatemyidae, Trionychidae and Carettochelyidae). In all marine turtles the buccopharyngeal 'mucosa' is heavily cornified and variously armed with sharply pointed papillae directed caudally; Winokur (1988) suggested that these modifications facilitate the swallowing of food with a minimum intake of salt water.

EXCRETION

Fox (1977) presented a review of the urogenital system in reptiles and a few illustrations of urogenital structures in turtles, from which the following is cited, unless otherwise indicated.

The kidneys are dorsal to the viscera, beneath the peritoneum, and the right kidney lies further forward than the left (Bellairs 1969).

Though a pronephros is present briefly during development, the mesonephros is the principal embryonic kidney, and adult turtles have a metanephric kidney. The urinary bladder is well-developed. The cloaca serves as a common external orifice for the digestive, urinary and reproductive systems.

The kidney is flattened, lobed and usually symmetrical. Its form and surface texture vary substantially, and its shape may be influenced by the impingement of coelomic viscera. Unlike squamates, the chelonian kidney lacks Henle's loop, a renal pelvis, pyramids and the tubular 'sex segment'. The postero-ventral ureter is short and has a two-layered *tunica muscularis*. A large urinary bladder joins the ventral wall of the cloaca. The ureters and bladder communicate separately with the cloaca.

Dantzler (1976) reviewed the components of urinary nitrogen in chelonians, though chelids were not mentioned. Values for aquatic turtles were: ammonia 20 to 25%, urea 20 to 25%, and urates 5%. Data given by Dantzler & Schmidt-Nielsen (1966) contrast values for an aquatic emydid, *Pseudemys scripta* (ammonia 4 to 44%, urea 45 to 95%, urates 1 to 24%), and a fully terrestrial desert tortoise, *Gopherus agassizii* (ammonia 3 to 8%, urea 15 to 50%, urates 20 to 50%).

Urinary nitrogen values for *Chelodina oblonga* and *C. steindachneri* demonstrate that both species excrete ammonia and urea when hydrated, but produce urates when dehydrated (Burbidge 1967). This change is more pronounced in the latter species, as discussed in Chapter 21. Apparently aquatic turtles absorb little water through the skin. If excess water enters via the gut, it can be voided in dilute urine (Bellairs 1969).

Chelonians can store water in the urinary bladder, in the cloacal bursae and probably as coelomic fluid. These reserves can be reabsorbed if necessary, as shown for *Chelodina oblonga* and *C. steindachneri* (Burbidge 1967). It is common for aquatic turtles and tortoises of all kinds to squirt varying amounts of water from the cloaca when handled, probably from the urinary bladder and/or the cloacal bursae.

Water comprises about 65% of body mass in turtles (Bellairs 1969). Freshwater turtles live in a low-sodium environment. The converse is true of marine turtles. Plasma osmolarity is variable, and ranged from 278 to 400 mOs/l in seven testudinid species and 258 to 436 mOs/l in *Chelodina oblonga* and *C. steindachneri* (Burbidge 1967); values for the chelids related with the state of hydration of the turtles. Marine turtles (*Chelonia* and *Caretta*) are able to live in fresh water. The osmolarity of a specimen of *Caretta* kept in fresh water for three years dropped from above 350 to 211 mOs/l. This change involved a decrease in sodium and chloride. Estuarine turtles (*Malaclemys*) survived after 14 days at 3.3% saline followed by 10 days at 6.6% saline. Over this period, plasma sodium rose to about 170 mEq/l in the hypertonic environment. The terrestrial emydid, *Terrapene*, survived only four days in 3.3% saline (Dessaur 1970).

The primary osmoregulatory strategy in freshwater turtles appears to be the production of dilute, low-sodium urine. *Apalone spiniferus* has special cells in the pharynx that can absorb sodium from water containing as little as 5 mM/l. Marine turtles and some estuarine turtles (*Malaclemys*) secrete excess salts in tears (Fig. 19.2) via enlarged lachrymal glands. The tears of *Caretta* have a concentration of 810 to 992 mM chloride (732 to 878 mM sodium) compared to 470 mM sodium in normal sea water (Bellairs 1969; Dessaur 1970; Dunson 1976).

SENSE ORGANS AND NERVOUS SYSTEM

The degree of encephalisation in turtles is similar to that in crocodiles and ranks between that of lizards and snakes. Brain weight expressed as a percentage of body weight in a very small sample of cryptodires ranged from 0.008% to 0.19% (Platel 1979).

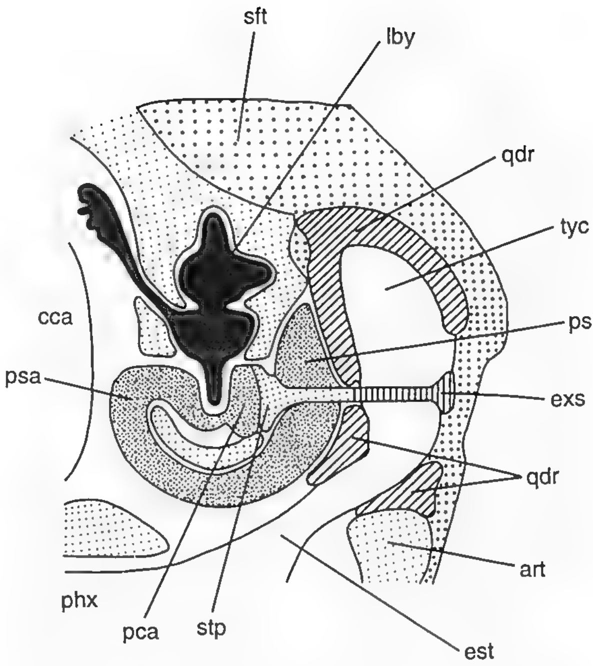

Figure 16.7 Schematic section through the middle ear and inner ear of a turtle. **art**, articular bone of lower jaw; **cca**, cranial cavity; **est**, eustachian tube; **exs**, extrastapes; **lby**, membranous labyrinth, shaded black; **pca**, perilymphatic capsule; **phx**, pharynx; **psa**, perilymphatic sac; **psi**, perilymphatic sinus; **qdr**, quadrate; **sft**, soft tissues; **stp**, stapes; **tyc**, tympanic cavity. (After Romer 1956) [T. Wright]

The eye has a generalised structure, similar to that of other amniotes, and functions well under a variety of conditions. The reptilian eye, and details of retinal structure and function were reviewed Underwood (1970), Peterson (1992) and Granda & Sisson (1992). The pupil in turtles is always round. The surrounding iris may be dark, or pale (golden, yellowish, or greenish) in sharp contrast with the pupil. Often a bright metallic-coloured ring is present on the rim of the pupil. The visible part of the eyeball surrounding the iris is usually dull coloured. Blotches of melanin may disrupt a brightly coloured iris, and blend with the pupil to form a stripe, which sometimes corresponds to a lateral head stripe. An uncamouflaged bright iris is very evident under water.

The supportive layer of the eyeball contains a ring of 6 to 13 scleral ossicles (Underwood 1970). All amniotes focus light on the retina by modifying the shape of a flexible lens. The muscular ciliary body surrounds the lens and, in turtles, remains in contact with the lens even when the muscle is relaxed. When the ciliary body is relaxed, the lens is 'set' at distant vision. When it contracts, the lens is squeezed and thickened antero-posteriorly for near vision.

The cornea does much of the work of focussing in land vertebrates (Romer & Parsons 1977). In turtles, however, focussing is accomplished either by the cornea on land, or the lens under water. Underwood (1970) compared eye structure in *Emys*, *Testudo* and *Caretta*. A typical semi-aquatic cryptodire, such as *Emys*, has a strongly convex cornea and a thick lens, and out of water the cornea is the principal refracting surface. *Testudo*, a completely terrestrial genus, has a cornea similar to that of *Emys*, but the lens is flatter and the ciliary body less well developed. *Caretta*, a marine turtle, which leaves the sea only to nest, has a reduced corneal curvature and the lens is significantly more curved than in *Emys*.

The retina contains single and double cones and one type of single rod. The cones have yellow oil droplets, like those of lizards. The double retinal cells may serve as detectors of polarised light (Underwood 1970). Verriest, de Rouck & Rabaey (1959) found both rods and cones in *Malaclemys*, *Pseudemys* and *Testudo*, but only cones in *Emys*. The most nocturnal turtles have more cones than rods. As a percentage of all rods and cones, rods form 40%, 2.5% and 25% in the retinas of *Chelydra serpentina*, *Chrysemys picta*, and *Emydoidea blandingii*, respectively (Underwood 1970).

Accessory ocular structures are the Harderian and lachrymal glands, the nictitating membranes, and the eyelids. The Harderian glands lie antero-medially to the eyeball, and the Harderian ducts enter ventrally between the nictitating membrane and the front of the eyeball. Harderian glands and ducts are absent in all Australian chelids and in all chelonian taxa which lack or have vestigial nictitating membranes. The lachrymal glands are situated postero-laterally to the eyeball, and the lachrymal ducts exit from the inner surface of the lower eyelid. Lachrymal glands occur in all chelonians. They secrete highly concentrated tears in marine turtles (Fig. 19.2) and some estuarine turtles such as *Malaclemys*. The secretion lubricates and cleans the conjunctival cavity (Bruno 1983; Legler & Bruno unpub. data). Good descriptions of the glands of *Chelonia* and *Caretta* appear in Abel & Ellis (1966). Turtles lack a nasolachrymal duct from the conjunctival cavity to the nasal passageways.

Nictitating membranes function in reptiles and birds as a third transparent inner eyelid that protects the eye without obscuring vision. They are absent in the cryptodiran families Kinosternidae, Dermatemyidae and Carettochelydidae, and are absent or rudimentary in many pleurodires of both families (Bruno 1983). The membrane is absent or vestigial in all Australian chelids, which have instead a translucent to transparent lower eyelid through which the eye is usually visible (see Chapter 21).

The external ear is absent. The middle ear is complex and unique in structure, and the inner ear is poorly known. Baird (1970) reviewed the turtle ear. The tympanic membrane lies flush with the side of the head and is covered with ordinary body skin. It is attached to the circular rim of the quadrate, and forms the outer wall of the air-filled tympanic cavity. The eustachian tube passes from the floor of the tympanic cavity to the pharynx. The slit-like pharyngeal eustachian orifices are easily seen when the mouth gapes widely. In preserved turtles, pressure exerted on the tympanic membranes will eject fine streams of fluid from the orifices.

Romer (1956) and Bellairs (1969) provided good diagrams of middle ear osteology. The quadrate divides the middle ear into a lateral tympanic cavity and a medial *recessus cavi tympani*. The latter contains most of the structures normally associated with the middle ear of other reptiles (Fig. 16.7, *cf.* Fig. 24.18). The stapes or columella is the only osseous element, or 'ossicle', in the middle ear. Its distal part is the cartilaginous extrastapes, an expansion of which is attached to the inner surface of the tympanic membrane. The extrastapes joins the stapedial shaft which passes through a foramen or an open notch in the quadrate, traverses the *recessus cavi tympani* and expands into a vertically oval footplate articulated to the vestibular or oval window (*fenestra ovalis*).

Part of the stapedial footplate abuts a fluid-filled sac, the paracapsular sinus. The shaft of the stapes lies upon the sinus and indents it dorsally. The sinus occupies most of the *recessus cavi tympani* and its posterior part lies against the lateral surface of the periotic sac. According to Baird (1970) the paracapsular sinus is a dampening mechanism unique to turtles and has no homologue in other reptiles.

The vestibular part of the osseus labyrinth is similar to, but simpler than that of lizards. The cochlear recess lies posterior to the vestibule rather than ventral. The vestibular window and stapedial footplate are almost vertical rather than horizontal. The utricle and semicircular ducts are like those of lizards. The saccule lies ventral to the utricle, as in *Sphenodon*, and is rounded but may be extended posteriorly (Baird 1970).

The auditory sensitivity of turtles is inferior to that of crocodilians and lizards, especially above frequencies of one to two kHz, and the ears of *Testudo* and *Terrapene* are responsive to sounds of about 110 Hz. The sensitivity of *Clemmys insculpta* for tones of up to 500 Hz is good, but declines rapidly above one kHz (Bellairs 1969). Some tortoises vocalise when mating and a few aquatic turtles make hissing or piping noises while breathing, but it has not been demonstrated that hearing these sounds is important to other turtles.

The nasal passages between the external nares and the internal nares in the roof of the buccal cavity are used in three basic ways — for normal aerial breathing, for olfactory purposes in the water and air, and for aquatic respiration. Most aquatic turtles practise buccopharyngeal pumping, during which water passes through the nose.

Of all reptiles, turtles have the most distinctive nasal anatomy, which Parsons (1970) considered to be primitive. Immediately inside the external naris is an expanded vestibule, which is linked to the expanded main nasal chamber by a short, narrow passageway. The roof of this chamber is lined with olfactory epithelium and Bowman's glands. The nasopharyngeal duct leads from the nasal chamber to the internal choanae. The length of this terminal choanal tube is directly related to the length of the secondary palate. The nasopharyngeal duct contains no olfactory epithelium (Parsons 1970; Romer & Parsons 1977).

Most turtles have widely scattered taste buds in the buccopharyngeal region (Winokur 1988). The olfactory epithelium is concentrated in the nose. The vomeronasal (Jacobson's) organ discriminates olfactory sensations from substances in the mouth (Romer & Parsons 1977). The vomeronasal region is not well separated from the rest of the nose in turtles, and there is controversy about its occurrence and homology in turtles.

SECRETORY ORGANS

The unpaired, almost spherical thyroid gland is situated ventral to the trachea and immediately anterior to the heart (Lynn 1970). A detailed account of thyroid anatomy in *Emys orbicularis* and *Testudo graeca* can be found in Naccarati (1922).

Clark (1970) illustrated the positions of the parathyroids, the thymus and the thyroid relative to the trachea and heart. Turtles do not respond dramatically to parathyroidectomy. The parathyroid, as in mammals, seems to regulate the calcium and phosphate concentration in body fluids. There are two pairs of parathyroids. The anterior pair is embedded and hidden in the tissue of the thymus. The posterior parathyroids lie near the arch of the aorta in close association with the left ultimobranchial body.

Gabe (1970) illustrated the adrenal glands in *Pseudemys scripta* and their relationship to the ventral surface of the kidney. The adrenal gland is closely adpressed to the ventral surface of the kidney, and comprises the interrenal cords, derived from coelomic epithelium, and the adrenal cells, originating from the neural crest. The histology of the adrenal organ resembles that of other vertebrates (Gabe 1970).

The brief review of pancreatic anatomy by Miller & Lagios (1970) includes Australian chelids. Illustrations of two cryptodires (*Lissemys punctata* and *Pseudemys scripta*) and one pleurodire (*Podnocnemis unifilis*) show the relative positions of pancreas, spleen, tubular gut and major arteries. The pancreas always lies in the loop formed by the duodenum and the pyloric end of the stomach, but the position of the spleen varies.

REPRODUCTION AND DEVELOPMENT

The gonads of both sexes lie immediately ventral to the kidneys. The testis is situated ventro-medially to the anterior half of the kidney. Testes are normally oval but may become elongate during the cycle of enlargement. The efferent ducts consist of a long coiled epididymis, and a short vas deferens which enters the dorsal wall of the cloaca just medial to the ureter. All male chelonians undergo a seasonal testicular cycle of hypertrophy and regression. Stages of spermatogenesis can be approximated by the degree of enlargement (Moll 1979). Fertilisation is by sperm produced in the preceding year. Mature sperm are produced after ovulation and

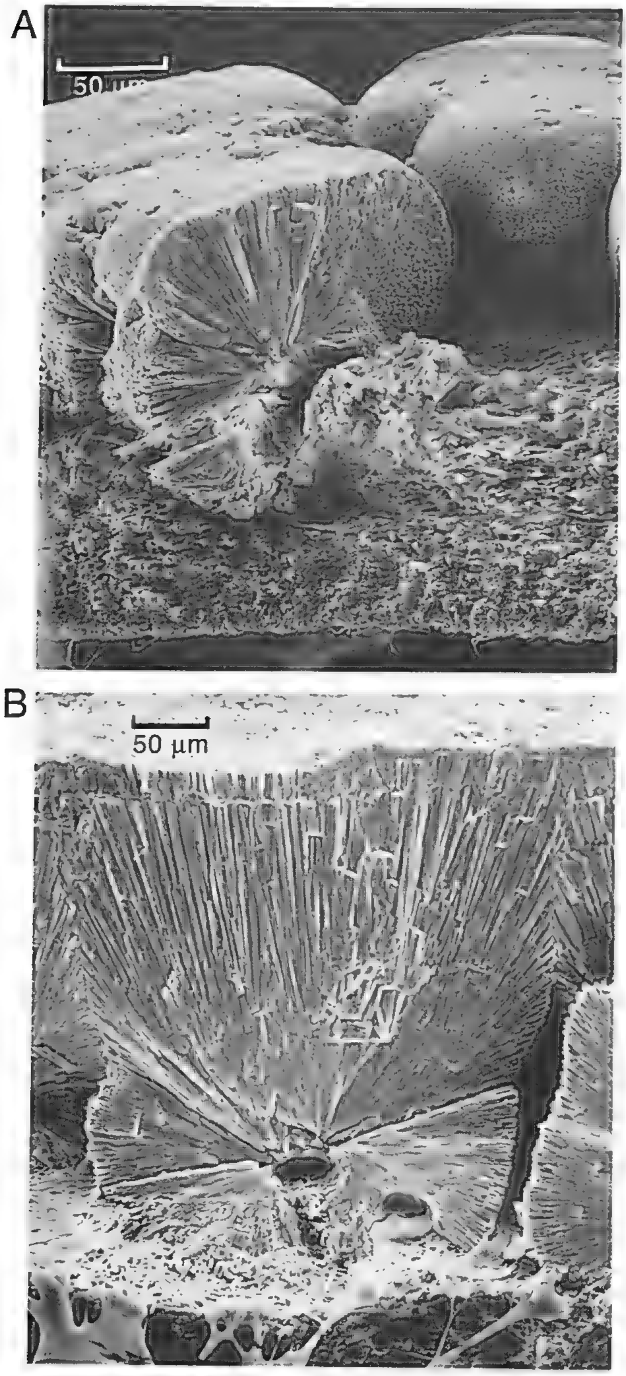

Figure 16.8 Scanning electron micrographs of oviducal egg of *Elseya dentata*, with the external surface of the eggshell at the top. **A**, a thin, undeveloped shell of specimen from Barramundie Creek, Northern Territory. Three rounded shell units are shown resting on a shell membrane. The broken shell unit in the foreground shows crystals radiating from the crystallisation nucleus. Note that shell units barely touch one another. **B**, a normally developed, thick shell from a specimen from Edith River, Northern Territory. Note hollow centre of crystallisation nucleus and potential zone of fracture passing through it. Flaking of the shell in late incubation may occur at this zone. Parts of other shell units are shown to the sides. Shell membrane and amorphous adhesive are shown below. [Photo by J. Legler]

oviposition have occurred. Engorgement and pallidity of the epididymides is an accurate indicator of motile, mature sperm.

The ovary is a sheet-like organ. Presumptive follicles are detectable as pale surface granules in juveniles. The oviducts lie ventral to the ovaries and enter the cloaca ventro-laterally. The proximal portion of the oviduct, nearest the ostium, is flattened and folded like a concertina, whereas the distal end, which communicates with the cloaca, is rounded, thicker walled and unfolded.

Most anatomical drawings show a neat arrangement of these structures in the dorsal posterior half of the coelomic cavity, but when the ovary bears large follicles and the oviduct is laden with oviducal eggs, these structures take up most of the available coelomic space and impinge upon other coelomic organs, including the lungs.

At puberty, presumptive follicles in each ovary accumulate yolk (vitellogenesis) and enlarge to ovulatory size at the beginning of each annual cycle, reaching a diameter approximating that of the mature egg. A follicle consists of the thinly-stretched ovarian wall surrounding a yellowish ovum. At ovulation the follicular wall ruptures and releases the ovum into the coelomic cavity. Ovulation of all follicles in a size group seems to be simultaneous in most turtles that have been studied. The empty follicle collapses and becomes a distinct, cup-shaped corpus luteum about 15 to 25% of the diameter of the mature follicle, and each has a bloody orifice where ovulation occurred. Corpora lutea begin to regress almost immediately but remain visible throughout the breeding season (and sometimes into the next). Their presence is evidence that ovulation has occurred. Corpora lutea are present in different stages of regression if more than one set of ovulations occur in one breeding season. Multiple ovulations can be predicted from detectable size groups in enlarging follicles. The annual reproductive potential can be calculated from the sum of all enlarged, preovulatory follicles and the number of corpora lutea of all stages.

Depending upon environmental factors, ovulation of all preovulatory follicles may not occur, and the reproductive potential may not be realised. Follicles not ovulated in a given season become dark and flaccid, or atretic, and are reabsorbed. Atretic follicles are usually identifiable late in the season.

Postovulatory ova lie free at least momentarily in the coelomic cavity. Extra-uterine migration is common, and ova from one ovary may go into either oviduct (Legler 1958). This may involve coelomic migration of ova, movement of the oviducal ostia or both. As the ovum passes through the oviduct, the clear albumenous material around the yolk, the shell membrane and the hard part of the shell are added to it in a series of layers. Coating proceeds quickly to the stage of a thin shell. The shell then thickens more gradually over a period of days. The rapidity of this process is indicated by the rarity of any stage earlier than a thin-shelled egg in the oviduct or the coelom in thousands of specimens examined (Legler pers. obs.)

Multiple layers of fibres orientated in different directions in the shell membrane impart a felt-like appearance under magnification. A variable number of layers can be separated mechanically. The configuration of the fibres determines whether the membrane will tear transversely, longitudinally or spirally at hatching. The mineralised layer consists of a single layer of shell units, each of which is a multi-sided inverted polyhedron with its apex attached to, or abutting, the shell membrane. Eggshell units begin as crystallisation nuclei (Ewert 1985) on the shell membrane and grow to final size by the addition of thousands of aragonite crystals. Initially the shell units are almost conical in shape, and become polyhedral as they abut on one another. The crystallisation nucleus becomes a hollow space near the apex of each shell unit (Fig. 16.8B)

Eggshells range from thin and flexible to hard and brittle (Ewert 1985; Legler 1985), the condition being characteristic of particular taxonomic groups. The shell may thicken in long-retained eggs. Under normal circumstances there is a single layer of shell units. Shell strength, rigidity and thickness depend on the height of the shell units and the extent of their fusion to one another (Fig. 16.8A, B).

Flexible-shelled eggs are rather rigid at laying. They become flexible and turgid as they absorb water and swell during incubation. This swelling necessarily involves movement between the shell units. Even hard-shelled eggs of medium shell thickness eventually expand, for example, in both groups of *Chelodina*, but not without cracking and flaking of part of the hard shell. The hardest-shelled eggs, such as those of *Elseya dentata*, have the thickest shells and do not expand at all. Thick-shelled eggs tend to have well-defined pores which are formed at points common to three or four shell units (Fig. 16.8B). Thin-shelled eggs usually lack pores (Fig. 16.8A).

Fully-shelled eggs normally are held in the oviduct until environmental conditions are suitable for laying. Development stops at the gastrula stage and does not proceed further until laying. This pre-ovipositional developmental arrest has been well-documented, but its causes have not been explained (Ewert 1985). Whatever the mechanism, it has a high selective advantage in permitting the nesting female to judge the suitability of conditions for nesting and therefore to determine the time that postgastrulatory development begins.

All living turtles are oviparous, and usually lay their eggs in nests dug in earth or sand near water. Australian freshwater turtles typically lay white ellipsoidal eggs (Fig. 17.1). Eggs of *Carettochelys insculpta* are spherical. The eggs of marine species are spherical (Fig. 17.2) and soft-shelled, as the calcareous layer is much reduced (Miller 1985). There is no evidence of the development of viviparity in turtles. Lack of viviparity or the inability to evolve viviparity has been discussed eruditely but never satisfactorily explained (Packard, Tracy & Roth 1977; Tinkle & Gibbons 1977; Shine 1985a). The chelonian body plan is remarkably preadapted as a protective enclosure for development, but the habits of most turtles do not favour temperatures that are high enough to facilitate optimal developmental rates. Even the marine turtles that are endothermic, for example, *Dermochelys coriacea*, make long journeys to deposit eggs. Viviparity would impair the tremendous fecundity of turtles by limiting or preventing multiple clutches. To evolve viviparity, turtles would have to retain eggs without developmental arrest, limit the formation of the eggshell, and redirect the distribution of calcium and nutrients to the embryo.

17. NATURAL HISTORY OF THE CHELONIA

Arthur Georges, Colin J. Limpus & C. John Parmenter

LIFE HISTORY

Females of all species of turtle (except perhaps *Chelodina rugosa*, see below) leave the water to deposit their eggs in cavities or depressions constructed in the surrounding sand, soil or litter. Turtles abandon the eggs once they are laid and do not protect the hatchlings. All species have distinct annual breeding seasons. Synchronisation of breeding with periods of ample food availability is unnecessary, because turtles can accumulate resources over time to provide for the demands of vitellogenesis (Chessman 1978; Georges 1983; Kuchling & DeJose 1989). This ability is carried to extremes in marine species, with *Chelonia mydas* taking in excess of one year to prepare for a breeding season (Limpus & Nicholls 1988). Nor is there a need for breeding to coincide with conditions suitable for copulation, as the male and female cycles are not particularly closely synchronised in chelonians. Males of most Australian species have sperm in the epididymides in all months, and females of some species overseas have been found to store sperm for several years.

There are three principal constraints on the reproductive patterns of chelonians. Firstly, females must nest when conditions are conducive to adult activity. They must also nest when the conditions to follow are conducive to embryo survival and ultimately, embryonic development. Thirdly, they must ensure that the hatchlings emerge when conditions are conducive to their survival. Knowledge of each of these constraints in the context of the ecology of a species is generally sufficient to explain its reproductive strategy.

A plethora of solutions for meeting these constraints has evolved. There is variation among species and plasticity among populations of the same species in the timing of egg laying, clutch size, clutch frequency and incubation period. Effective incubation may be prolonged by cold torpor arrest during the winter months, embryonic diapause, delayed hatching, embryonic aestivation, and delayed emergence from the nest after hatching (Ewert 1985).

Reproductive Patterns for Freshwater Turtles

Two broad reproductive patterns can be identified among Australian freshwater turtles — one temperate and one tropical — though whether there is an overriding taxonomic influence on these patterns is debatable (Legler 1985; Kuchling 1988).

Winter provides a major interruption to adult activity and growth, and an impediment to embryonic development, for turtles of the temperate zones. *Emydura krefftii* from Fraser Island in Queensland exhibits a typical reproductive pattern for temperate-zone turtles of both the northern and southern hemispheres (Georges 1983). Mating occurs all year round with peaks in the autumn and spring. Sperm are present in the epididymides of males all year round, but spermatogenesis is post-nuptial with a peak in testicular activity in autumn and a cessation of testicular activity during the breeding season. Yolk begins to accumulate in the ovaries of females in late summer and continues through winter, presumably by a transfer of material from fat stores to the ovaries. Ovulations and nesting begin in early spring. Up to three clutches are laid by each female between early spring and mid summer. Clutch size ranges from four to ten eggs, depending upon the size of the female. Hatchlings emerge from nests in mid to late summer and make their way to the water. There is ample time for incubation and hatching to occur before the onset of winter.

Although it is the most prevalent pattern, spring nesting and summer hatching is not universal among Australian freshwater turtles, even within the temperate zones (see Chapter 21). For example, *Chelodina oblonga* nests in the spring, early summer and mid summer. *Pseudemydura umbrina* nests in the spring. In both species, hatching is initiated by winter rains (Burbidge 1981; Clay 1981). *Chelodina expansa* nests in the autumn and winter (Goode & Russell 1968; Georges 1984; Legler 1985).

Tropical freshwater species are freed from the constraints of reduced winter temperatures, and show the greatest diversity in reproductive patterns. Rainfall throughout the Australian tropics is markedly seasonal (Taylor & Tulloch 1985). There is typically a dramatic rise in water levels in the monsoonal wet season (December to March) and a corresponding drop in water levels in the wet-dry transitional months (April, May) and the following dry season (June to August). Freshwater species inhabiting the tropics often have only a very short period in which to find the relatively dry ground suitable for nesting, and they have solved the problem in a variety of ways. *Chelodina rugosa* lays eggs underwater or in saturated soils (Kennett, Christian & Pritchard 1993a). *If local conditions have dried, C. novaeguinea* may move to more permanent water bodies or aestivate until conditions are appropriate (Covacevich, Couper, McDonald & Trigger 1990a; Kennett, Georges, Thomas & Georges 1992) (see Chapter 21).

Tropical *Emydura* spp. inhabit permanent water and, unconstrained by seasonal disappearance of water, they nest at the same time as their southern counterparts (Fig. 17.1). Their eggs incubate and hatch during the northern dry-season. Pig-nosed turtles, *Carettochelys insculpta*, also inhabit permanent water, and nest between late August and mid November (Webb *et al.* 1986; Georges & Kennett 1989).

After about 65 to 70 days of incubation, and rapid development for eggs of their size, *Carettochelys* embryos are at a final stage of development and are quite capable of hatching. Instead, they enter

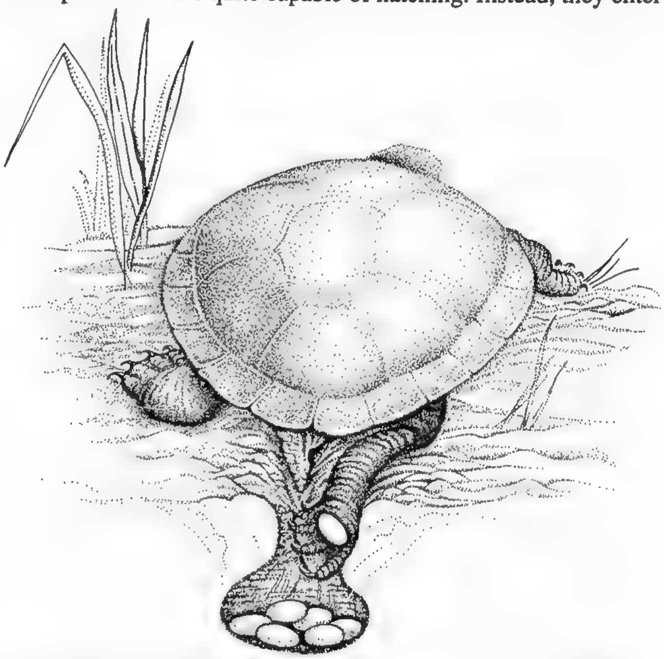

Figure 17.1 Egg laying in the chelid *Emydura macquarii*. [T. Wright]

a form of embryonic aestivation. Their metabolic rate and demand for oxygen drops precipitously (Webb *et al.* 1986) and they wait for an appropriate stimulus before hatching. Webb *et al.* (1986) showed that immersion in water was sufficient to arouse the torpid offspring and hatching followed. In the field, both flooding and torrential rain can stimulate hatching (Fig. 22.2; Georges 1987).

Clearly, hatching of the young turtles is delayed until the first heavy rains of the wet season flood the nests or saturate the surrounding sands. Presumably the hatchlings gain some benefit from this strategy, hatching into water where there may have been none before, and the rain may have opened up new areas into which the hatchlings can disperse to feed and seek shelter. Hatching in response to a discrete stimulus may ensure synchronised hatching and so help to overcome variation in development rates caused by thermal gradients in nests (Georges 1992; Thompson 1989). predators may be satiated as a result of simultaneous hatching of all nests on a nesting bank (Carr 1967), and the floodwaters responsible for hatching may have dispersed potential predators previously concentrated in the contracted waterbodies.

Reproductive Patterns for Marine Turtles

Marine turtle eggs require nest temperatures between 25° to 33°C and a nest in a low salinity, well-ventilated substrate with high humidity, placed where it has a low probability of being flooded or eroded (Miller 1985; Maloney, Darian-Smith, Takahashi & Limpus 1990). These conditions can be met above the storm surge level on most tropical or subtropical beaches protected from strong wave action by headlands or intertidal reef flats. Nesting is distinctly seasonal and restricted to the summer months on subtropical beaches (Limpus 1971a). Closer to the equator, the period of suitable temperatures is longer and some beaches may be suitable for successful incubation all year round (Limpus, Miller, Baker & McLachlan 1983a). The success of a rookery depends upon environmental parameters, such as beach stability, the seasonal mosaic of nest temperatures that determine hatching success and hatching sex ratio, and the proximity of offshore currents for dispersal of hatchlings to suitable oceanic feeding areas.

With the onset of the breeding season, adult males and females migrate from feeding grounds to copulate near the nesting area (Limpus, Miller, Parmenter, Reimer, McLachlan *et al.* 1992; Limpus, Parmenter, Baker & Fleay 1983c; Parmenter 1983). There is no pair bond between individuals and copulation with a number of different partners during the mating season is normal (Fig. 19.3; Limpus 1993; Harry & Briscoe 1988). The female stores the sperm from her several mates for use later in the breeding season. At the completion of mating the males depart, presumably returning to the distant feeding grounds (Limpus 1993). Each female moves to an area adjacent to her selected nesting beach and commences production of eggs, fertilising them from her sperm store. Because of the mixture of sperm she carries, several males usually contribute to the fertilisation of any one clutch (Harry & Briscoe 1988). The female comes ashore to nest, usually at night, several weeks after her first mating (Fig. 17.2). For those beaches fronted by reef flats, nesting coincides with the higher tides.

Within the one nesting season, each female typically lays several clutches at about two weekly intervals (Hirth 1980; Limpus 1985; Limpus, Fleay & Baker 1984a; Limpus, Fleay & Guinea 1984b). Between clutches the female moves just offshore from the nesting beach to make the next clutch of eggs, again fertilising them from stored sperm. Breeding turtles do not feed, or else feed to only a limited extent, while migrating, courting or making eggs at the nesting beach area. They live on the fat reserves deposited before the breeding season.

The number of eggs and egg size varies among species. *Natator depressus* lays about 50 billiard-ball size eggs per clutch and three clutches per breeding season (Limpus 1971a; Limpus *et al.* 1984a). *Eretmochelys imbricata* lays about 132 ping pong ball-sized eggs per clutch in about three clutches per season, while *Chelonia mydas* lays about 115 intermediate-sized eggs per clutch and about six clutches per breeding season (Limpus, Parmenter, Baker & Fleay 1983d). Females lay their eggs high up on the beach usually within the vegetated strand. Miller (1985) has described the embryology of marine turtles. Eggs hatchs at about 6–13 weeks after laying, depending on incubation temperature, as described further in Chapter 19.

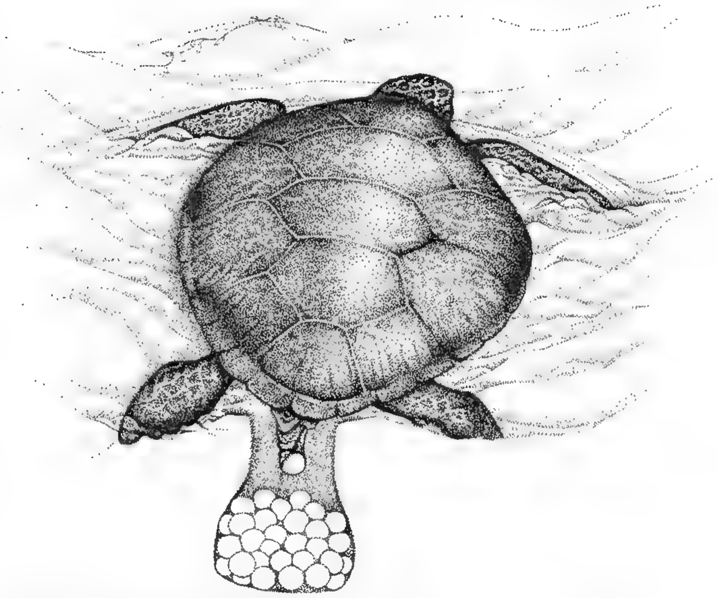

Figure 17.2 Egg laying in the cheloniid, *Chelonia mydas*. [T. Wright]

Females usually return to the same beach or island to lay several clutches within the one nesting season. However, a small percentage will lay on more than one beach within a few hundred kilometres of the initial nesting site (Limpus *et al.* 1984a, 1984b). At the completion of the nesting season the female returns to the same feeding ground that she left at the start of her breeding migration (Fig. 19.3; Limpus *et al.* 1992). Individual females breed every 2 to 8 years, generally returning to nest on the same beach (Limpus 1985; Limpus *et al.* 1984a, 1984b). This behaviour, and the annual use of traditional nesting beaches, has led to the assumption that a marine turtle returns to nest on the precise beach of her birth. In reality, the homing is probably not so exact. Genetic studies suggest that the female returns to breed in the general region of her birth (Bowen, Kamezaki, Limpus, Hughes, Maylan *et al.* in press; Norman, Moritz, Limpus & Prince in press; Gyuris & Limpus 1988).

Sex Determination

Sexual differentiation of the embryo is profoundly influenced by incubation temperature in many marine, freshwater and terrestrial turtles (reviewed by Bull 1980, 1983; Ewert & Nelson 1991). For most species, females are produced at high temperatures and males at low temperatures. A very narrow range of temperatures, referred to as the threshold or pivotal temperature, produces both males and females (Bull 1983). A few species have upper and lower thresholds, and females are produced at the extremes of temperature (Yntema 1976; Gutzke & Paukstis 1984). Sex determination is not temperature dependent in those Australian chelids studied to date (Bull, Legler & Vogt 1985; Georges 1988a; Thompson 1988; Palmer-Allen, Beynon & Georges 1991), whereas *Carettochelys insculpta* (Webb *et al.* 1986; Georges 1992) and all marine species (Limpus & Miller 1980; Limpus, Reed & Miller 1985) have the trait.

Eggs of *Carettochelys insculpta* incubated at a constant 32°C, or hotter, produce 100% females whereas those incubated at 30°C or cooler produce 100% males (Webb *et al.* 1986). In the field, hot exposed nests produce females, cool shaded nests produce males, and nests intermediate in temperature produce hatchlings of both sexes (Georges 1992). In nests that produce hatchlings of both sexes, males tend to emerge from the deepest, coolest eggs and females tend to emerge from the uppermost, hottest eggs. The ecological significance of temperature dependent sex determination is obscure.

Sex determination in marine species has been better studied. Females spread their nesting over a series of beaches which encompass a range of nest temperatures either side of the pivotal temperature, the theoretical temperature that should produce a 1:1 sex ratio (Limpus, Reed & Miller 1983b). As a result, the sex ratio for each species, or breeding stock, depends on the proportion of clutches laid in each of these warm and cool nesting areas. Cyclones, with their associated high rainfall and cooling effect on the beaches, can modify the general seasonal trend in hatchling sex ratio from a rookery. A cyclone can cause short-term cooling events with up to 5°C drops in nest temperature over a few days. Should this happen at mid-incubation, clutches can contain all males, while clutches emerging a few days earlier or later than these may contain all female hatchlings (Reed 1980).

Growth and Demography

The order Chelonia includes some of the most fecund amniotes on earth. Estimates of reproductive potential range from 4.4 for the chelid, *Pseudemydura umbrina*, to 690 per year for the cheloniid, *Chelonia mydas*. Typically, there is a strong positive relationship between clutch size and maternal body size (Georges 1983; Miller 1989); reproductive potential in these species may increase with age.

High fecundity is matched by vulnerability of the egg and hatchling stage to predation. Parmenter (1985) estimated that in the absence of predation, survivorship of *Chelodina longicollis* eggs at Laurendale near Armidale was 72%, but predation reduced this figure to 37%. Predation in the study areas was estimated to be much higher, and close to 100%. Predators included the European Red Fox, *Vulpes vulpes* and domestic cat, *Felis catus*. Water rats, goannas and crows exacted a high toll on nests of *Emydura macquarii* in South Australia, and foxes alone preyed on an estimated 93% of nests (Thompson 1983). In contrast, nest predation is rare among *Emydura* sp. on Cooper Creek in central Australia (Thompson 1983) where foxes are rare. Juvenile turtles probably fare much better in the water. Gibbons (1968) reported that the chance of survival of hatchlings in the North American species, *Chrysemys picta*, was very high, although only 2% of the eggs survived to hatch. There are no useful data for post-hatching survival in Australian species.

There are few direct estimates of recruitment to freshwater turtle populations in Australia, but it can be reasonably assumed that the populations are sustained by a trickle of new recruits, or by successful recruitment in the few years when conditions allow many nests to survive to hatching. The longevity of adults is necessary for populations to be sustained by such low or intermittent recruitment.

The difficulties of studying growth in a long-lived slow growing vertebrate have discouraged research on this topic in Australia, and few relevant studies have been published. In the temperate zones, freshwater turtles have an annual cycle of growth, even at latitudes that permit activity and feeding in all months (Georges 1982a). Growth of *Emydura krefftii* (Fraser Island) is poorly correlated with body size, so it is not possible to calculate a satisfactory relationship between age and size. In general, juveniles of all species so far studied grow faster than adults, and growth rate drops abruptly at the onset of maturity, when available resources are redirected to reproduction (Georges 1985). Females of *Emydura* and *Chelodina* species tend to grow faster than males and to reach larger maximum sizes (Parmenter 1976; Chessman 1978; Georges 1982a). *Pseudemydura umbrina* is the only species in which the males grow to larger sizes than females (Burbidge 1981). Onset of maturity typically occurs between seven and 12 years of age (Burbidge 1981; Georges 1982a; Parmenter 1985). Females tend to mature at larger sizes than males. There are no data on longevity for any Australian turtle, although Georges (1982a) estimated that if a specimen of *Emydura krefftii* (Fraser Island) grew at the fastest observed rate of any turtle in its size cohort, it would take at least 69 years to reach maximum size.

There are relatively few estimates of population densities of freshwater turtles in Australia. *Chelodina longicollis* is very abundant in the permanent dune lakes of the Jervis Bay Territory (up to 163.8 ± 34.2 turtles/ha; 9.9 ± 2.1 per 10 km of shoreline; Georges, Norris & Wensing 1986), and in lentic waters of the New England Tableland (up to 400/ha in farm dams; Parmenter 1976). Density estimates for *Chelodina longicollis* from Gippsland ranged from 160 turtles/ha for lagoons and 240 turtles/ha in farm dams, equivalent in both instances to about 70 kg/ha (Chessman 1978). Population densities for *Carettochelys insculpta* in the upper reaches of the South Alligator River have been estimated at 33.8 ± 11.3 turtles/ha (equivalent to 67 turtles/km of channel or 227.4 kg/ha) (Georges & Kennett 1989). These estimates are high in comparison with estimates for species of freshwater turtles on other continents (Iverson 1982; Congdon, Greene & Gibbons 1986). However, in each of these studies, the turtle densities were probably inflated above the carrying capacity of the waters in which they were found because of seasonal contractions of their aquatic habitat (Georges & Kennett 1989; Kennett & Georges 1990).

An estimate of sustainable density is available for *Emydura krefftii* on Fraser Island. In Lake Coomboo, they have a population density of 87 turtles/ha, equivalent to 28.8 ± 0.7 kg/ha. Biomass production was 18.5 ± 3.4 kg/ha (Georges & Legler in press).

The population structure of freshwater turtle populations is highly variable, presumably dependent upon recent history of recruitment. Generally adults predominate or are present in equal numbers to juveniles (Georges 1985), but age structures have not been determined for any Australian species. Sex ratios are typically close to 1:1 for chelid turtles, which have genotypic sex determination, but skewed in favour of females for *Carettochelys insculpta* which has environmental sex determination (Georges 1988a).

Most marine turtle eggs are laid on islands where potential egg predators are scarce. The principal threats to egg survival in Australia are early infertility and/or embryonic death, flooding and erosion, and possibly microbial invasion (Parmenter 1980; Limpus 1985; Limpus *et al.* 1983a, 1983d, 1983b). At most rookeries, approximately 60 to 80% of eggs can be expected to produce hatchlings which reach the beach surface. Exceptions are the eggs of *Caretta caretta*, which are subject to predation by *Vulpes vulpes* on the mainland north of Bundaberg, and those of *Natator depressus* which are eaten by pigs (*Sus* sp.) and varanids on the mainland south of Bamaga and in the Northern Territory. At most rookeries, there is < 2% loss of hatchlings to terrestrial predators during the beach crossing (Limpus 1973), unless nocturnal predators are present (Limpus *et al.* 1983d).

The most intense predation on hatchlings probably occurs in the sea, however recruitment and survivorship in feeding areas are poorly documented. The principal predators of large marine turtles are tiger sharks, crocodiles, toothed whales and man (Balazs 1980; Limpus *et al.* 1983d; Caldwell & Caldwell 1969). Survivorship from egg to breeding adult is low, estimated at between a few per thousand and a few per ten thousand for *C. caretta* (Limpus 1985; Frazer 1986). Marine turtles in Australia display slow growth and are decades old at first breeding; for example > 30 years for *C. mydas*, *C. caretta* and *E. imbricata* in the southern Great Barrier Reef (Limpus & Walter 1980; Limpus 1985, 1992a). Because of the long period before sexual maturity, survivorship of large immature and adult marine turtles must be very high and the adult must have a long breeding life to maintain population stability (Crouse, Crowder & Caswell 1987). Consequently marine turtle populations consist of a large proportion of immature turtles (Limpus & Reed 1985a; Limpus 1985, 1992a). These same studies have identified widely varying sex ratios for *C. mydas*, *C. caretta* and *E. imbricata* inhabiting the southern Great Barrier Reef. Of these species *E. imbricata* occurs at the lowest density (3.34 turtles/km^2, and with a low biomass (0.82 kg/ha) (Limpus 1992a).

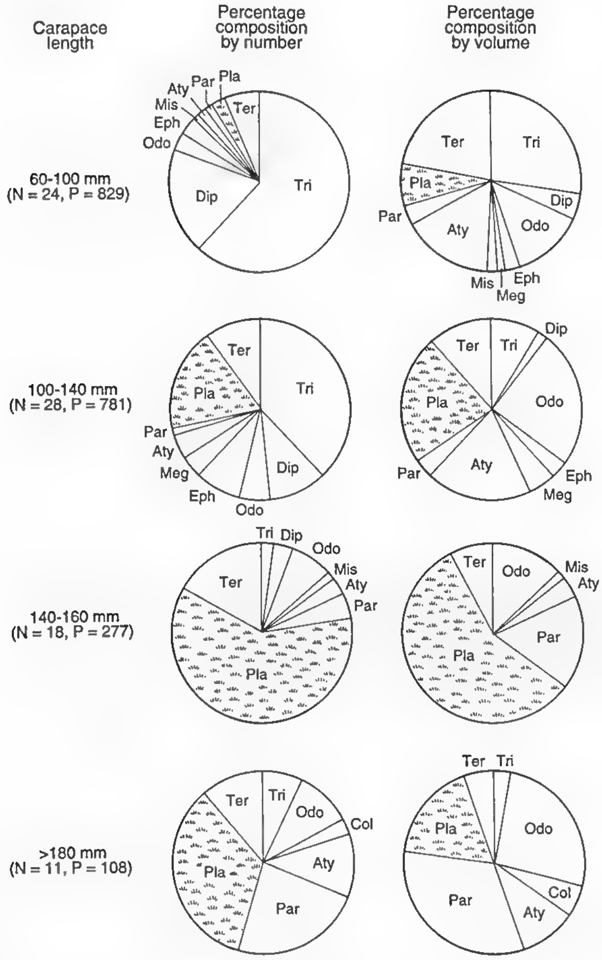

Figure 17.3 Variation in the composition of the diet of *Emydura krefftii* with increasing body size, as measured by the frequency of occurrence of prey in stomachs by number or by volume. **aty**, atyid crustaceans; **col**, coleopteran larvae; **dip**, dipteran larvae and pupae; **eph**, ephemeropteran nymphs; **meg**, megalopteran larvae; **mis**, miscellaneous aquatic insects; **odo**, odonate nymphs; **par**, parastacid crustaceans; **pla**, plant material; **ter**, terrestrial arthropods; **tri**, trichopteran larvae. [W. Mumford]

ECOLOGY

Diet

Turtles, with their rounded body form and heavy investment in bony skeletal elements, are not renowned for their agility, and this has placed restrictions on the foods they can exploit (Pritchard 1984). Most freshwater turtles are omnivorous, although some species have resorted to herbivory (for example, testudinids), and there are a few carnivorous specialists, such as *Pseudemydura umbrina*, *Chelus* species from South America and *Claudius* species from Mexico. Carnivorous turtles may feed upon invertebrate prey even slower than themselves, while others rely upon stealth to secure more mobile prey.

Australian freshwater turtles typically are omnivorous (Fig. 17.3; Chapter 21). Temperate species of *Emydura*, for example, consume a broad range of foods including filamentous algae, periphyton (including sponges), a wide variety of aquatic macrophytes, aquatic macroinvertebrates, terrestrial insects which fall or are blown onto the water, and carrion (Legler 1976; Georges 1982b; Chessman 1986). There is a general tendency for juveniles of omnivorous species to be more carnivorous than adults (Fig. 17.3; Georges 1982b; Moll & Legler 1971).

Omnivorous species of the wet-dry tropics, such as *Carettochelys insculpta*, *Elseya dentata*, *Emydura victoriae* and *Emydura 'australis'*, rely heavily upon the seeds, fruits and leaves of riparian vegetation during the dry season, supplemented with aquatic macrophytes, algae, macroinvertebrates and carrion (Fig. 17.3; Legler 1976; Georges & Kennett 1989).

There is considerable overlap, especially among omnivorous species, in the dry season habitat preferences and diets of the tropical turtles. It may be that these similarities do not persist during the wet season, and that unique aspects of habitat and food preferences among species would emerge if studies were conducted then. Alternatively, the highly variable nature of the tropical climate, and the interconnectedness of aquatic environments in wet seasons, may result in interchange and re-invasion of river systems by ecologically similar species, at a greater rate than the slow process of competitive exclusion.

Newly hatched marine turtles presumably feed on the macroplanktonic algae and/or animals in surface waters. Juvenile marine turtles, except *Dermochelys coriacea*, are principally benthic feeders during residence in shallow waters of the continental shelf. *Dermochelys coriacea* is a plankton feeder throughout life, feeding principally on jellyfish and planktonic tunicates (Brongersma 1972). In Australian waters, *C. mydas* feeds mostly on seaweed, seagrass and mangrove fruits, *C. caretta* and *Lepidochelys olivacea* feed mostly on shellfish and crabs, *N. depressus* feeds mostly on soft corals and sea pens, and *E. imbricata* eats sponges primarily. All species eat jellyfish and Portuguese man-of-war on occasions (Lanyon, Limpus & Marsh 1989; Moody 1979; Guinea & Limpus unpub. data).

Patterns of Habitat Use

Chelonians have specialised along two major paths with respect to habitat utilisation. Marine turtles of both the Cheloniidae and Dermochelyidae migrate as adults (Meylan 1982) and have a planktonic dispersal phase as young (Carr 1986). Such highly mobile animals can utilise widely separated habitats, enabling them to optimise feeding and survival for different age/size classes and select specialised breeding habitats. This is made possible by the relative stability and predictability of the marine ecosystem.

In freshwater and brackish water ecosystems the habitat is fragmented and a turtle will require wider physiological and morphological capabilities if it is to disperse widely as it will have to traverse terrestrial or marine habitats. In reality, these capabilities are limited. As a result, freshwater and brackish-water turtles tend to be restricted to particular river systems. Consequently, their lifestyle needs to be more closely adapted to deal with the vagaries of local climate and ecology.

Many species of Australian freshwater turtle occupy only permanent water of riverine and lentic ecosystems. Often several species will co-occur in the one river drainage (Fig. 21.7). For example, six species of freshwater turtle occur in the Fitzroy-Dawson drainage of Queensland (Legler & Cann 1980). The dominance of each in different microhabitats, as described in Chapter 21, together with variation in diet, presumably allow these species to co-exist in the same drainage. In discussing similar patterns of habitat fidelity on Fraser Island, Georges, Norris & Wensing (1986) speculated that the combined presence of *Emydura krefftii* and *Chelodina expansa* in the permanent dune lakes might virtually exclude *C. longicollis* because of competition for food. Such competition may be exacerbated by the presence of fish (Chessman 1988).

Competition between species is remarkably difficult to demonstrate, primarily because the effects of passive competitive exclusion and character displacement are most evident at evolutionary time scales. Theories of passive competition for resources that explain the distribution and abundance of freshwater turtles in Australia have very little direct experimental support and remain speculative.

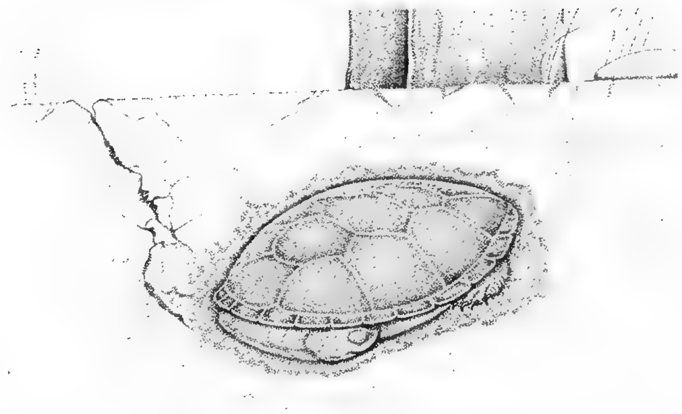

Figure 17.4 Position and posture of the chelid *Chelodina rugosa* during aestivation. [T. Wright]

Ephemeral aquatic environments are generally highly productive, particularly if they have dried completely before refilling. In addition, species that would otherwise compete with turtles for food, such as fish (Chessman 1984), are often unable to invade isolated ephemeral swamps. However, the numerous species of freshwater turtle that do exploit the benefits of such environments are still subject to the problem of periodic and often unpredictable habitat loss. Many species aestivate during such dry periods, including *Pseudemydura umbrina*, *Chelodina rugosa* (Fig. 17.4), *C. steindachneri* and *C. novaeguineae*. *Chelodina longicollis* migrates to more permanent water.

In southern New South Wales, *Chelodina longicollis* migrates overland to seek refuge in permanent dune lakes when ephemeral swamps and ponds dry during periods of low rainfall. At such times, the number of turtles in the lakes reflects the carrying capacity of both the permanent and ephemeral waters of the region, and may well exceed the carrying capacity of the lakes alone. Exceptionally high population densities were recorded for these lakes at the end of 1978–1983 drought (Georges *et al.* 1986). As a result, turtles were in poor body condition, grew slowly and failed to breed in 1986 (Kennett & Georges 1990).

Following a drought, *Chelodina longicollis* returns to the ephemeral waters as they become available again, and act as the focus for reproduction, recruitment and growth. Rain appears to stimulate a very rapid migratory response in this species. The migratory tendencies of *C. longicollis* probably first evolved in response to selection for an ability to exploit productive ephemeral waters in the absence of competition from fish (Chessman 1984) and other species of turtle (Georges *et al.* 1986; Chessman 1988). Once populations grew to approach the carrying capacity of both the ephemeral and permanent waters of a region, individuals would have often found themselves occupying more restricted permanent water during extended dry periods, where intense intraspecific competition for food would cause a sharp decline in growth and reproductive output, as described above. In turn this would enhance selection for a rapid migratory response and preference for ephermeral habitats.

Reproductive potential and onset of sexual maturity depend on size and not age in turtles (Gibbons 1982), so any delay in growth while occupying a drought refuge would have considerable consequences for reproduction of individuals. Under these circumstances, occupation of ephemeral waters would afford much greater selective advantages than could have been predicted from a comparison of production in ephemeral and permanent waters alone.

In the tropics, *Chelodina rugosa* and *C. novaeguineae* attain highest densities in ephemeral waters. They take advantage of high production during the wet season and survive the dry season by migrating to permanent water or by aestivation. *Chelodina rugosa* occupies shallow ephemeral waterbodies of floodplains in low lying country adjacent to the Gulf of Carpentaria and between the Arnhem Land and Kimberley plateaux. At the end of the dry season, *C. rugosa* buries beneath the mud of the waterbody in which it lives, to await the wet season innundation (Fig. 17.4). It obtains its oxygen through a breathing hole until the ground dries and cracks. This cycle of aestivation and activity of *C. rugosa* is annual.

Chelodina novaeguineae occupies more marginal xeric environments where annual rainfall is less predictable. When the ephemeral waterbodies dry, individuals migrate to the surrounding scrub and aestivate beneath litter, in the burrows of other animals or in drainage crevasses. Aestivation by *C. novaeguineae* is not necessarily annual, and the species can aestivate for two or more years (Cann pers. comm.).

Marine turtles utilise traditional nesting beaches in tropical and warm temperate regions and feed throughout the tropical and temperate seas of the world at some stage in their life cycles. *Dermochelys coriacea* migrates to tropical nesting beaches from open ocean feeding grounds as far afield as the high latitude waters adjacent to pack ice (Pritchard 1971; Goff & Lien 1988). Along Australian shores, *D. coriacea* nests infrequently in south-eastern Queensland, but it is commonly encountered feeding along the continental shelf to the south of the Great Barrier Reef and off south-western Western Australia (Limpus & McLachlan 1979).

Natator depressus nests only on continental islands and the mainland coast of Australia, largely avoiding beaches fringed by coral reef (Limpus, Gyurus & Miller 1988; Parmenter in press). Unlike other marine turtles, post-hatchling dispersal does not include an oceanic component and this species spends most of its life over the Australian continental shelf (Walker & Parmenter 1990). The species is captured most frequently over soft bottom inshore habitats of the Great Barrier Reef, within the Gulf of Carpentaria and throughout the Arafura Sea (Limpus *et al.* 1983c; Poiner & Harris in press).

The remaining marine turtle species have an oceanic post-hatchling dispersal phase in the life cycle (Fig. 19.4; Carr 1986). In Australian waters, *Chelonia mydas* nests principally on islands near the oceanic margin of the continental shelf, from the tropics northwards. *Eretmochelys imbricata* nests on islands on the inner margin of the Continental shelf within the tropics, and *Lepidochelys olivacea* nests principally on continental islands in north western Arnhem Land. *Caretta caretta* nests on the mainland and adjacent islands near the Tropic of Capricorn on both the east and west coasts (Limpus 1982, unpub. data).

The adult and immature turtles of these species occupy a diversity of feeding areas within a radius of some 2600 km of their rookeries (Limpus *et al.* 1992). *Chelonia mydas* feeds principally in coral reef and inshore seagrass pastures in tropical and warm temperate areas (Lanyon *et al.* 1989). *Eretmochelys imbricata* is most commonly found feeding in coral and rocky reef habitats in tropical areas (Limpus 1992a; unpub. data), while *Lepidochelys olivacea* feeds over soft bottomed habitats across northern Australia (Harris in press; Poiner & Harris in press). *Caretta caretta* feeds across a diversity of habitats including shallow coral reefs to deeper soft bottomed habitats of the continental shelf along all but the southern coast of Australia, although it may be most abundant in warm temperate habitats (Limpus unpub. data).

BEHAVIOUR

Mating

Mating behaviour in turtles has been little studied. In freshwater species, mating behaviour appears to vary between species (Murphy & Lamoreaux 1978), though cloacal touching precedes mounting in all species studied, as described in Chapter 21. In marine species, the males and females aggregate for mating in the vicinity of the nesting beach (Limpus 1993). The male mounts on top of the female, using all four flippers, and enlarged claws in cheloniid turtles, to grasp the carapace of the female (Fig. 19.3).

He then curls his elongate tail under the female to bring the cloacae together, allowing for insertion of the penis (Booth & Peters 1972; Bustard 1972). Although a pair may be joined for many hours, copulation may occur for a much shorter time.

Nesting

Typically, many freshwater turtles undertake nesting activity at night, triggered by rain that falls during the breeding season (Goode 1967; Vestjens 1969). Water temperatures appear important for other species, such as *Carettochelys insculpta*, (Georges unpub. data) and a period of starvation followed by a flush of food availability is an important factor in the successful ovulation and nesting of *Pseudemydura umbrina* (Kuchling & DeJose 1989).

Nesting behaviour has been observed for a number of Australian chelids. After digging a cavity, *Emydura macquarii* deposits its eggs (Fig. 17.1), fills the excavation with soil, and then drops its shell hard onto the ground to compact the soil in the filled nest (Goode 1965; see also Chapter 21). This tamping of the soil has been observed also in *Chelodina longicollis* (Vestjens 1969), *Chelodina oblonga* (Clay 1981), *Chelodina expansa* (Georges pers. obs.) and *Pseudemydura umbrina* (Kuchling in press).

The nesting behaviour of all marine turtle species is very similar (Bustard & Greenham 1969; Bustard, Greenham & Limpus 1971). The female searches out a nest site above the high tide level and excavates a depression (body pit) of variable depth, using all four flippers, and places her body down to the level of relatively firm sand. She then excavates a vertical, flask shaped egg chamber under the tail using the hind flippers. The eggs are laid such that they drop directly into the egg chamber (Fig. 17.2). At the completion of laying, moist sand is scooped into the chamber with the hind flippers, and tamped down at intervals as the chamber fills. The tamping action of smaller species (*L. olivacea*, *E. imbricata*, *N. depressus*) may be quite vigorous. When the egg chamber is filled, the female then digs her way forward for a variable distance, using her front flippers to dig sand from the front and fling it back, and the hind flippers to push sand to the middle back of the body pit. After the pit is refilled, the female returns directly to the sea. The duration of nesting varies from about an hour (*L. olivacea*, *E. imbricata*, *N. depressus*), to one and a half hours in *C. caretta* and *D. coriacea*, and three hours in *C. mydas*.

Following pipping, the hatchling remains for a day or so at the egg shell while it uncurls and internalises the remains of the yolksac (Miller 1985). The hatchlings dig as a group to the surface over several days and emerge from the nest, usually at night (Bustard 1967b; Limpus 1973, 1985). On emergence, they orientate to low elevation light horizons (Limpus 1971b; Salmon, Wyneken, Fritz & Lucas 1992) which will normally direct them seawards. There is evidence of imprinting of the hatchlings to the earth's magnetic field at the nest (Lohmann 1991), and possibly to the water that they first contact (Grassman, Owens, McVey & Marquez 1984). Immediately the hatchlings reach the water they begin swimming, and orientate perpendicular to wave fronts, a behaviour which normally takes them into deeper water (Salmon & Lohmann 1989). The hatchlings at this stage live on yolk from the yolksac and do not feed or sleep while on the beach or while swimming out to sea.

Thermoregulatory behaviour

Chelonians, like all reptiles, are ectothermic. They rely upon ambient temperatures remaining within the range conducive to their general activity, or when this is not so, the animals use thermal sources and sinks within their environment to maintain body temperatures within the preferred range. Reptiles have a vast repertoire of behaviours to regulate their body temperatures within fairly narrow limits while active, quite irrespective of ambient temperatures, but turtles are limited in this regard because the water in which they live is thermally conductive and they lack effective insulation. While large turtles can be expected to have considerable thermal inertia, and circulatory mechanisms exist to minimise heat transport from body core to the surface (Hutchison 1979), for most freshwater turtles, any elevation in body temperature achieved is quickly dissipated in the surrounding water.

Freshwater turtles thermoregulate primarily by seeking out warmer strata, typically at the water surface or in slower moving shallow waters (Fig. 17.5), by basking in the sun's rays while floating at the surface, or by leaving the water altogether and basking (Fig. 17.6; Chapter 21). Basking is a major component of daily activity in Australian chelids (Webb 1978), and occurs in two major periods for *Emydura* sp. and *Elseya latisternum*. These shortnecked chelids bask until they exhibit signs of discomfort similar to those reported in the Panamanian *Pseudemys* (Moll & Legler 1971). These consist of tear secretion, gular movements,

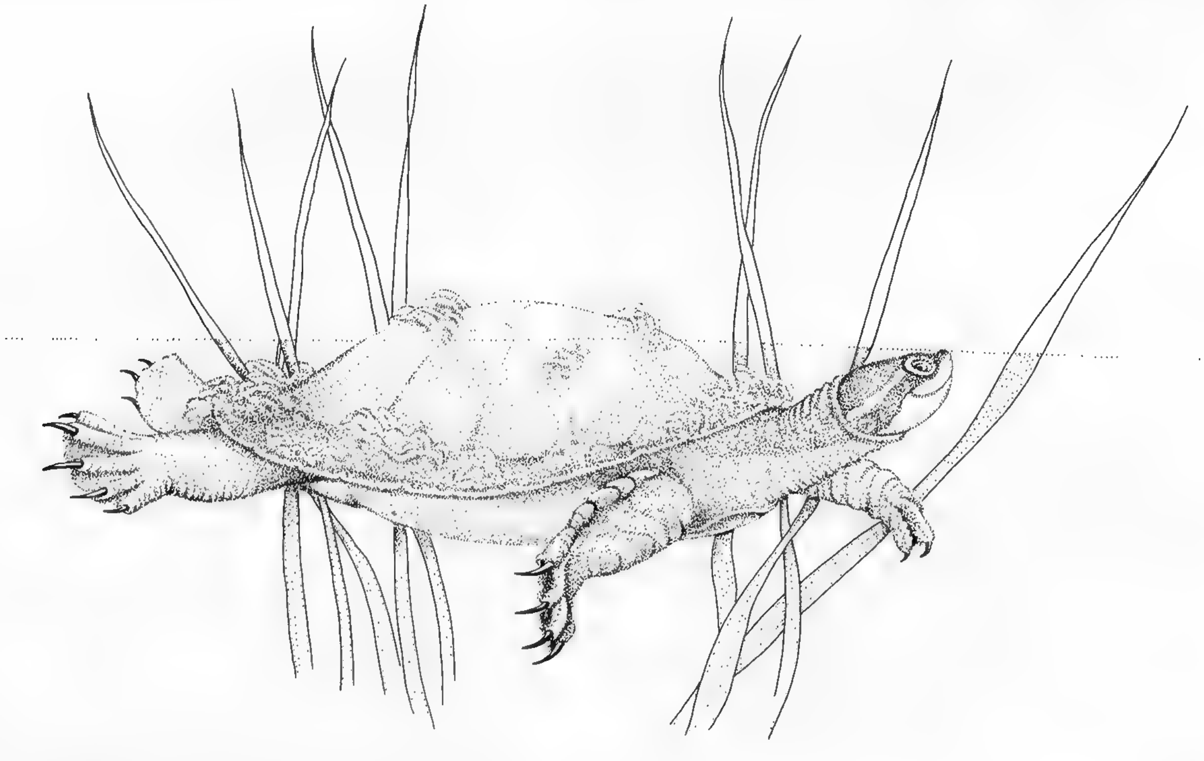

Figure 17.5 Aquatic basking posture of the chelid, *Emydura krefftii*. (After photo by J. Cann/ANT) [T. Wright]

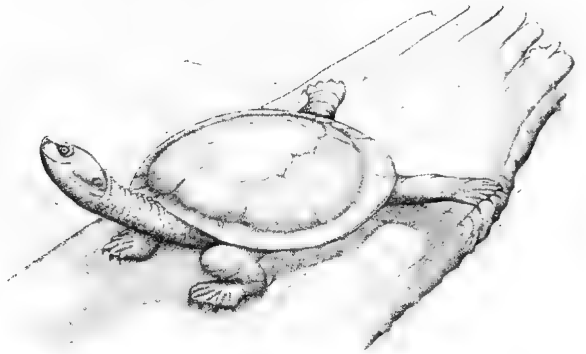

Figure 17.6 Aerial basking posture in the chelid, *Emydura macquarii*. [T. Wright]

panting, frothing from the mouth and wiping tears or water over the surface of the head. *Chelodina expansa* and *C. longicollis* bask only occasionally (Webb 1978).

Of the marine turtles, only *Chelonia mydas* leaves the water to bask and does so most frequently at breeding time (Whittow & Balazs 1982; Garnett & Crowley 1985). *Chelonia mydas*, *Caretta caretta*, *L. olicacea* and *N. depressus* may bask by floating high at the water surface (Sapsford & van der Reit 1979; Limpus unpub. data). During sunny days basking can result in elevated body temperatures (Whittow & Balazs 1982; Sapsford & van der Reit 1979). However, since *C. mydas* will bask on beaches even at night when they would be losing heat, it is doubtful if these basking activities are always primarily for thermoregulation (Garnett & Crowley 1985; Limpus unpub. data).

ECONOMIC SIGNIFICANCE AND MANAGEMENT

Research

Research on freshwater turtles for management purposes requires information on distribution and abundance, in order to assess the current population status of the species, to determine its specialisation for particular microhabitats, and to establish a baseline for monitoring population trends. Hoop traps, baited with bread, sardines, meat, fish or a combination of these, are most useful for capturing freshwater turtles (Legler 1960a). Hoop traps yield samples of *Emydura krefftii* (Fraser Island) that are unbiased with respect to size and sex (Georges 1985).

Capture rates of turtles in baited hoop traps in the Northern Territory are very low, with notable exceptions, and a modification of the design to enable accumulation of turtles over a period of days or weeks has been developed by Kennett (1992). Diving may be precluded by risk of attack by saltwater crocodiles. Turtles can be collected in relatively clear waters using a dip-net and spotlight from a punt at night. This is particularly successful for capturing *Carettochelys insculpta*, *Emydura victoriae* and *Elseya dentata*. Baited traps readily catch *Chelodina longicollis*, *C. rugosa* and all species of *Emydura* and *Elseya*, but they are of limited use with *C. expansa* and *Pseudemydura umbrina*, species which feed principally or solely on live animals. Other methods of capture are discussed in Chapter 14.

Chelid turtles can be permanently marked by cutting notches in the marginal scutes and underlying peripheral bones with a file or small hacksaw. A semi-binary code (Fig. 17.7) is preferable to minimise the number of adjacent notches in any one quarter of the carapace. Notching is inappropriate for *Carettochelys insculpta*, which lacks scutes. Further, the carapace margin is well-vascularised, and cutting the peripheral plates, visible beneath the overlying skin, results in unacceptable bleeding and such notches are not permanent (Georges & Kennett 1988). Though cattle ear tags can be attached to the shell through a hole drilled in the lateral margins of the carapace, these are only useful for one to two years. A tagging system similar to that used on marine turtles (Limpus 1992b), or freeze branding, are alternatives worthy of investigation for marking this species.

Once a marked population is established, it is possible to estimate population sizes using one of many mark-recapture techniques (Seber 1973). Catchability among individuals varies considerably (Georges 1982a) and use of techniques catering for such variation, such as the regression methods or frequency of capture methods (Seber 1973), should be explored as alternatives to the traditional Peterson and Jolly-Seber methods, unless sampling intensity is high (>75% of the population marked).

Traditionally, reproductive biology of freshwater turtles has been studied by killing turtles on a monthly sampling basis and examining the reproductive organs (Georges 1983). However, such destructive sampling is rapidly becoming ethically unacceptable, and is not feasible for assessment of species at risk. Radiography (Gibbons & Greene 1979), laparoscopy (Limpus & Reed 1985a) and ultrasound scanning (Kuchling 1989) provide practical alternatives to dissection and direct examination of reproductive organs. Radiography can detect and allow counting of shelled oviductal eggs, but soft parts such as corpora lutea or enlarged ovarian follicles are not revealed. Long-term effects of repeated exposure of turtles to X-rays is not known.

Gonadal structure can be examined, measured and biopsied by laparoscopy, but there are limitations on accurate counting and some measurements (Limpus 1992a). Ultrasound scanning is an accurate method to measure and count large structures such as eggs and follicles. However, there are limitations on the depth of reliable viewing with large animals, and small structures, such as corpora albicantia, may not be resolved in the images produced. Though these new technologies have their strengths and weaknesses, they have the potential to contribute significantly to population studies.

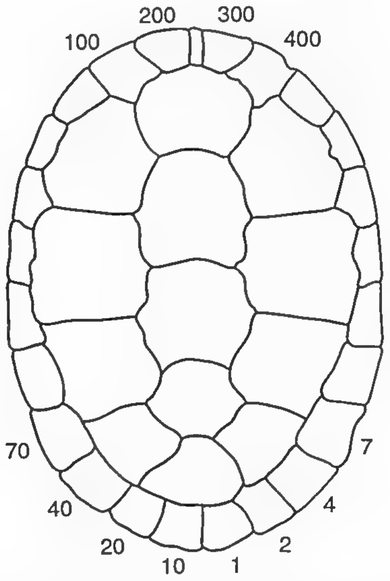

Figure 17.7 Diagram showing the marking scheme used to identify individuals of *Emydura krefftii*. Notches are cut into the marginal scutes and underlying peripheral bone with a file or small saw, to form a permanent and unique pattern. Individuals are identified by adding the numbers assigned to particular scutes; for example turtle number 3 is marked by notching scutes 1 and 2 on the right rear of the carapace. [D. Wahl]

Stomach contents can be obtained by stomach flushing (Legler 1977). A 12V submersible pump is used to supply a steady flow of water, which is passed into the stomach through a flexible plastic tube (Georges *et al.* 1986). The water then passes back up the oesophagus carrying food particles with it. Water flow is adjusted for turtles of different sizes by interchanging tubes of different diameters. The food particles are caught in gauze and transferred to 70% ethanol for later sorting and identification.

Percentage composition of the diet by number, weight or volume, and occurrence (Windel & Bowen 1978) are traditionally used to assess the relative importance of various food types in the diet. Caution must be exercised in the interpretation of diet from stomach contents, as the proportional representation of foods in the stomach does not reflect diet in a strictly quantitative sense. Different foods differ in their digestibility and rate of passage through the gut. Nor do animals forage at random, so foods found in the stomach of an individual at one time do not necessarily provide a random selection of foods eaten by that individual over time. To assess the degree of dietary specialisation, one must compare the foods eaten with the foods potentially available in the environment, either qualitatively or quantitatively (Georges *et al.* 1986).

Criteria for Setting Conservation Priorities

Australian freshwater turtles do not often fall into the category of species in conflict with community goals, values and aspirations. Nor are they a major economic resource, at least for Australian communities. Priorities for their conservation must therefore be based on values that cannot be measured on an economic scale.

There are three intrinsic attributes with a bearing on the conservation priority accorded a species. The first is distinctiveness, important because it may enhance both its aesthetic and scientific value. If a species is taxonomically distinct, then it will lack close relatives which may share some or many of its features, and much may be lost if such a species becomes extinct. The second attribute is rarity. Rarity in the colloquial sense may increase the aesthetic value of a species, and so increase public pressure for adequate conservation measures. Rarity in the biological sense combines both abundances and distribution (Rabinowitz, Cairns & Dillon 1986). An abundant species with a geographically restricted distribution can be quite vulnerable to extinction through habitat destruction, climatic change or disease, whereas an ubiquitous species with low abundances throughout its range may be quite secure. The third attribute is a species' intrinsic vulnerability to decline and eventual extinction. Rarity, low fecundity, susceptibility to disease, specialisation on particular foods or other environmental attributes are all examples of factors contributing to a species' vulnerability to extinction.

Extrinsic factors also have a role to play in setting conservation priorities. Are there current threats to populations, and is there a pressing need for intervention to negate or offset the deleterious effects of human activities or natural events? Opposing factors include logistic constraints — whether they be legal, economic, social or biological — that diminish the feasibility of conservation measures or render them impractical. Feasibility must be gauged against the objectives of management, namely to preserve the current Australian turtle diversity by preventing further extinctions. A second objective, and one that requires more investment to achieve, is to conserve species in the context in which they evolved so that we also preserve the processes that maintain genetic diversity and lead ultimately to speciation.

Conservation Priorities

Among freshwater forms, *Pseudemydura umbrina* sits high on the list of priorities. It is distinctive both taxonomically and morphologically. It represents a monotypic genus, and its nearest living relatives may be among the chelids of South America (Legler 1981). The species is exceptionally rare (Burbidge 1981; Kuchling & DeJose 1989), being restricted to a wild population of less than 30 individuals near Perth in Western Australia. It is vulnerable by its inflexible preference for ephemeral waters, even when permanent water is available and accessible (Burbidge 1983), in a climatic regime where its habitat is flooded in the colder months of the year. It also has the lowest fecundity of any Australian chelid, laying only one clutch of three to five eggs per season. The species is threatened by habitat loss through past draining of swamps for land reclamation and by predation on eggs and adults by introduced foxes, which are devastating predators of freshwater turtles throughout their range (Parmenter 1976; Thompson 1983; Palmer-Allen *et al.* 1991). Current measures are directed at captive breeding and re-introduction to an area within its former range (Burbidge, Kuchling, Fuller, Graham & Miller 1990; Kuchling & Bradshaw 1992; Kuchling & DeJose 1989; Kuchling, DeJose, Burbidge & Bradshaw 1992).

Carettochelys insculpta is Australia's most distinctive turtle, both morphologically and taxonomically. It is the sole remaining species in its family, and as such represents all that remains of 40 million years of evolution independent of any other extant lineage (Chen, Mao & Ling 1980). The species was once considered to be one of the rarest turtles in the world (Groombridge 1982), but it now appears that where it is found, it may be locally quite abundant (Georges & Kennett 1989). It is rare in the sense of being geographically restricted, as a family, to southern New Guinea and northern Australia. In Australia, it is distributed from the Victoria River in the west to the Goomadeer River in the east, but abundant only in the Daly and Alligator drainages. The species is vulnerable by virtue of its limited distribution, and because stereotyped nesting habits render it susceptible to over-exploitation. Adults and their eggs are highly regarded as food by indigenous peoples throughout its range, and exploitation for food is thought to be threatening populations in New Guinea (Groombridge 1982). Habitat degradation is the major potential threat to Australian populations (Georges 1988b).

Third on our list of priorities for freshwater turtles is *Rheodytes leukops*. It is distinctive enough to be placed in a monotypic genus, and has no clear affinities with any other Australian freshwater turtle (Georges & Adams 1992). Morphologically, it is quite striking because of its capacity to extract oxygen from water using well-vascularised gills in a well-ventilated cloaca (Chapter 16). The species is restricted to a single drainage, the Fitzroy-Dawson system of central Queensland, and while there are no data on abundances, it is considered quite rare by virtue of its limited distribution. The species is vulnerable as a result, and because it is specialised for life in the riffle — fast flowing broken water. With increasing numbers of dams and weirs, riffle is an endangered microhabitat. The biology of *Rheodytes leukops* is poorly known, and its conservation priority may change with further study.

Other distinctive species are largely ignored during considerations on conservation, because they are so poorly studied. Many are undescribed. The three undescribed species of *Elseya* in New South Wales, the new genus colloquially known as shortnecked alpha, the Arnhem Land *Chelodina* are all restricted in distribution, but nothing is known of their biology or population status. *Emydura subglobosa* of the Jardine River on Cape York, is rare, but not considered a high priority because it is not taxonomically distinct above the species level and it is common in New Guinea.

Rare species are not the only ones to attract the attention of conservation biologists. Recent biochemical studies (see Georges & Adams 1992) have shown *E. macquarii* from the Murray-Darling drainage, *E. krefftii* from coastal Queensland and *E. signata* from coastal New South Wales to be a single species, sharing even rare alleles. However, morphological and genetic variation suggest that they are in the process of allopatric speciation. This speciation process could be brought to an abrupt halt if exchange of specimens between drainages is artificially enhanced, say by distribution of hatchling *Emydura* by the pet trade. In contrast, specimens of *Chelodina longicollis* frequently migrate overland and may easily migrate from drainage to drainage. Genetic and morphological variation throughout its range is slight, and commercial distribution of hatchlings and subadults would have little impact on genetic processes leading to speciation. These are important considerations if we are to address seriously the second conservation objective listed above.

Among the marine turtles, *C. caretta* populations that nest in eastern Australia, have declined by more than 50% in the past decade. This decline has been attributed mostly to accidental drowning in fishing gear in Australian waters (Limpus & Reimer in press). There is wide spread and large-scale hunting of *C. mydas* and *E. imbricata* populations that nest in northern Australia. There is no evidence to suggest that the populations are large enough to support the current harvests in the long term. The small number of *L. olivacea* which drown in fishing gear annually in Australia may be excessive for the small nesting populations that occur in Australia. For these species at least, there must be concern for the long term viability of the species in Australia and active conservation management of their populations is required both in Australia and in neighbouring countries.

Management must address a wide range of problems which may be grouped into three broad areas: fishing, development and predation by feral animals. Traditional and commercial harvests of turtles are often carried out in remote areas where enforcement is difficult; fishermen are often reluctant to modify fishing gear in order to reduce turtle capture and death. Development of coastal areas for tourism, agriculture and real estate have negative impacts on turtle nesting and feeding habitat. Predation of eggs and hatchlings by feral foxes and pigs in Queensland may result in future declines in *C. caretta* and *N. depressus* populations.

18. BIOGEOGRAPHY AND PHYLOGENY OF THE CHELONIA

John M. Legler & Arthur Georges

The earliest known turtles, *Proganochelys*, had unspecialised cervical vertebrae (Gaffney 1990) and presumably were unable to retract the head beneath the shell. This innovation was later achieved in two ways. One lineage, the suborder Cryptodira, evolved a mechanism whereby the neck flexes in the vertical plane when retracted beneath the shell. In these forms, the head is still pointed in a forward direction when retracted. The suborder comprises nine extant families, and most of the living species. The majority occur in the temperate region of the northern hemisphere, and in the tropics. The only Australian representatives are the marine turtles, families Cheloniidae and Dermochelyidae, and the freshwater pig-nosed turtle, *Carettochelys insculpta*.

In the second lineage, the suborder Pleurodira, the neck flexes in the horizontal plane so that the head points towards the left or right when retracted. The suborder comprises two families. The Pelomedusidae includes five genera *Erymnochelys*, *Pelomedusa*, *Peltocephalus*, *Pelusios* and *Podocnemis*. Though presently restricted to the South American and African continents, they were once widely distributed across the northern hemisphere. The Chelidae includes five genera *Chelodina*, *Elseya*, *Emydura*, *Pseudemydura* and *Rheodytes* currently found in Australia, New Guinea, the island of Roti (Lesser Sunda Islands, Indonesia), and South America. There are reports of fossil chelid turtles from Europe, North Africa and India, but the diagnosis of these fossils as chelids is either incorrect or has been brought into serious question (Williams 1953, 1954b). There is no well accepted evidence that fossil chelids occur outside the range of extant taxa (Pritchard 1979b; Pritchard & Trebbau 1984). As such, chelid turtles are the only reptile group with clear Gondwanan origins.

DISTRIBUTION

Freshwater turtles are cosmopolitan with breeding populations occurring in suitable habitats in temperate and tropical regions of major continents, large islands, and some oceanic islands. There are epicentres of diversity in the eastern United States of America and southern Asia (Fig. 18.1).

The five extant genera of marine turtles have worldwide distributions in tropical and temperate waters, except for *Natator depressus* which is endemic to the Australian region.

Cryptodires are now the only turtles of the Northern Hemisphere, but they occur also in the Southern Hemisphere. Pleurodires now occur only in the Southern Hemisphere. There is a substantial fossil record for pelomedusid turtles in the Northern Hemisphere, but there is no evidence that chelids ever occurred there.

Cryptodires exhibit extremes in geographic range. Painted turtles (*Chrysemys picta*) and snapping turtles (*Chelydra serpentina*) of Canada have the most northerly distribution (about 52°). These turtles probably occur at or near the northern limits for oviparous reptiles. This distribution is equalled only by a few oviparous snakes (*Opheodrys*, *Pituophis* and *Storeria*) (Conant 1975). *Geochelone chiliensis*, a terrestrial tortoise has the most southerly distribution, and occurs at 43°S in Argentina. The emyidid, *Pseudemys scripta*, ranges from 42°N to 36°S, a total of 78° of latitude, possibly the widest breeding range of any freshwater turtle (Legler 1990). Sea turtles may range widely to the north and south of their breeding ranges. *Dermochelys coriacea* has the largest latitudinal range of any known turtle, from the north coast of Iceland to 47°S, a total latitudinal range of 113°.

Most chelid turtles occur in temperate or tropical latitudes. There is a varied fauna of pelomedusids and testudinid tortoises at or near the southern tip of Africa (*ca.* 35°S). *Phrynops geoffroanus* is the southern-most South American chelid (30°S). Australian chelids occur to the latitudinal extremes of the continent, but have epicentres of diversity between 23° and 25°S in eastern Queensland (see Chapter 21).

Limiting Factors

All extant Australian chelids are aquatic. Their geographic distribution is generally limited by the presence of permanent water or its seasonal yet predictable occurrence in natural drainage systems (Anon. 1967; Leeper 1970) as discussed in Chapter 21. A notable exception is *Chelodina steindachneri*, which occurs in

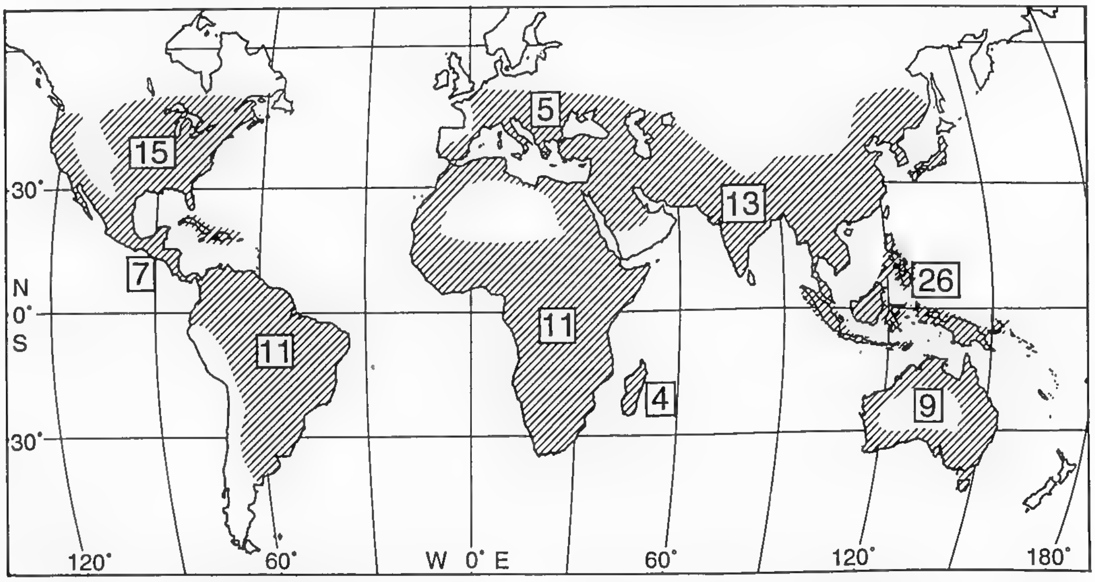

Figure 18.1 Worldwide distribution of the freshwater chelonians. Numbers of genera are indicated for each of eight regions: North, Central and South America, sub-saharan Africa, with Madagascar as a subset, Europe and North Africa, India, South-East Asia, and Australia. [W. Mumford]

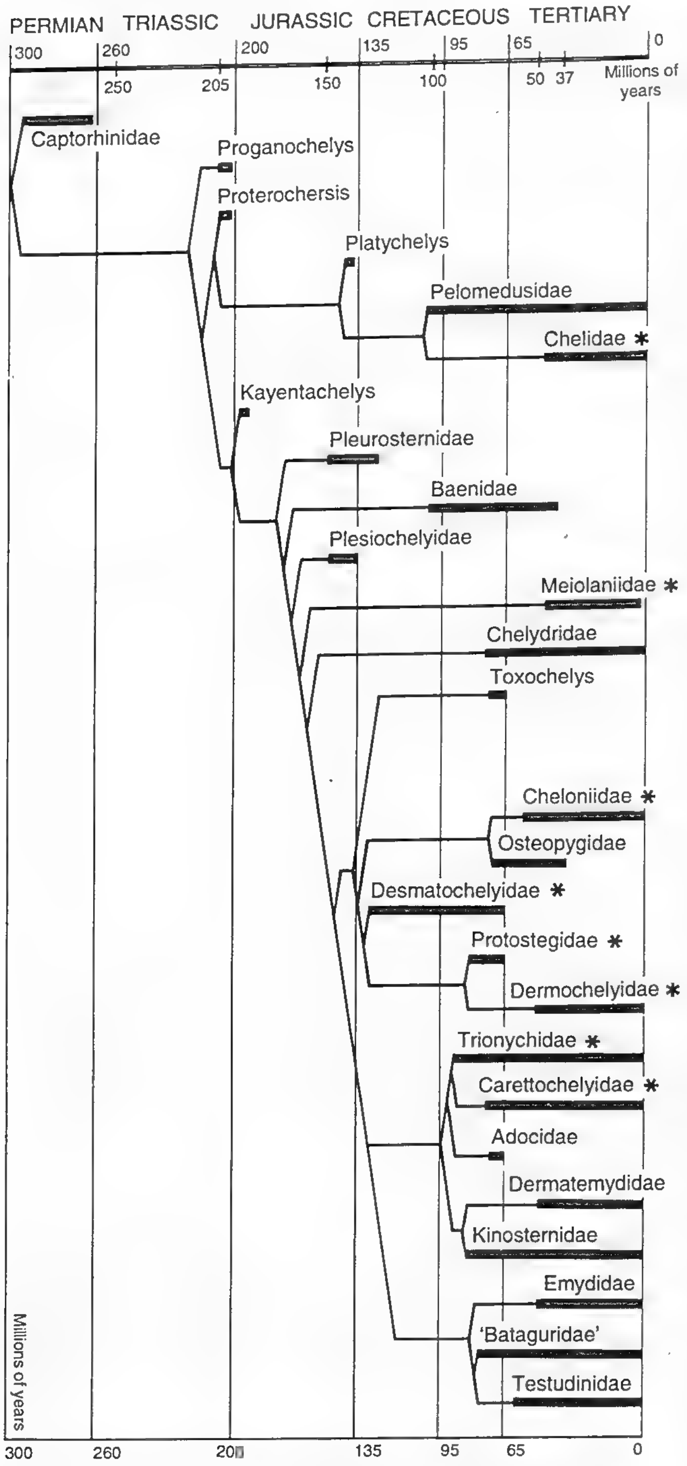

Figure 18.2 Phylogenetic tree showing the relationships of living and fossil turtles. (After Gafney & Meylan 1988) [D. Wahl]

water courses that fill unpredictably and which may be dry for well over one year.

However, in well-watered temperate regions, temperature is probably a limiting factor in its effect on the incubation of eggs and the digging of nests. Turtles are oviparous and must rely on a warm season long enough for nesting and at least partial embryonic development. Overwintering of eggs and hatchlings is known (Carr 1952; Ernst & Barbour 1972; Ewert 1979). Turtles seem to prefer microhabitats in which they can voluntarily move into different temperatures. Temperatures of approximately 25°C are probably close to optimum, but there is evidence to suggest that temperate aquatic turtles (including chelids) can move about comfortably, eat, mate, and nest at body temperatures of 15°C or lower (see Chapter 16). Southern Hemisphere turtles in general, and chelids in particular, never experience the vicissitudes of temperature of a boreal winter. Water seems to be a far greater limiting factor in the Southern Hemisphere.

Substrates which do not permit the digging of nests may limit distribution in various areas of otherwise favourable habitat. In streams draining to the Murray-Darling system from the New England Tableland, there is usually a distinct fauna above falls or cascades and another below. The intervening zone contains few or no turtles and, although the water in this zone is fast, it is probably the lack of nesting sites that excludes the turtles.

PHYLOGENETIC ORIGIN

The oldest known turtle, *Proganochelys quenstedti* from the Upper Triassic of Bavaria, lived approximately 200 million years ago (Gaffney 1990). The species was first described by Jaekel (1914, 1918). More recently, Gaffney (1990) prepared a monograph on a series of six specimens, including some that were virtually complete skeletons, such that this species is now one of the best known skeletally. Gaffney's restorations and illustrations of *P. quenstedti* suggest an animal with habits, habitat, body form, and general mass similar to the large North American Snapping Turtle, *Chelydra serpentina*. *Proganochelys* has some primitive characters that are absent in living chelonians, but is otherwise quite clearly a *bona fide* turtle. By Triassic times, *Proganochelys* already possessed most of the adaptive modifications that are diagnostic of turtles. In particular, the shell had evolved fully and surrounded the limb girdles.

Unfortunately, *P. quenstedti* provides little or no information about the evolutionary steps leading from the generalised tetrapod body plan to the unique turtle body plan.

The search for turtle ancestry relies heavily on osteological comparisons (usually of the skull) between *bona fide* turtles and groups of reptiles at or near the base of the amniote stock, usually referred to as Stem Reptiles. The two best supported hypotheses of chelonian origin identify different fossil groups of reptiles as the sister group of the Chelonia. Gaffney & Meylan (1988) used the Captorhinidae, a group of anapsids that would necessitate an origin for turtles as early as the early Permian or even late Carboniferous. This hypothetical ancestor would require a gap of approximately 100 million years between the origin of turtles and the oldest material of *P. quenstedti* (Fig. 18.2). Gaffney & Meylan (1988) built their hypothesis on four sets of shared, derived characters (synapomorphies) of the cranium, not all of which are unique to the chelonians and the captorhinids.

Reisz & Laurin (1991) invoked the procolophonids, a group of small tetrapod reptiles (or 'parareptiles') from the Permian of South Africa, as the ancestors of turtles. They supported this hypothesis on one postcranial and nine cranial synapomorphies, all of which are unique to the two sister groups. The hypothesis implies an origin for turtles as late as the late Permian, necessitating a much shorter gap in evolutionary history.

Although these hypotheses are of great interest and importance, neither really addresses the matter of the transition from a generalised tetrapod body plan to that of a turtle. Nor does either have an impact on an understanding of chelonian evolution since the Triassic, or of relationships between existing groups within the order Chelonia.

To date, Deraniyagala (1939) has been the only author to suggest and illustrate a body plan (a whole hypothetical organism) that constitutes a stage intermediate between a generalised tetrapod and a pre-chelonian. His 'saurotestudinate' ancestor from the Permian or Carboniferous, although somewhat fanciful, combines many of the characters that most current turtle biologists would predict in an ancestral group (see Chapter 16).

AFFINITIES WITHIN THE CHELIDAE

Morphology has played an important part and, until recently, the only part in the classification of Australian chelids. However, Burbidge, Kirsch & Main (1974) utilised a serological approach to the classification of the Chelidae, and Georges & Adams (1992) recently presented an analysis of relationships within the

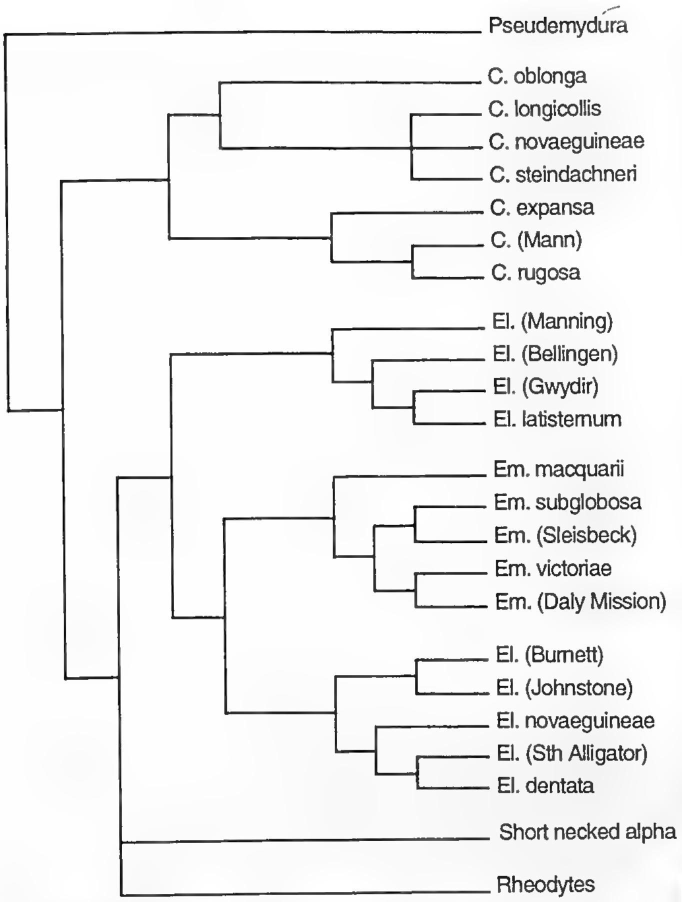

Figure 18.3 Cladogram of relationships within the Chelidae. (After Georges & Adams 1992) [D. Wahl]

Australian chelids, based on biochemical data (Fig. 18.3). There is a general congruence between their findings and those of Legler (1981), based on a phenetic analysis of morphological characters (see Chapter 21). Evidence from both studies, together with that from the recent cladistic analysis of Gaffney & Meylan (1988) strongly support the monophyly of the family Chelidae, and the common ancestry of South American and Australian chelids.

The simplest biogeographic scenario to explain monophyly involves the presence of chelids on the large southern continent, Gondwana. The land mass split into South America and Australia-Antarctica during the Palaeocene or Eocene, 50 to 65 million years ago. Following the separation of Australia and Antarctica, about 45 to 49 million years ago, the Australian plate was completely isolated as it drifted 15° northward, until it collided with the Asian plate about 10 to 15 million years ago (Runcorn 1962; Irving 1964; Dietz & Holden 1970; Doutch 1972; Raven & Axelrod 1972; Tarling & Tarling 1975; Tyler 1979).

The origin of the longnecked freshwater turtles, *Chelodina* and *Hydromedusa* from a common longnecked ancestor is well supported. *Hydromedusa* is known from the early Eocene of South America (Wood & Moody 1976), probably before the isolation of that continent from Gondwana. The longnecked chelids are, therefore, more likely to be monophyletic (Gaffney & Meylan 1988) than convergent (Pritchard 1984). It seems logical that the longnecked condition is derived; *Hydromedusa* is, therefore, regarded as already too specialised to have been ancestral to both longnecked and shortnecked groups (see also Chapter 21).

The evidence for shortneck lineages is not so clear and is not supported by fossils. Cann & Legler (1993) placed Australian shortnecked chelids in three distinct groups. *Pseudemydura*, which is not closely related to any Australian chelid and might be related to *Platemys* of South America (see also Chapter 21); *Emydura*; and the '*Elseya* complex', containing the *Elseya dentata* group, the *Elseya latisternum* group, *Rheodytes*, and shortneck alpha (see Chapter 21). Although *Emydura* and the *Elseya* complex almost certainly have a common ancestry, the present authors do not regard the relationship between these two groups to be as close as do some other authors (for example, Gaffney & Meylan 1988; MacDowell 1983), who place them all in the genus *Emydura*.

BIOGEOGRAPHY

The modern Australian chelonian fauna can be considered in three categories.

The ancient autochthonous fauna includes the chelids, which constitute the dominant continental turtle fauna of Australia. They are the only modern family of turtles common to Australia and South America.

An Asian element of Tertiary origin has entered Australia via the Indo-Australian Archipelago since the Australian and Asiatic plates collided 10 to 15 million years ago. The Australian reptile fauna is predominantly oriental (Tyler 1979), with a large component derived after Australia collided with the Asiatic plate. *Carettochelys insculpta* is probably a part of this oriental group and occurs only in a few river systems in northern Australia and in southern New Guinea. The cryptodiran genus *Pelochelys* belongs in this group if southern New Guinea is considered as a part of the Australian continental plate.

The cosmopolitan element includes the marine turtles of the families Cheloniidae and Dermochelyidae. These occur worldwide and are subject to few or no distributional barriers, with the exception of *Natator depressus*, known only from Australian and New Guinean coastal waters.

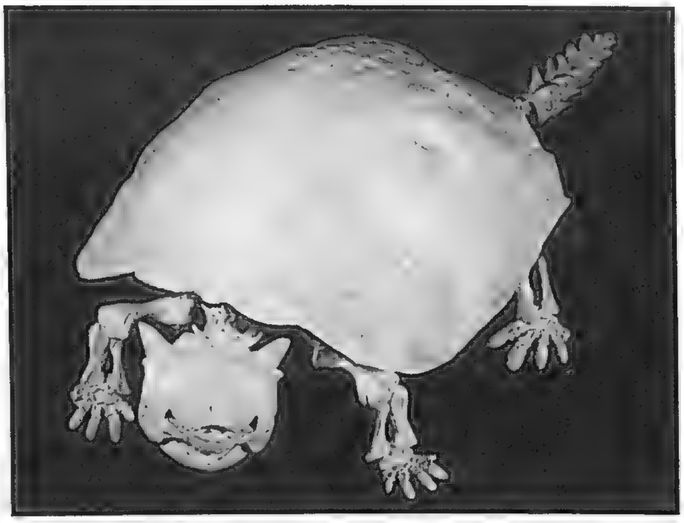

Figure 18.4 Fossil skeleton of *Meiolania platyceps*. [Photo by Australian Museum]

FOSSIL RECORD

The Australian fossil record has yielded sparse but identifiable specimens of the Chelidae and Carettochelyidae, two taxa of Early Cretaceous marine turtles included in the Chelonioidea and specimens of the extinct cryptodiran families Meiolaniidae and Trionychidae (Gaffney 1981). The chelonioid fossils are some 110 million years old. Fossils presently not clearly assigned to any higher taxon, such as *Chelycarapookus* of the Lower Cretaceous of Victoria (Chapman 1919), provide tantalising examples of what may yet be discovered in the fossil record. Warren (1969) was unable to determine the suborder, although the species was assigned recently to a new family, the Chelycarapookidae.

Meiolaniidae

Meiolaniids are considered to be the only real Australian novelty provided by the fossil record. They occur from the Miocene to the Pleistocene on mainland Australia, in the Pleistocene of Lord Howe Island and New Caledonia, and in the Cretaceous and Eocene of South America (Gaffney 1981).

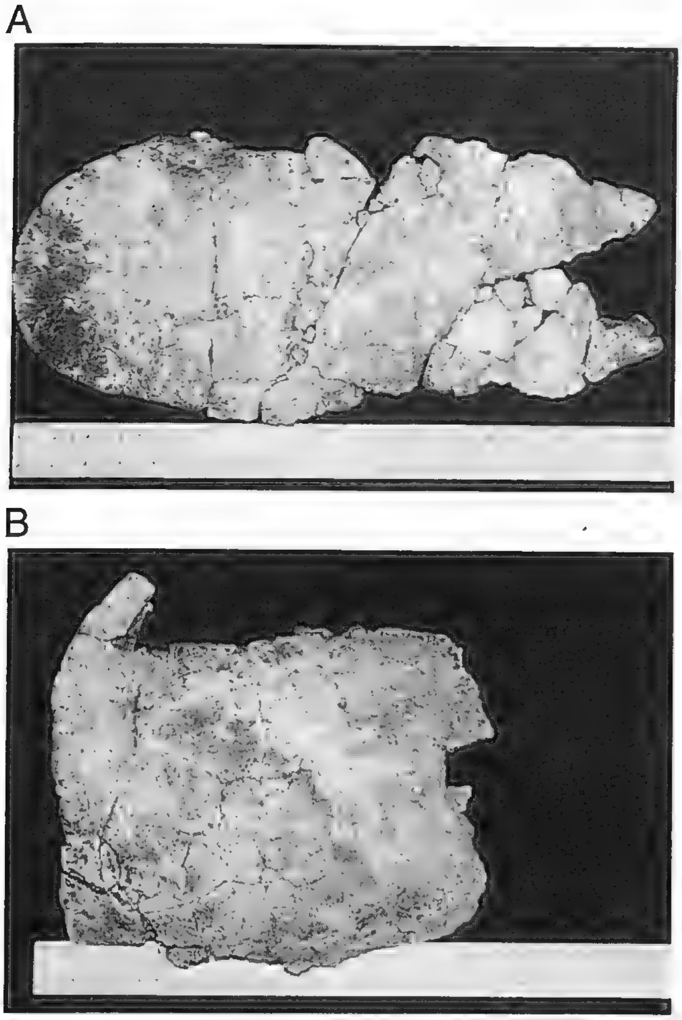

Figure 18.5 Fossil plastron and carapace of *Elseya*. [Photo by J. Cann]

The best known fossil specimens are of *Meiolania platyceps* of Lord Howe Island (Fig. 18.4). They were large terrestrial turtles with cranial horns and frills, cervical ribs, a bony club at the end of their tails and numerous epidermal ossicles (Gaffney 1983, 1985a). Their bizarre appearance led to much confusion when early palaeontologists endeavoured to identify the fossil remains. Their ecology is unknown, but it is thought likely that they had habits similar to the testudinids of the Galapagos and Aldabra Islands (Gaffney 1985b).

Trionychidae

The trionychids are soft-shelled turtles which occur today in Africa, Asia and North America but not in South America or Australia. *Pelochelys bibroni* of New Guinea probably reached the Australasian region from Asia (Darlington 1957).

Fossil material from Australian deposits is fragmentary, but has been diagnosed as Trionychidae on the basis of surface texture pattern and a natural distal edge to the costals, rather than a suture, suggesting that peripheral bones were absent (Gaffney & Batholomai 1979). Trionychids were widespread through Queensland in the late Cainozoic and possibly as early as the Miocene.

Carettochelyidae

Carettochelys insculpta is found today in the southern flowing rivers of New Guinea and the larger rivers of the Northern Territory in Australia (Cogger 1992). It is the sole surviving species of a family that was widespread in the late Tertiary.The genus is represented in the Australasian fossil record by a specimen from the Miocene of New Guinea (Glaessner 1942). A fossil from Western Australia was misidentified as *Carettochelys* by Goster & McNicoll (1978) (Gaffney 1981).

Chelonioidea

The oldest turtles from Australia with definitive stratigraphic data are the marine chelonioids *Cratochelone* and *Notochelone* from the Early Cretaceous Toolebuc Limestones of Julia Creek (Gaffney 1981, 1991).

Chelidae

The Chelidae dominate the extant freshwater turtle fauna of Australia, and are also the most common and widespread fossil turtles. Chelids are restricted in distribution to Australasia and South America, both as living and fossil forms. They range in age from Miocene to Recent in Australian deposits. Chelids are distinguished from other turtles by the presence of a pelvis that is fused to the carapace and plastron, but in the absence of fossil evidence of this character, Australian material often is assigned to the family if neural bones are absent (Gaffney 1981). Fossil specimens have been assigned to the genera *Chelodina*, *Emydura*, *Elseya* and *Pseudemydura* on the basis of diagnostic scute arrangements of the carapace and plastron (Fig. 18.5; Gaffney 1977, 1981; Gaffney, Archer & White 1989). New insight into the evolution of the chelid fauna awaits discovery.

Four of the six extant genera of Australian freshwater turtles are monotypic (*Pseudemydura*, *Rheodytes*, shortnecked alpha, and *Carettochelys*), represented by species that are distinct both morphologically (Ramsay 1886; Siebenrock 1901; Legler & Cann 1980; Cann & Legler 1993) and biochemically (Georges & Adams 1992). Each of these genera arises from lineages of considerable antiquity, as *Chelodina* and *Pseudemydura* may have their closest living relatives among South American forms (Gaffney 1977; Legler 1981). *Carettochelys insculpta* represents an independent lineage of some 40 million years standing (Chen, Mao & Ling 1980). Although today Australia is the driest continent after Antarctica (see Chapter 21), this was not always so. The extant freshwater turtle fauna probably should be considered a relict of a much more diverse fauna of wetter times.

This assertion is not well supported by the fossil record, in part because of little attention having been paid to the turtle elements of Australian fossil collections until recently and, in part, because the morphology of extant forms is poorly known in detail. As Gaffney (1981) pointed out, it is not possible to deal realistically with fossil chelid material at the species level because of the paucity of skeletal material and descriptive work for extant forms. The new taxa described by de Vis around the turn of the century can be diagnosed to family only, and no extinct species can be substantiated at present (Gaffney 1981).

19. FAMILY CHELONIIDAE

Colin J. Limpus & Jeffrey D. Miller

DEFINITION AND GENERAL DESCRIPTION

The Cheloniidae, comprising the hard-shelled marine turtles, is one of only two surviving cryptodiran families from the past diverse marine turtle faunas (Pritchard & Trebbau 1984). The family is characterised by non-retractable, large, paddle-like flippers each with one or two claws (Fig. 15.3A), and keratinised epidermal scutes on the head, flippers, carapace and plastron. The ribs are fused to the overlying pleural bones which, in turn, are fused to each other to form the shield-like bony carapace in adults. The head can be withdrawn partially beneath the carapace, and there are no cusps on the upper jaw sheaths (Pritchard & Trebbau 1984).

The family is represented in Australia by five species, each referred to a separate genus: *Caretta caretta* (loggerhead turtle), *Chelonia mydas* (green turtle), *Eretmochelys imbricata* (hawksbill turtle), *Lepidochelys olivacea* (pacific ridley turtle), and *Natator depressa* (flatback turtle). All species have a worldwide distribution in tropical and temperate waters, except for *N. depressa* which is endemic to the Australian region. Data presented in this chapter refer to the Australian populations, unless otherwise indicated.

Cheloniid turtles have a chromosome number of 2n = 56, with little detectable variability in chromosomal morphology between genera (Kamezaki 1990).

HISTORY OF DISCOVERY

Marine turtles have been known to coastal peoples since ancient times. The eggs and meat were used as food and the carapace scutes were used in constructing ornaments and utilitarian items as well as sacred objects. *Caretta caretta*, *Ch. mydas* and *E. imbricata* were described from the Atlantic Ocean basin by Linnaeus (1758, 1766). *Lepidochelys olivacea* (Eschscholz, 1829) was first described from the Philippines, and *N. depressa* was described from northern Australia by Garman in 1880 (Cogger, Cameron & Cogger 1983).

During early exploration in northern Australia, cheloniid turtles were sought actively for fresh meat. The keratinised scutes, or tortoiseshell, of *E. imbricata*) were traded (Parsons 1962). Explorers like Dampier, Cook, Bligh, Flinders, King, Stokes and Jukes recognised *Ca. caretta*, *Ch. mydas* and *E. imbricata* (Jukes 1847), and their journals provide insights into the abundance and distribution of turtles at the time of early European contact with Australia. While the Australian endemic *N. depressa* had been described as early as 1880, its generic classification was not resolved for a further century (Limpus, Gyuris & Miller 1988; Zangerl, Hendrickson & Hendrickson 1988). *Lepidochelys olivacea* was not recognised as being part of the Australian fauna until 1969 (Cogger & Lindner 1969).

MORPHOLOGY AND PHYSIOLOGY

Details of morphology and physiology may be found in the synopses and recent reviews of the species — *Ch. mydas* (Hirth 1971), *Ca. caretta* (Dodd 1988), *E. imbricata* (Witzell 1983), *L. olivacea* (Marquez 1976) and *N. depressa* (Limpus *et al.* 1988; Zangerl *et al.* 1988).

External Characteristics

The weight of adult cheloniids ranges from 35 to >200 kg. Carapace length varies from 0.8 m for *L. olivacea* up to 1.2 m for *Ch. mydas*.

The carapace is oval to round and the head, carapace and plastron are covered in keratinised scutes (Fig. 19.1). In *E. imbricata* the carapace scutes are thick and imbricate (Pl. 3.2), while in the other genera, regular flaking of the surface layers keeps the scutes thin. In *N. depressa* (Pl. 3.4) the keratin layer is so thin that it has a skin-like texture similar to that of *Dermochelys corriacea* (Dermochelyidae) (Limpus *et al.* 1988). Cheloniid turtles vary in dorsal colour from uniform grey (*L. olivacea*; Pl. 3.6) to mottled black, brown and olive (*Ch. mydas*; Pl. 3.5) and are pale ventrally.

Hatchlings are also variable in colour, but tend to be darker dorsally than the adults. The dorsal colours of *Ch. mydas* and *Ca. caretta* are black and red-brown, respectively. Hatchlings of *E. imbricata* are brown, and those of *L. olivacea* are dark olive-grey to blackish dorsally. The carapace scutes of *N. depressa* are greyish with black margins (Pl. 3.3).

Cheloniids have elongate and paddle-like front flippers and short, oval rear flippers. The digestive tract and urinogenital system open into a common chamber, the cloaca, which opens to the outside through a single vent on the ventral surface of the tail. External sexual dimorphism is limited. In the pubescent or adult male, the tail is longer and the plastron is flatter or slightly more concave than in a female.

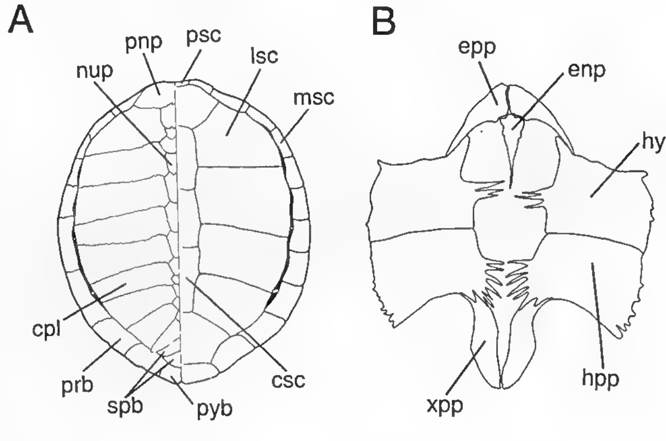

Figure 19.1 Carapace and plastron of *Natator depressus*. **A**, scutes and bones of the carapace; **B**, bones of the plastron. **cpl**, costal plate; **csc**, cental scute **enp**, entoplastron; **epp**, epiplastron; **hpp**, hypoplastron; **hyo**, hyoplastron; **lsc**, lateral scute; **msc**, marginal scute; **nup**, neural plate; **pnp**, preneural plate; **prb**, peripheral bone; **psc**, precentral scute; **pyb**, pygal bone; **xpp**, xiphyplastron. (After Zangerl *et al.* 1988) [T. Wright]

Body Wall and Skeletal System

The general skeletal and cranial morphology of all genera have been described by Deraniyagala (1939), Gaffney (1979), Pritchard & Trebbau (1984) and Zangerl *et al.* (1988). The relatively inflexible carapace consists of an outer epidermal layer with keratinised scutes, a thin dermal tissue layer overlying expanded dermal bones (pleural, proneural, neural, suprapygal, peripheral and pygal bones) which are fused to each other and to the underlying ribs and vertebrae (Fig. 19.1A). The plastron is less rigid, with substantial midline fontanelles reduced or contained by the nine plastron bones (Fig. 19.1B); it is not as cartilaginous as in the Dermochelyidae. The Cheloniidae has a typical anapsid skull (Fig. 12.2), with an inner neurocranium encasing the brain and an outer dermal cranium encasing the extensive muscles operating the jaws and anterior neck. There is little emargination or reduction in thickness of dermal bone to lighten the skull (Fig. 16.4C, D).

Locomotion

When swimming, the Cheloniidae appear to fly through the water, using their front flippers as birds use their wings; the hind flippers function as rudders and elevators (Walker 1971). As with birds and bats, the thrust from the anterior girdles is transferred to a fused vertebral column for pulling the body forward. Though they are capable of speeds up to 4 to 7 km/hr over limited distances (Hirth 1971; Whitzell 1983; Dodd 1988), chelonians can maintain steady swimming for extended periods. *Caretta caretta* and *Ch. mydas* can maintain average speeds of 30 to 40 km/d over thousands of kilometres during migration (Limpus, Miller, Parmenter, Reimer, McLachlan & Webb 1992). On land, the body slides along the ground. Two gaits are used when on land: hatchlings and large *Ca. caretta*, *E. imbricata* and *L. olivacea* use a quadrupedal walking gait. A breast-stroke-like gait in which the two front flippers push together, aided in part by the hind flippers, is used by large *Ch. mydas* and *N. depressa* (Bustard 1972).

Feeding and Digestive System

Hatchlings of all genera commence life as carnivores feeding on surface zooplankton. As youngsters they change to a benthic feeding lifestyle. Diet varies among the genera, and the jaws and keratinised sheaths are specialised to cope with their respective diets. The jaws of *Ca. caretta* and *L. olivacea* form large crushing plates with associated powerful muscles for breaking hard-bodied molluscs and crustaceans (Dodd 1988; Marquez 1976; Moodie 1979). *Eretmochelys imbricata* has pointed, sharp-edged jaws for prying sponges out of crevices (Meylan 1985). As an adult, *Ch. mydas* is almost totally herbivorous and uses its serrated jaws for cropping algae, sea grass and mangroves (Lanyon, Limpus & Marsh 1989). Thomson (1980) has described the anatomy and histology of the digestive tract of *Ch. mydas* and *Ca. caretta*. Adaptations for herbivory in *Ch. mydas* include a large crop, stomach and colon, larger than those of the carnivorous *Ca. caretta*, and a functional caecum. *Chelonia mydas* depends on a rich cellulolytic microflora (bacteria) and microfauna (protozoa) in the caecum and colon for fibre digestion (Fenchel, McRoy, Ogden, Parker & Rainey 1979), and it can digest cellulose as efficiently as ruminants and dugong. However, in *Ch. mydas* the low digestibility of protein in sea grass probably is a result of most cell wall digestion occurring in the hind gut (Bjorndal 1979, 1980). Wood (1974) identified nine, possibly ten, essential amino acids required in the diet of young *Ch. mydas*. While this is significant for preparation of artificial diets, it may not be significant for diets containing natural proteins.

Circulatory, Respiratory and Excretory Systems

The anatomy of the circulatory system of cheloniid turtles has been neglected (for example, *Ca. caretta*, Dodd 1988), but is assumed to resemble that of other chelonians (Jackson 1979). In an assay of 27 blood chemistry properties and packed cell volume (PCV) for wild *Ch. mydas*, only levels of uric acid and cholesterol differed between the sexes. Thirteen blood properties were correlated to turtle size and PCV was independent of sex and size of the turtles (Bolten & Bjorndal 1992). Blood chemistry and morphology for *Ca. caretta* has been reviewed by Dodd (1988). The lungs of *Ca. caretta* are comparable to those of marine mammals and are adapted to prolonged diving and a high metabolic activity (by reptilian standards). There is a wide intrapulmonary bronchus with complete cartilage rings, cartilage in the large trabeculae of the tubular chambers, well-vascularised, alveolus-like structures, and a partial single capillary net and well developed pulmonary musculature (Perry, Darian-Smith, Alston, Limpus & Maloney 1989). *Caretta caretta* can dive to 233 m with breath-holds up to 21 minutes (Sakamoto, Uchida, Naito, Kureha, Tujimura & Sato 1990) to avoid turbulent surface waters. The kidney in *Ch. mydas* is predominantly ammoniotelic as would be expected for an aquatic species (Khalil 1947), but it does not contribute significantly to electrolyte/water balance. The latter is the function of the lachrymal salt gland (Fig. 19.2) which is functional from the time the hatchling leaves the nest. Young *Ch. mydas* have the highest Na^+ secretion rate for any reptile and a secretion rate similar to that of many marine birds. Hatchlings are capable of excreting the Na^+ content of approximately 0.2 to 0.5 ml of sea water per hour with osmotic concentrations of lachrymal gland tears 1.5 to 2.0 times that of sea water (Marshall & Cooper 1988). These glands enable *Ca. caretta* and *Ch. mydas* to maintain plasma homeostasis without access to fresh water (Bennett, Taplin & Grigg 1986; Marshall & Cooper 1988).

Cheloniid turtles secrete high-molecular-weight, water-soluble proteins from the inguinal and axillary (Rathke's) glands, but not all genera secrete lipids. The function of these secretions is not known (Mason 1992).

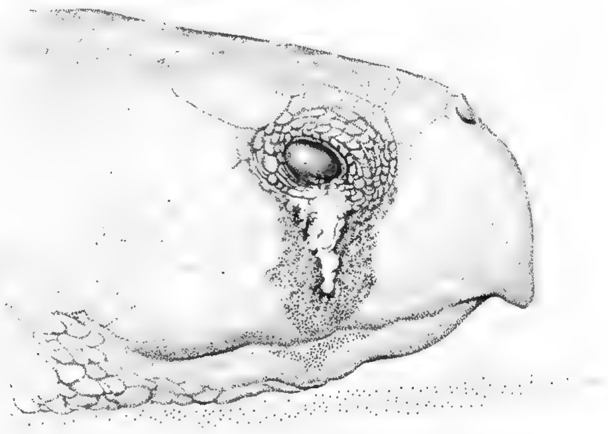

Figure 19.2 Secretion of surplus salt from the eye of *Caretta caretta*. The lachrymal gland is the primary osmoregulatory organ in marine turtles. (After photo by J.P. Ferrero/Auscape International) [T. Wright]

Thermoregulation

Cheloniid turtles are only able to maintain their deep body temperature to within about 3°C above the ambient water temperature (Mrosovsky & Pritchard 1971) and do not have a thermoregulatory capacity comparable to that of the Dermochelyidae (see Chapter 20). While some heat may be obtained through the dark dorsal surface during basking, body heat can be also generated via muscular activity. The pectoral muscle in actively swimming adult *Ch. mydas* is about 7°C warmer than in inactive turtles (Standora, Spotila & Foley 1982). Thermal inertia resulting from large body size can contribute to slow cooling rates during deep dives into cold water, while increased cooling rates can be achieved by flushing the stomach with cold water, if required (Sakamoto *et al.* 1990).

Sense Organs and Nervous System

Cheloniid turtles have an acute sense of smell (but not taste) that can operate underwater. The functioning of the olfactory epithelium of the nasal passages can be blocked by Zn^{++} ions (Manton 1979). In the sea, cheloniids are constantly sampling their surroundings by flushing water from the buccal cavity into the nasal cavities and out through the nostrils. The anatomy of chemical reception in chelonians was reviewed by Scott (1979). The role of chemoreception in the life of the marine turtle remains unclear.

The eyes of cheloniid turtles are well developed and conform to the general chelonian eye, in which cones predominate in the retina, but the lens is more strongly curved (Granda 1979). The colour vision of *Ch. mydas* extends at least from near-ultraviolet to green (360 to 500 nm), while that of *Ca. caretta* extends minimally from near-ultraviolet to red (360 to 700 nm) (Witherington & Bjorndal 1991a). *Chelonia mydas* has a greater spectral sensitivity for shorter wavelengths than *Pseudemys scripta*, with spectral sensitivity peaking at 520 nm and secondary peaks at 600 nm and 450 to 460 nm (Granda 1979).

Endocrine and Exocrine Systems

Hormones appear to play an important role in facilitating specific physiological events during spermatogenesis, vitellogenesis, migration, ovulation and oviposition. Adult male *Ca. caretta* exhibit a prenuptial spermatogenic cycle that coincides with increased concentrations of serum testosterone. Levels of testosterone remain high during migration to the breeding area and mating (Wibbels, Owens, Limpus, Reed & Amoss 1990). Four to six weeks before adult female *Ca. caretta* migrate, a significant rise occurs in serum oestradiol-17β (E_2) concentration, which decreases towards and during migration. Serum testosterone levels also increase in the months before migration. Concentrations of E_2, serum testosterone and serum progesterone are high at oviposition for each of the successive clutches laid during the breeding season, except for the last clutch of the season when they are low (Wibbels *et al.* 1990).

Surges in serum concentrations of follicle stimulating hormone, luteinising hormone and progesterone occur in *Ca. caretta* and *Ch. mydas* within 20 to 50 hours, following oviposition. Concentrations of serum testosterone decline and fluctuations in oestradiol are low or not detectable in the same period (Wibbels, Owens, Licht, Limpus, Reed & Amoss 1992). Similar surges occur in luteinising hormone and progesterone during the ovulatory and nesting cycle of *L. olivacea* (Licht, Owens, Cliffton & Penaflores 1982). The function of follicle stimulating hormone and luteinising hormone in turtles may be different from their function in mammals (Licht 1980).

Prostaglandins have an active role in nesting behaviour and ovulation in *Ca. caretta*. Prostaglandin PGF_{2a} apparently stimulates oviducal contractions to expel eggs, while PGE_2 may be more important in promoting cervical relaxation (Guillette, Bjorndal, Bolten, Gross, Palmer, Witherington & Matter 1991). Owens (1980) and Licht (1980) provide detailed reviews of marine turtle endocrinology.

Reproduction

Age at sexual maturity for eastern Australian cheloniids is probably about 30 to 50 years (Limpus & Walter 1980; Limpus 1991, 1992). The adult female has massive, paired ovaries, which produce mature ovarian follicles > 2.5 cm in diameter. The oviducts are up to 6 m long (Deraniyagala 1939; Owens 1980; Limpus 1985). Copulation usually occurs before the first ovulation for the season (Fig. 19.3). A female may mate with a series of males and stores sperm in the oviducts for use later in the breeding season (Owens 1980; Limpus, Fleay & Guinea 1984a; Limpus 1993). Cheloniids produce white, spherical eggs that average 35 to 55 mm in diameter (depending on the genus), with flexible calcareous shells (Miller 1985). Individual females normally do not breed in successive years (Hirth 1980; Limpus, Fleay & Baker 1984b; Limpus 1985). The egg laying period may be distinctly seasonal (summer in eastern and western Australia), or all year round with a dry season peak in activity, as occurs across northern Australia (Cogger & Lindner 1969; Limpus 1971a; Bustard 1972). Within a breeding season females lay one to 11 clutches, containing on average 50 to 132 eggs, at about two weekly intervals. Nests are 43 to 70 cm deep, depending on the species, and are dug in the supratidal, frontal sand-dunes (Hirth 1980; Limpus 1971a; Limpus, Miller, Baker & McLachlan 1983a). Hatchlings emerge from nests approximately two months after the eggs are laid (Miller 1985). Hatchlings of a single clutch may have different fathers as a result of fertilisation by sperm from several males having been stored in the oviducts (Harry & Briscoe 1988).

Male *Ca. caretta* appear to be annual breeders, but this may not apply for other genera (Wibbels *et al.* 1990; Limpus 1993). Testes are abdominal and a single grooved penis is erectile from within the cloaca.

Embryology and Development

The cleidoic eggs of cheloniids follow typical turtle embryological development. At oviposition the embryos are at middle gastrulation (Stage 6, Miller 1985). For successful incubation, they must be laid in well ventilated, low salinity, high humidity nest substrate, which is not subjected to flooding (Ackerman 1980; Miller 1985; Maloney, Darian-Smith, Takahashi & Limpus 1990). Embryos can be killed by rotation of the eggs during incubation (Limpus, Baker & Miller 1979; Parmenter 1980).

Nest temperature, which may range from 25° to 33°C, determines the length of the incubation period, of approximately 6 to 13 weeks (Miller 1985). The sex of hatchlings is a function of nest temperature during middle incubation (Miller & Limpus 1981; Yntema & Mrosovsky 1980, 1982; McCoy, Vogt & Censky 1983). The theoretical temperature that produces a 1:1 sex ratio with constant temperature incubation (pivotal temperature), varies between species and breeding units. For eastern Australian *Ca. caretta*, the pivotal temperature is 28.6°C (Limpus, Reed & Miller 1983b; Limpus 1985). Two heterogeneous nuclear

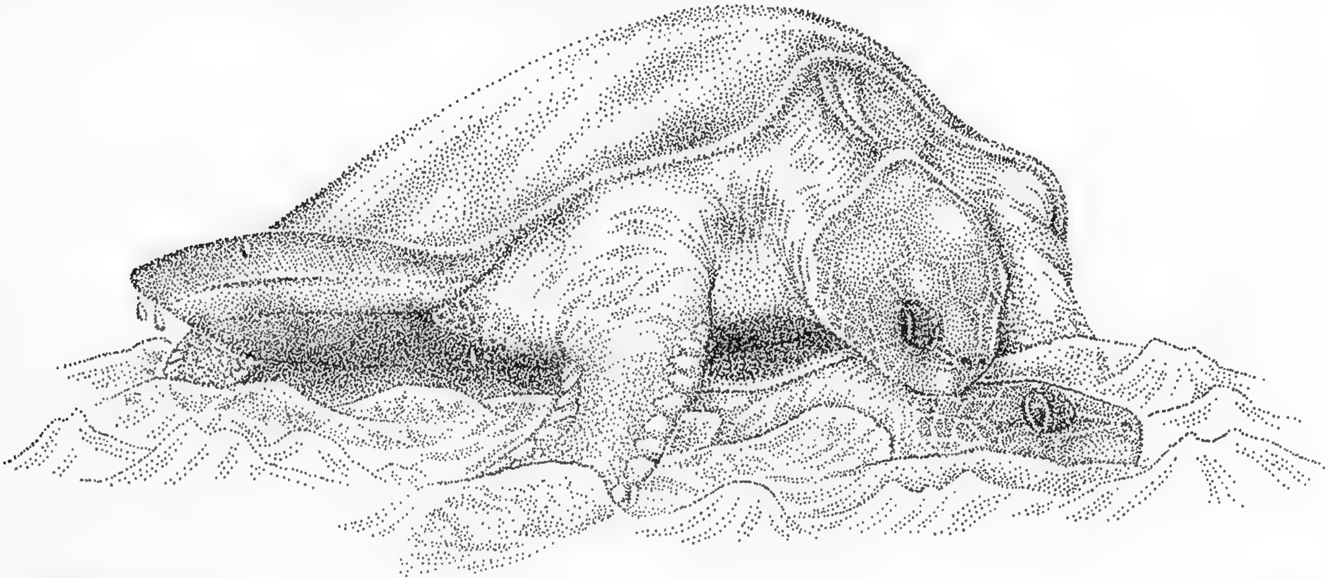

Figure 19.3 Mating in *Natator depressus*.

[K. Couper]

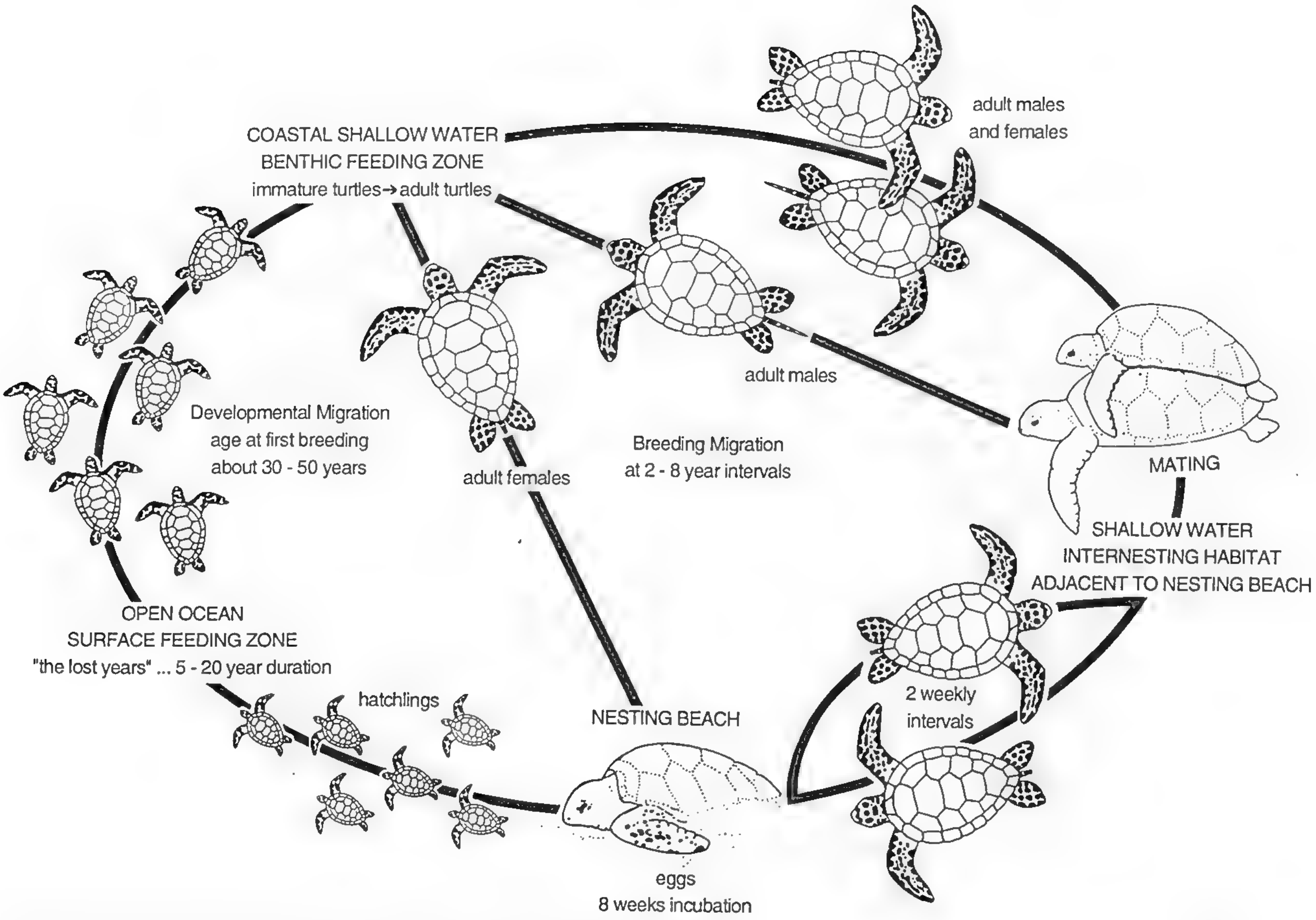

Figure 19.4 Generalised life cycle for a marine turtle. (After Lanyon, Limpus & Marsh 1989)

[D. Wahl]

ribonucleoprotein particles that are differentially expressed in male and female embryonic urinogenital systems at different incubation temperatures are implicated in sexual differentiation of *Ca. caretta* (Harry, Williams & Briscoe 1990).

NATURAL HISTORY

Life History

After they emerge from the nest, hatchlings swim out to sea where they are dispersed by currents into the open ocean (Carr 1986). Post-hatchlings of *N. depressa* are exceptions, as they are entrained over the Australian continental shelf (Walker & Parmenter 1990). During this post-hatchling, planktonic phase, the juveniles are believed to feed on macrozooplankton at the surface convergence lines. After several years and one or more circuits of the ocean gyre, the young of most species select a feeding area within continental shelf waters and change to benthic feeding when they are approximately 300 to 400 mm in carapace length or greater, depending on the species (Fig. 19.4; Carr 1986).

The distribution and biology of post-hatchlings in Australian waters is poorly understood. An immature turtle remains associated with the same continental shelf or inshore feeding area for years. However, it may make one or more shifts in feeding site before selecting the feeding area it occupies as an adult (Limpus 1982, 1985; Limpus & Reed 1985a). In the tropics, at least, an adult associates with the one feeding area, possibly for life, which it leaves only during its breeding migrations (Limpus 1989; Limpus & Reimer 1992; Limpus *et al.* 1992). Turtles migrate from widely scattered feeding areas to breeding areas (Fig. 19.4).

The slow growth to maturity is reflected in the large proportion of the total population that is immature. Sex ratios are variable and often significantly biased towards females (Limpus 1985, 1992; Limpus & Reed 1985a, 1985b; Wibbels, Martin, Owens & Amoss 1991). Reliable predictive population models are scarce because of difficulties in estimating the age of individuals and the survivorship of cohorts over the vast feeding areas of a single population. It appears that large immature and adult *Ca. caretta* require a high annual survivorship and a long breeding life to maintain population stability (Frazer 1983; Crouse, Crowder & Caswell 1987).

Ecology

Most ecological studies of marine turtles have been conducted on the nesting beaches. Conversely, there have been few ecological studies of marine turtles in their aquatic habitats. *Chelonia mydas* principally inhabits areas with abundant seagrass and algae, especially coral reefs, rocky reefs and seagrass flats, and it appears to have a positive feed-back effect on the seagrass community. As a result of the hind gut digestion of fibre and the incomplete removal of nutrients, especially nitrogen, during the passage of seagrass through the gut, the turtle returns to the environment a coarsely cut and partly digested faecal product with a C:N nutritional quality that is superior to the original seagrass (Thayer, Engel & Bjorndal 1982). Thus the turtle increases the rate of movement of nitrogen and other elements through the food web of sea grass beds. On the other hand, the migrating female transports substantial quantities of nutrients from the feeding areas in the form of mature follicles which she deposits as eggs at the rookeries. Some of these nutrients then enter the food web at the rookeries as decaying eggs on the beach, and as eggs and hatchlings eaten by predators (Lanyon *et al.* 1989). While slow growth, delayed sexual maturity and long intervals between breeding seasons of wild *Ch. mydas* are probably under nutritional control rather than genetic control (Bjorndal 1980, 1985), they may also be characteristic of the family (Lanyon *et al.* 1989). Limpus & Nicholls (1988) have demonstrated that regional climatic events, such as the El Niño southern oscillation (ENSO), determine the proportion of adult female *Ch. mydas* available to breed in any one year, and hence presumably the timing between breeding seasons. A similar ENSO effect has not been detected in the other genera.

Within Australia the other species are associated with different foraging habitats. *Caretta caretta* is most frequently found in shallow bays and reefs with abundant molluscs and crabs. *Lepidochelys olivacea* seems to be associated with soft-bottom habitats which are deeper than those used by *Ca. caretta*, and *E. imbricata* is mostly associated with hard-bottomed habitats. *Natator depressa* occurs in similar soft-bottomed habitats to *L. olivacea* (Limpus 1975a; Limpus *et al.* 1984b; Limpus 1985, 1992).

Nesting marine turtles can have some negative impacts on strand vegetation communities (Rogers 1989). However, while nesting they bury nutrients (eggs, humus, vegetation) and seeds back into the soil. In loose coralline sand, the grass and tree roots enhance the ease with which a nesting turtle can construct an egg chamber and hence deposit her eggs (Bustard & Greenham 1968). Regularly nesting under trees, however, could be a disadvantage to the turtle population in providing relatively cooler sand and thus affecting the sex ratio. The warm, brown sand beaches of mainland eastern Australia produce mostly female hatchlings of *Ca. caretta*, and the cooler, white sand beaches of the adjacent coral cays and shaded habitats produce mostly males (Limpus, Reed & Miller 1983b; Limpus, Reed & Miller 1985). In the southern Great Barrier Reef, *Ch. mydas* clutches laid on the northern, sunny side of islands produce mostly female hatchlings and the clutches on the southern shaded areas produce mostly males (Limpus *et al.* 1983b; Limpus *et al.* 1984a).

Behaviour

The hatchling is imprinted by the earth's magnetic field at the nesting beach as it leaves the nest (Lohmann 1991). Imprinting to the smell of the nest substrate or to the water that the hatchling first contacts may also occur (Grassman, Owens, McVey & Marquez 1984). Genetic studies provide convincing evidence that the breeding adult does return to the region of birth (Gyuris & Limpus 1988; Bowen, Meylan, Ross, Limpus, Balazs & Avis 1992; Karl, Bowen & Avise 1992). It remains to be demonstrated however, whether this fidelity is the result of imprinting to the natal beach during the egg or hatchling phase, or whether the hatchling is imprinted to the general region of her birth and subsequently imprinted to the specific rookery as an adult during the first breeding season (Limpus *et al.* 1992).

The hatchling does not feed or sleep between leaving the nest and moving into deep, offshore water. Hatchlings orient to low elevation light horizons when moving from the nest to the sea (Limpus 1971b; Salmon, Wyneken, Fritz & Lucas 1992). They can be disoriented by bright lights, although not by the yellow wave lengths of low pressure sodium vapour lights (Mrosovsky & Shettleworth 1975; Witherington & Bjorndal 1991b). By swimming perpendicular to wave fronts, the hatchlings are directed to swim out to the open ocean (Salmon & Lohmann 1989).

Each adult female migrates faithfully between its particular feeding area and rookery, although different paths are followed on their breeding migrations (Fig. 19.4). While some migrate in excess of 2600 km, most migrate less than 1000 km to their rookeries. Recaptures of females tagged at the south-eastern Queensland rookeries have been recorded from Indonesia, Papua New Guinea, Solomon Islands, New Caledonia, Fiji, and in Australia, Northern Territory, Queensland and New South Wales (Limpus *et al.* 1992). *Natator depressa* does not migrate beyond the Australian continental shelf (Limpus, Parmenter, Baker & Fleay 1983c). Adult females display a high degree of fidelity to their chosen nesting beach, with most females returning to the same small beach for their successive clutches within a breeding season and in successive breeding seasons (Carr, Carr & Meylan 1978; Limpus 1985; Limpus *et al.* 1984a; Limpus *et al.* 1984b; Limpus 1992).

The Cheloniidae and the Dermochelyidae display remarkably similar nesting behaviours. The female selects a nest site above the tide level and clears the loose sand by excavating a body pit with the front and rear flippers; below the body pit she digs a vertical sided, flask-shaped egg chamber with the hind flippers; she lays the eggs in the egg chamber and then conceals them with sand using first her rear flippers, then all four flippers (Fig. 19.5; Bustard & Greenham 1969; Bustard, Greenham & Limpus 1971; Pritchard 1971).

Economic Significance

Harvests of eggs and turtles have been reviewed by Parsons (1962, 1972), Marquez (1976), Milliken & Tokunaga (1987) and Groombridge & Luxmoore (1989). Wherever there has been human contact with cheloniid turtles they have been harvested for food (either as eggs or the turtles for meat), oil, skin for leather and scale for tortoiseshell or bone: *Ch. mydas* in particular has been eaten as meat and in soup; *E. imbricata* has been harvested for tortoiseshell (= *bekko* in Japanese); *L. olivacea* has been taken for leather. Overharvest of most populations for extended periods has caused significant global declines in marine turtle numbers and there is now an embargo on international trade in marine turtle products under the Convention for International Trade in Endangered Species (see Chapter 14). Significant internal trade in *Ch. mydas* and *E. imbricata* occurs in Papua New Guinea, Indonesia and Cuba, while commercial egg harvesting is common in Indonesia and South-East Asia. With increasing interest in ecotourism, sea turtle rookeries have potential use as a non-harvested commercial resource. Ecotourism is established at Australian nesting sites (Bundaberg and Heron Island in the

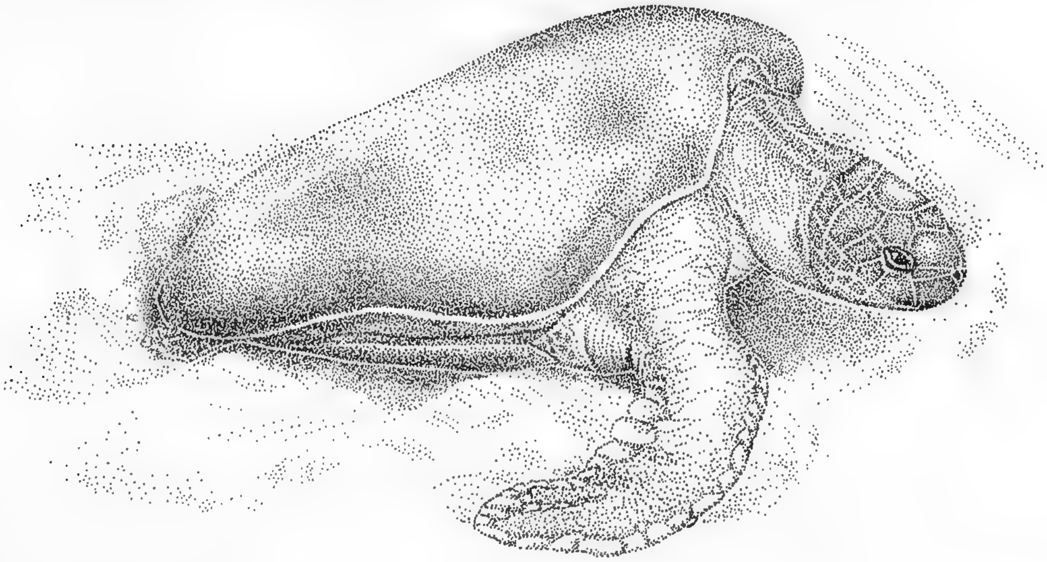

Figure 19.5 Female *Natator depressus* nesting. [K. Couper]

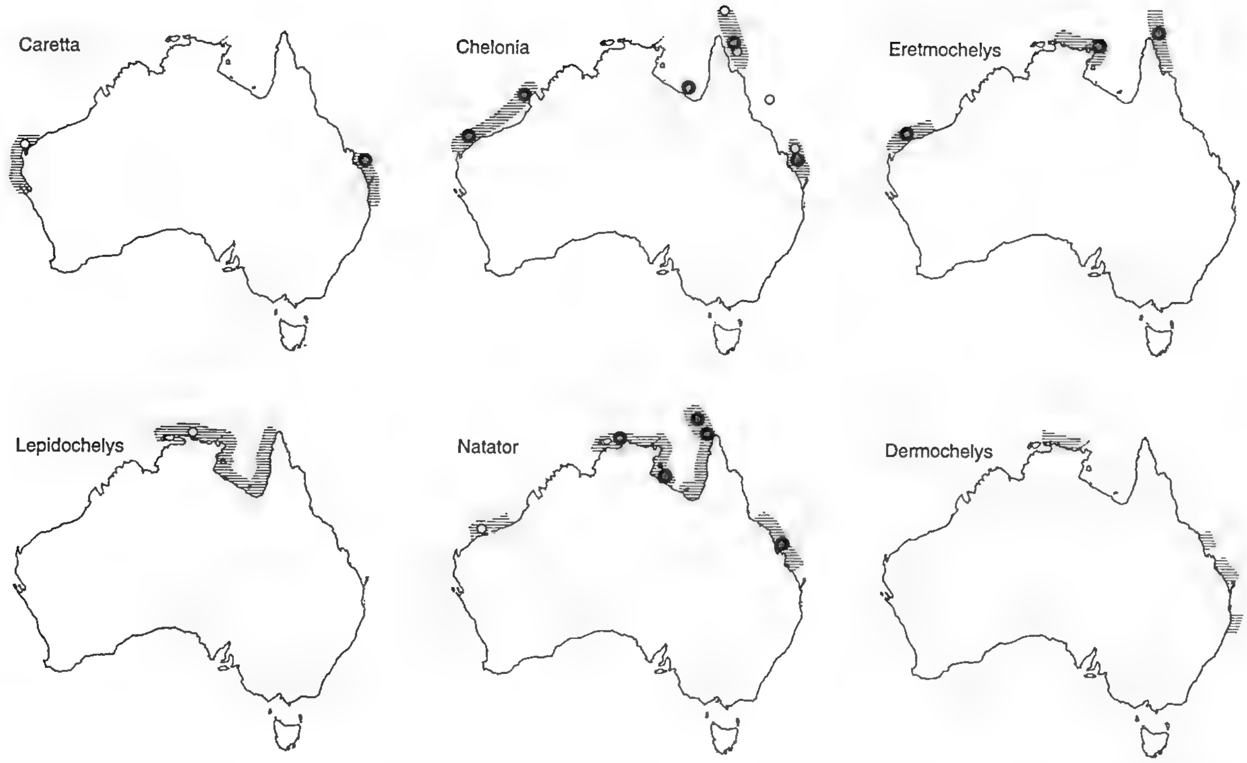

Figure 19.6 The primary breeding areas of the cheloniids *Caretta caretta, Chelonia mydas, Eretmochelys imbricata, Lepidochelys olivacea, Natator depressus,* and for *Dermochelys coriacea.* Shading indicates the primary breeding areas: major nesting colonies (> 1000 females/year) and minor colonies (hundreds of females/year) are indicated by closed and open circles, respectively. [W. Mumford]

southern Great Barrier Reef), and draws more than 35 000 visitors each summer, and in South Africa (Hughes pers. comm.).

BIOGEOGRAPHY AND PHYLOGENY

Distribution

All cheloniid genera except *Natator* have a worldwide distribution in tropical and temperate waters. The feeding distribution of *N. depressa* is confined almost totally to the Australian continental shelf, and nesting is confined to Australian territory. All five species are present in northern Australian waters, but the major rookeries are more restricted in distribution (Fig. 19.6; Limpus 1982, 1985; Miller & Limpus 1991; Limpus *et al.* 1988). *Caretta caretta* nests in the Capricorn-Bunker Groups and adjacent Bundaberg mainland in the southern Great Barrier Reef, and on Murion Island on the southern North West Shelf. *Chelonia mydas* nests in the Capricorn-Bunker Groups of the southern Great Barrier Reef, on Raine Island and Moulter Cay and associated islands of the outer northern Great Barrier Reef, on the Wellesley Group in the Gulf of Carpentaria, and on the Lacepede Islands, Monte Bello Islands and Barrow Island in northern Western Australia. *Eretmochelys imbricata* nests in the northern Great Barrier Reef and Torres Strait, on Truant Island in north east Arnhem Land, and on Rosemary Island on the North West Shelf. *Lepidochelys olivacea* nests in the McCluer Island Group of western Arnhem Land. *Natator depressa* nests in the Peak and Wild Duck Islands in inshore southern Great Barrier Reef, on Crab Island and Deliverance Island of the northeast Gulf of Carpentaria and western Torres Strait, in the Sir Edward Pellew Group in the Gulf of Carpentaria, on Cobourg Peninsula and Greenhill Island in western Arnhem Land, and on Delambre Island on the North West Shelf.

The widely spaced breeding concentrations for each species should be managed as separate stocks because there is little potential for recolonisation of depleted populations from other distant breeding concentrations (Bowen *et al.* 1992; Karl *et al.* 1992).

Affinities with other Groups and Fossil Record

The Cheloniidae is one of six families of marine turtles known from the fossil record. Four families have been recorded in Australia, including the Dermochelyidae, and the extinct Desmatochelyidae (*Cratochelone, Notochelone*) and Protostegidae (Pritchard & Trebbaum 1984; Gaffney 1991). Of the 31 genera attributed to Cheloniidae, only five are extant — the monospecific *Caretta, Chelonia, Eretmochelys* and *Natator*, and *Lepidochelys*, which includes two species. All five genera are represented in Australia (Pritchard & Trebbaum 1984).

20. FAMILY DERMOCHELYIDAE

Colin J. LIMPUS

DEFINITION AND GENERAL DESCRIPTION

The Dermochelyidae (leatherback turtles) is one of only two families surviving from the past diverse marine turtle faunas. It is represented by a single extant species, *Dermochelys coriacea* (Pritchard & Trebbau 1984). The family is characterised by large paddle-like flippers which lack claws, the absence of keratinised epidermal scutes except in hatchlings (Fig. 15.3E), separate ribs, a mosaic of small, polygonal dermal bones covering the body, a strongly ridged carapace, and pronounced tooth-like cusps on the upper jaw. These turtles can be readily identified from photographs and reliably distinguished on the basis of size, colour and the ridged carapace (Pls 3.7, 3.8). Their occurrence on nesting beaches can be recognised from the wide tracks, which may exceed two metres (Limpus & McLachlan 1979).

HISTORY OF DISCOVERY

Although a formal description of *D. coriacea* was first given by Vandelli in 1761 from a specimen collected in Italian waters, the species had been recorded pictorially at least as early as 1554 (Fretey & Bour 1980). Together with other marine turtles, the species was well known to early mariners. For example, Dampier described four marine turtle species in 1717, including the trunk-turtle (*D. coriacea*) which had rank flesh (Masefield 1906). In Australia, the species was known to Aborigines before European contact, and it was represented occasionally in Aborginal art and rituals (McCarthy 1955). Backhouse described a specimen of *D. coriacea* from Moreton Bay, Queensland in 1843. The low level of breeding by this species in south-east Queensland was documented by Limpus (1974) and Limpus & McLachlan (1979) provided the first detailed review of the widespread feeding distribution and limited breeding of the species in Australia.

MORPHOLOGY AND PHYSIOLOGY

In general anatomy, *Dermochelys coriacea* resembles the cheloniid turtles. However the physiology and function of this species has received little study.

External Characteristics

Dermochelys coriacea is the largest living turtle (up to 916 kg; Morgan 1989) and the next largest living reptile after the large crocodilians. Adults are usually at least twice the size of other marine turtles (Hirth 1980). The elongate carapace tapers posteriorly and bears five longitudinal ridges formed by rows of enlarged dermal bones (Deraniyagala 1939; Pritchard 1971). The dorsal surface of adults is black, with small, light coloured spots (Pritchard & Trebbau 1984). The front flippers are the longest of any marine turtle (Pl. 3.7, 3.8). Other external features are compared with those of cheloniids in Chapter 19.

Body Wall and Skeletal System

The smooth skin lacks keratinised scutes and protuberances. A mosaic of small dermal bones overlies the carapace and plastron, and the deposits of subepithelial fat, 60 to 70 mm thick (Deraniyagala 1939; Brongersma 1969; Goff & Lien 1988). The general skeletal structure and cranial morphology has been described by Deraniyagala (1939), Gaffney (1979a) and Pritchard & Trebbau (1984). The carapace is largely cartilaginous and characterised by a reduction in bone compared with other turtles. Neural, costal or marginal bones are absent and the ribs are separated (Fig. 20.1A). The plastron lacks an entoplastron bone and the remaining four pairs of elongate bones which form a ring around the plastron provide little structural support (Fig. 20.1B).

The skeleton of *D. coriacea* remains extensively cartilaginous even in adults (Pritchard & Trebbau 1984). The epiphyses are vascularised perichondrally and transphyseally, and the medullary bone is not remodelled, features that are unique among extant reptiles (Rhodin, Ogden & Conlogue 1981; Fig. 20.2). These features may reflect adaptation to a marine diving lifestyle, because they occur also in cetaceans and sirenians, and to some extent in extinct marine reptiles such as ichthyosaurs and plesiosaurs (Rhodin *et al.* 1981).

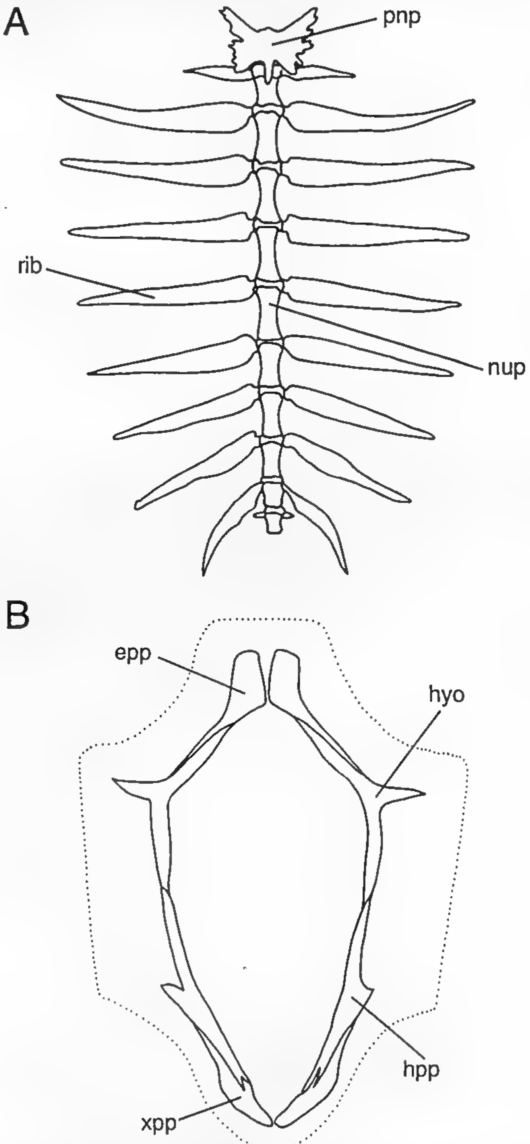

Figure 20.1 Skeleton of *Dermochelys coriacea.* **A**, carapace; **B**, plastron. **epp**, epiplastron; **hpp**, hypoplastron; **hyo**, hyoplastron; **nup**, neural plate; **pnp**, preneural plate; **rib**, rib; **xpp**, xiphyplastron. (After Pritchard & Trebbau 1984) [T. Wright]

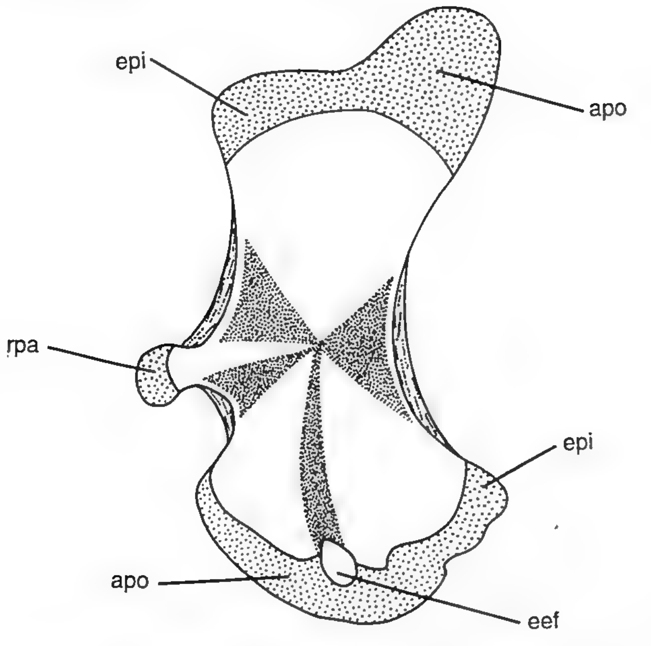

Figure 20.2 Longitudinal section of the humerus of *Dermochelys coriacea*, to show light-coloured endochondral bone and dark periosteal bone, the absence of a medullary cavity and poor differentiation of compact and cancellous bone. **apo**, apophysis; **epi**, epiphysis; **eef**, ectepicondylar foramen; **rpa**, radial process apophysis. (After Rhodin, Ogden & Conlogue 1981) [D. Wahl]

Locomotion

These turtles are unable to support their bodies off the ground on land, and they haul themselves across beaches by pushing with all four flippers together. As adults, their terrestrial gait resembles that of the cheloniid turtles *Chelonia* and *Natator*. However, of all marine turtles, only hatchlings of *D. coriacea* move with this breast-stroking gait (Limpus & McLachlan 1979). The limited data suggest that *D. coriacea* swims at speeds (1.9 to 9.3 km hr^{-1}) comparable to those of other marine turtles and the great white shark, *Carcharodon carcharias* (Standora, Spotila, Keinath & Shoop 1984).

Feeding and Digestive System

The jaws of *D. coriacea* are comparatively light in weight and lack the thick bone and crushing plates of cheloniid turtles. The sharp edged jaws are deeply notched, and suited to grasping and cutting soft-bodied prey (Pritchard 1971). The backwardly directed, flexible papillae that line the throat and oesophagus of marine turtles are best developed in *D. coriacea* and prevent the prey from sliding back out of the anterior gut (Pritchard 1971).

Circulatory System and Body Temperature

The cardiovascular system resembles that of other chelonians. It consists of a three-chambered heart, an arterial system, and a venous system that includes a well-defined renal portal system (Jackson 1979 and references therein). However, *D. coriacea* has a circulatory feature unique among reptiles, in the form of a single, well-defined bundle of closely packed veins and arteries at the base of each flipper. This functions as a countercurrent heat exchange system to reduce heat loss via the flippers (Greer, Lazell & Wright 1973).

Body temperatures are often well above those of the seawater. The core body temperature of breeding female *D. coriacea* off tropical nesting beaches in the Caribbean of South America was 30.6°C, some 3° warmer than the ambient water temperature and 1° to 2° warmer than the core body temperature of sympatric, nesting female cheloniid turtles (Mrosovsky & Pritchard 1971). A captive study by Frair, Ackman & Mrosovsky (1972) suggests that *D. coriacea* can maintain a core body temperature up to 18°C above an ambient water temperature of 7.5°C. Standora *et al.* (1984) demonstrated that an inactive subadult could maintain an elevated deep body temperature relative to ambient air temperature in the absence of an external heat source. This would be facilitated by the insulating subepithelial fat deposits, the large body size and hence low surface area to volume ratio, and the countercurrent heat exchange system. However, an endogenous heat source would be necessary, possibly utilising thermogenic brown fat tissue (Eckert 1992). Endogenous heat could be supplemented by heat generated during muscular activity and from radiation absorbed through the dark dorsal surface when the turtle basks at the ocean surface (Standora *et al.* 1984; Eckert 1992). This combination of adaptations enables *D. coriacea* to function in the low water temperature it encounters during deep dives and migrations to low latitudes.

Sense Organs and Nervous System

Visual cues are important for hatchlings to find the ocean for the first time (Mrosovsky & Shettleworth 1975). *Dermochelys coriacea* may vocalise when injured (Carr 1952). The sounds made by nesting *D. coriacea* are variable and most intense in the 300 to 500 Hz frequency range, as in other turtles. However, sound production may be of minor functional significance (Mrosovsky 1972).

Reproduction

The female has paired ovaries and paired oviducts. Copulation, sperm storage and egg production within the female are poorly documented. Mature ovarian follicles are 36 to 39 mm in diameter. The eggs are spherical with flexible calcareous shells averaging 82 g and 53 mm in diameter. Testes are abdominal and a single grooved penis is erectile from within the cloaca.

Embryology and Development

Dermochelys coriacea lays cleidoic eggs that follow typical turtle embryological development (Deraniyagala 1939; Ackerman 1980; Mrosovsky 1984; Miller 1985). Oviposition occurs at stage six (early to middle gastrulation) approximately eight days after fertilisation and subsequent albumen and shell deposition in the oviducts. For successful incubation, eggs require a temperature range of 25° to 33°C and a high humidity, low salinity, well-ventilated nest substrate that is not subject to flooding. Nest temperature determines incubation period (69 days at 29°C) and the sex of the hatchling.

NATURAL HISTORY

Life History

The breeding cycle of *D. coriacea* in Australia is typical of populations breeding elsewhere (Deraniyagala 1939; Hirth 1980; Limpus, McLachlan & Miller 1984c; Tucker & Frazer 1991). Age at sexual maturity has not been determined, although Pritchard & Trebbau (1984) predict maturity is reached in less than three years. Females do not normally breed in successive years. The egg laying season spans December to January, and within a single breeding season the individual female may lay as many as four clutches of 83 eggs per clutch over 9 to 11 days. Nests are 0.9 m deep and dug in the frontal sand dune of the supratidal region. Male breeding cycles have not been recorded.

Dermochelys coriacea makes transoceanic migrations between nesting beaches and feeding areas, and it regularly migrates further than any other species of marine turtle (Pritchard 1976; Meylan 1982). The species is long-lived and breeds over many years. Adults are presumed to return to the region of their birth to breed. Hatchlings disperse to open oceanic waters from the beaches and the adults maintain a solitary, totally pelagic lifestyle, although they may aggregate in areas of abundant food and off nesting beaches (Bustard 1972).

Ecology

Dermochelys coriacea is primarily an inhabitant of open waters. It is the deepest diving reptile, and reaches depths in excess of 315 m (possibly in excess of 1000 m), on dives of up to 37 minutes, presumably in search of zooplanktonic food (Eckert, Eckert, Ponganis & Kooyman 1989). On average, dives last 9.9 minutes to a depth of 62 m. Within Australia, it is recorded most frequently in the southern temperate waters (Limpus & McLachlan 1979) and it is the most frequently recorded turtle in New Zealand waters (McCann 1966).

The diet of *D. coriacea* consists primarily of large zooplanktonic invertebrates such as jellyfish and tunicates (for example, *Pyrosoma* and salps) as well as associated commensal fish and amphipods, and the fish prey of the jellyfish (Brongersma 1969). Surface living and deep water siphonophores (Cnidaria: Hydrozoa) are also eaten (Bacon 1969; den Hartog 1980). In Australian waters, the rhizostome jellyfish, *Catostyus mosaicus*, forms part of the diet (Limpus & McLachlan 1979; R. & V. Taylor pers. comm.). Though primarily a water column feeder, *D. coriacea* will also feed on the ocean floor of the continental shelf (Limpus 1984).

The species ventures into cold temperate waters more often than any other marine reptile (Bleakney 1965; Goff & Lien 1988). As a summer migrant to the temperate North Atlantic waters, *D. coriacea* is regularly recorded in water at 9° to 15°C and it can remain active among pack ice in approximately 0°C water (Goff & Lien 1988). Specimens are usually obtained following accidental capture in fishing gear, such as shark nets and float lines to lobster pots.

Behaviour

Nesting behaviour is typical of all marine turtles (Pritchard 1971); the nesting female returns faithfully to her particular nesting beach to lay successive clutches of eggs in the same breeding season, and in successive breeding seasons (Eckert, Eckert, Adams & Tucker 1989).

Dermochelys coriacea must lay its eggs on warm beaches in order to obtain the necessary temperatures for hatching, and to produce a viable mixture of both sexes (Mrosovsky 1984; Miller 1985). Nesting usually occurs on open sand beaches and rarely on beaches fronted by rocky or coral reefs (Pritchard 1971).

Economic Significance

In some countries, *D. coriacea* is killed for its meat, oil and/or eggs, while elsewhere a high proportion of eggs are harvested commercially. In Malaysia, the decline in numbers of nesting turtles resulting from past overharvesting of eggs is threatening a significant tourist industry based on viewing the nesting turtles (Mrosovsky 1983).

Mortality has increased because of gut blockage following ingestion of plastic bags presumably mistaken for jellyfish (Balazs 1985).

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Dermochelys coriacea occurs in all oceans. It feeds mostly in temperate waters and breeds at traditional nesting sites in the tropics (Pritchard 1971). Within Australia, it is seen mostly from southern Queensland to Victoria and in south-west Western Australia (Fig. 19.6). The few nesting turtles in south-east Queensland may be waifs from the larger nesting population in New Guinea (Limpus & McLachlan 1979).

Affinities and Fossil Record

The marine turtles have their origins in the late Jurassic to early Cretaceous and the surviving families, Cheloniidae and Dermochelyidae, probably diverged in the early Cretaceous (Gaffney 1991). The fossil record for dermochelyids is poor. Four extinct genera are recorded. *Cosmochelys* and *Eosphargis* are known from the Eocene of Nigeria, and early Eocene of Europe, respectively. *Psephophorus* occurred in the Eocene-Pliocene of Europe, North Africa and North America, and *Pseudosphargis* in the late Oligocene of Germany. *Dermochelys* is not known from the fossil record (Pritchard & Trebbau 1984).

21. FAMILY CHELIDAE

John M. Legler & Arthur Georges

DEFINITION AND GENERAL DESCRIPTION

Chelids are all aquatic or semi-aquatic freshwater turtles. In Australia, the presence of distinct ankle joints and webbed feet, each with four or five claws (Fig. 15.3B), readily distinguishes this family from marine turtles and *Carettochelys*, which have flipper-shaped limbs. The posterior parietosquamosal arch is usually present (absent in *Chelodina*), but the quadratojugal is absent. The vomer is always present and usually separates the palatines. The presence of nasal bones (except in *Chelus*) is diagnostic for the family Chelidae, if living forms only are considered (Gaffney 1979). A splenial bone is present.

Chelids are typical pleurodirans in respect of features associated with the mechanism of head withdrawal. The cervical vertebrae have strong lateral processes, closely juxtaposed or fused postzygopophyses, and well developed central articulations which are never double (Williams 1950). The trochlear processes of the pterygoids are well developed, to accomodate the pleurodiran arrangement of the external adductor tendon (Gaffney 1979).

Horny scutes overlie the bony shell. The plastron is made up of nine bony plates, covered by 13 plastral scutes. A mesoplastron is lacking. The carapace is bordered by 11 pairs of peripheral bones covered by 12 marginal scutes, and a precentral scute is present in all but the genus *Elseya*. The pelvis is fused to both the carapace and plastron, which are joined by a rigid bridge. Neural bones are frequently reduced or absent. The fifth and eighth cervical centra are biconvex and there are never any saddle joints.

Australian chelids are often considered in the categories of 'shortnecks' and 'longnecks'. These useful terms are seldom defined. In a live chelid, the neck can be bent gently to the side that so it arcs continuously from its joint with the first thoracic vertebra. In longnecks, the tip of the snout will reach to a point somewhere on the posterior quarter of the plastron (*Chelodina longicollis* group), or beyond the posterior edge of the carapace (*Chelodina expansa* group). In shortnecks, the snout tip extends at most to the middle of the bridge.

The chromosome number in the Chelidae ranges from $2n = 50$ to 64 (96 in triploid *Platemys*), and is $2n = 50$ in Australian shortnecks or $2n = 54$ in Australian longnecks (Bull & Legler 1980).

In Australia, the family is represented by the five named genera, *Chelodina*, *Elseya*, *Emydura*, *Pseudemydura* and *Rheodytes* (Pls 3.10–3.15). Three additional genera are yet to be described (Legler unpub. data). Useful illustrated references on Australian chelids are those of Cann (1978), Goode (1967) and Worrell (1963). More comprehensive references include those of Pritchard (1967), Pritchard & Trebbau (1984) and Ernst (1989).

HISTORY OF DISCOVERY

The first described Australian chelid turtle *Chelodina longicollis* (Pl. 3.11), collected by Sir Joseph Banks from the east coast of Australia on Cook's first voyage in 1770. The species was formally described as *Testudo longicollis* by Shaw (1794), and transferred to the genus *Emys* (Schweigg, 1814) before it was considered distinct enough to be placed in the new genus *Chelodina* (Fitzinger, 1826). As the Australian continent was explored, more genera of freshwater turtles became known.

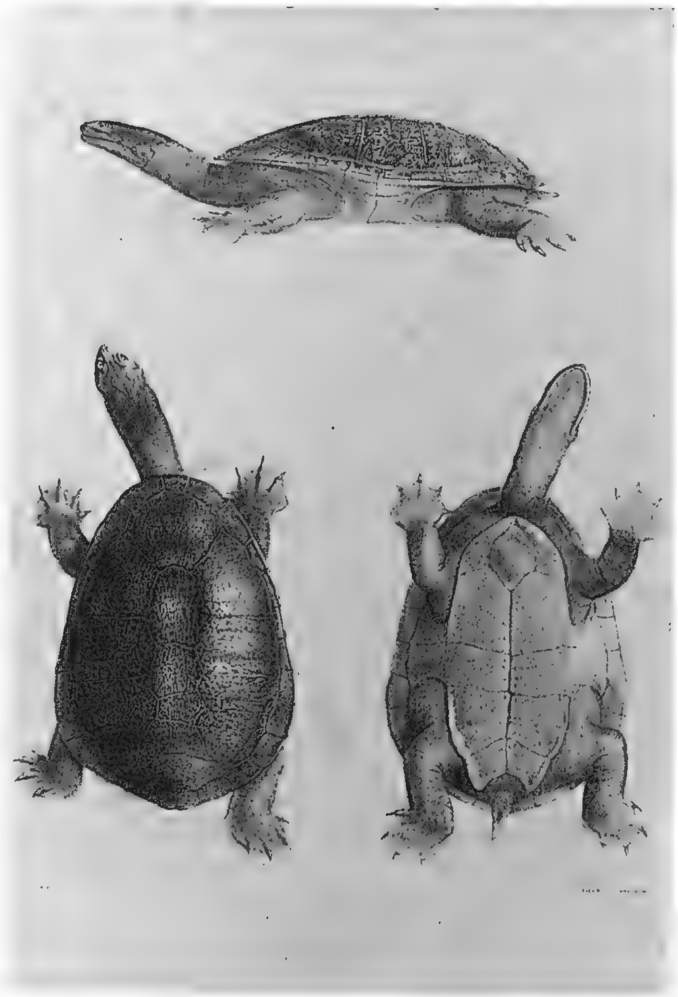

Figure 21.1 *Chelodina oblonga*, described by Gray in 1841, is one of only three species of freshwater turtles known from Western Australia. (After Gray 1856) [Photo by Australian Museum]

Emydura macquarii was collected by the French explorers and naturalists Lesson and Garnot in 1825 and described by Gray (1830), and *Elseya dentata* (Pl. 3.15), named for the collector, Dr J.A. Elsey, who was surgeon and naturalist on Gregory's expedition from the Victoria River of northern Australia to Moreton Bay in Queensland (Goode 1967).

The description of many species from single, isolated specimens of vague geographic origin which were shipped to European museums, often led to considerable confusion. For example, *Pseudemydura umbrina* (Pls 3.13, 3.14) was first described in 1901 from a specimen found in 1839 (Siebenrock 1901). In 1953, a specimen was discovered in the possession of a schoolboy and taken to the Western Australian Naturalist's Club annual Wildlife Show. The specimen was described as a new species *Emydura inspectata* by Glauert (1954), but Williams (1958) showed that it was in fact, *Pseudemydura umbrina*, described over 50 years earlier.

Many discoveries of Australian turtles are much more recent. *Rheodytes leukops* (Pl. 3.12) of the Fitzroy River in Queensland was first described in 1980 (Legler & Cann 1980). Perhaps the most perplexing is the species unofficially called 'shortneck alpha' or the petshop turtle. For more than two decades, it was known to science only from petshops in Victoria, and the source of the specimens could not discovered, despite thorough investigative work by Cann, Legler and others. An electrophoretic study by Georges and Adams showed that it was not a petshop hybrid, as it had many unique alleles. Finally, in 1990 the species was found by Cann in its native habitat of the Mary River, Queensland (Cann & Legler 1993).

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Australian chelids are small to moderate in size. As adults, they range in size from *Pseudemydura* (carapace length of smallest female 120 mm; Burbidge 1967) and males of *Emydura* from some eastern coastal drainages (carapace length approximately 100 mm) to a maximum of 485 mm in *Chelodina expansa* (usual range 250 to 350 mm). *Elseya dentata* and shortneck alpha attain lengths close to 400 mm. Most specimens of *Emydura*, *Elseya latisternum* and *Rheodytes* are intermediate in size (Cann & Legler 1993).

Though the sexes are difficult to distinguish by external characters before sexual maturity, the development of secondary sexual characteristics at puberty simplifies this processs in adults. The form of adult size dimorphism is variable in Australian chelids. Males are larger in *Pseudemydura*, the sexes are of equal size in *Rheodytes*, and males are smaller than females in all other genera. The hypothesis proposed by Berry & Shine (1980) that larger male size is associated with forcible mating, whereas larger females are able to select their mating partner, has yet to be corroborated for Australian chelids. The tendency for shells of females to be deeper and more commodious than males would be adaptive in facilitating the periodic storage of eggs. The precloacal part of the tail, which accommodates the penis, is almost always deeper, longer and in general more heavily developed in males than in females.

Australian chelids tend to be drab in colour and unpatterned. The young are generally more brightly coloured than the adults. Hatchlings of *Chelodina longicollis* have a bright orange and black plastron. Bright yellow, orange, pink markings, alone or in combination, mark the head and neck of adults in some populations of *Emydura victoriae*, *E. subglobosa* and *Elseya latisternum* and pale areas of the plastron and ventral soft skin may be suffused with pink. In juveniles of some populations of *E. latisternum*, melaninistic marks on the plastron contrast brightly with yellowish or pinkish colour.

Chelids show little colour dimorphism, except for males of *Rheodytes*, in which the head is characteristically orange in colour.

Skeletal System

The sutural articulations which firmly join elements of the carapace and plastron may co-ossify in old adults. The only Australian genus to show any reduction of the rigid joints in the shell is *Pseudemydura*, in which the articulation between carapace and plastron contains fibrous connective tissue, or is syndesmotic, and is at least slightly movable. The adaptive significance of these slight modifications is unclear, though they may permit the animal to lay a relatively large hard-shelled egg.

The skull roof is complete, feebly or not emarginate posteriorly, but with variable emargination between the orbit and the tympanum. Emargination is least in *Pseudemydura*, resulting in extensive dorsal roofing. Greater emargination in other Australian shortnecks leaves a posterior temporal arch of moderate width. Ventral emargination is complete in both groups of *Chelodina*, in which parietosquamosal contact has been lost completely.

Feeding & Digestive System

Usually, the mandible is lightly constructed and the dentary bones are unfused medially. Jaw structure is correlated with diet. The occlusal surfaces of the jaws consist principally of the maxillary bones above and the dentary bones below. The palatine and premaxillary bones make a variable and minor contribution to the upper member. The occlusal surfaces are covered by the cornified epithelium of the jaw sheaths.

Each jaw ramus bears an outer, vertical tomial ridge and an inner, horizontal, triturating (crushing) surface. The mandibular tomium occludes with the inner surface of the maxillary tomium to form an efficient shearing device. This is used for general initial feeding movements, for shearing or scoring of vegetation too large to swallow whole and for grasping objects to be torn apart by the foreclaws. *Rheodytes* uses the tomial apparatus to scrape food off submerged rocks. Slightly modified tomia and triturating surfaces are characteristic of generalised, opportunistic omnivores, such as the *Elseya latisternum* group and most *Emydura*.

Three basic adaptive modifications to the jaw structure are found in Australian chelids. Secondary alveolar ridging may be present on the triturating surfaces, the tomium and triturating surfaces may be reduced in those chelids that use the suck and gape mode of feeding (both groups of *Chelodina*), or the opposed triturating surfaces and associated osseous structures are developed extensively to form a crushing plate. This last form is associated with megacephaly, as described later in this section.

The *Elseya dentata* group are the only Australian chelids with median alveolar ridging. Such ridging provides additional shearing or crushing planes. The median alveolar ridge of the lower jaw fits closely inside its counterpart on the upper jaw. Another ridge, here

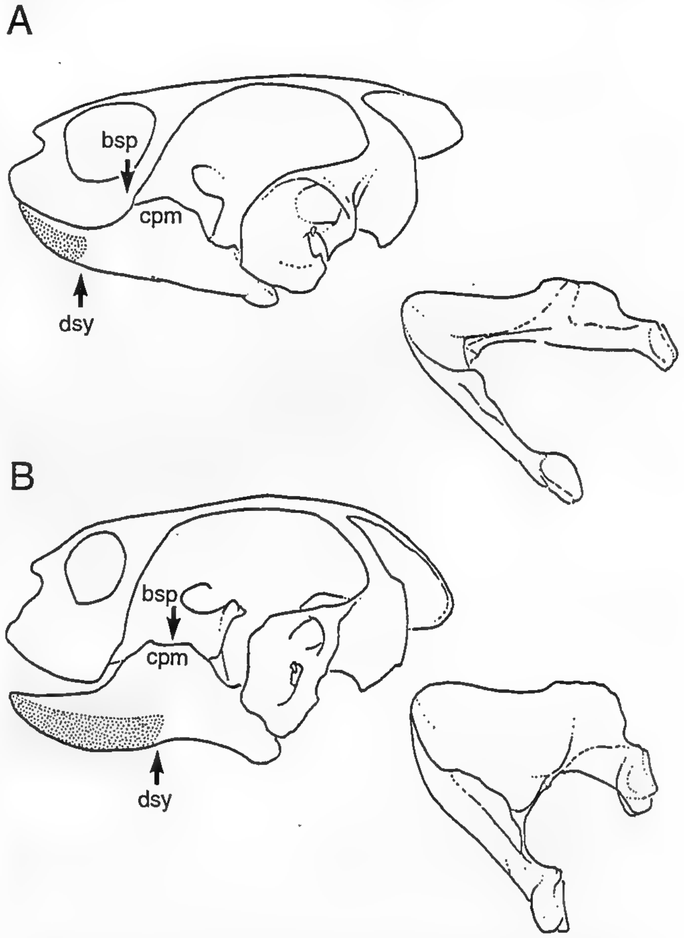

Figure 21.2 Lateral view of skull, and oblique view of mandibles of female *Emydura victoriae*. **A**, small, young adult, showing basic proportions of palate and dentary symphysis present at hatching; **B**, large, old megacephalic adult, showing extreme megacephaly, especially in the development of the dentary symphysis. **bsp**, posterior extent of bony secondary palate; **cpm**, coronoid process of mandible; **dsy**, posterior extent of dentary symphysis (shaded). [J. Legler]

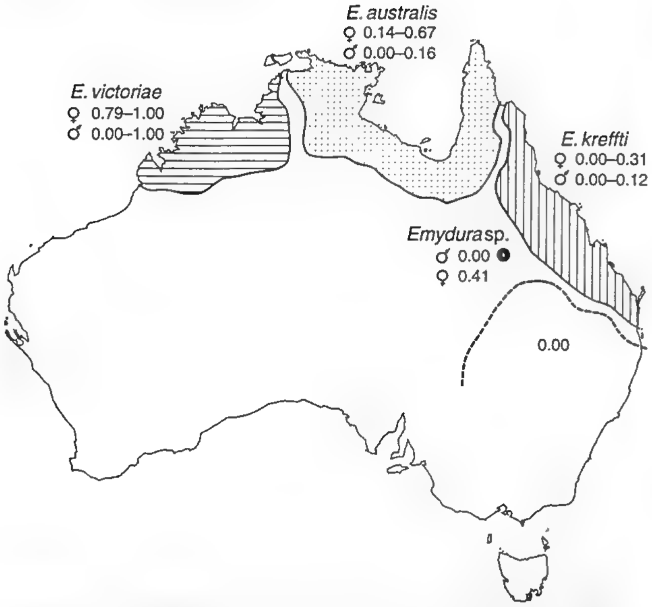

Figure 21.3 Distribution of *Emydura victoriae*, *E. australis*, *E. kreffti*, *E. macquarii* and a distinctive, unnamed species of the Cooper's Creek drainage, illustrating the percentage frequencies of megacephalic adults in various subpopulations. The broken line indicates the southern limit of megacephaly, which includes the entire range of *E. macquarii* and several distinctive coastal populations in southeastern Australia. (From Legler unpub. data) [W. Mumford]

termed the 'secondary maxillary ridge' develops variably on the extreme medial edge of the maxillary triturating shelf, and serves to deepen the groove into which the dentary alveolar ridge fits. Alveolar ridging is an adaptation associated with herbivory. It has evolved convergently several times within the order, for example, in *Chelonia* (Cheloniidae), *Pseudemys* (Emydidae), *Batagur* (Bataguridae) and *Dermatemys* (Dermatemyidae).

Megacephaly is a phenotypic state in turtles in which the head is normally but often grossly enlarged (Figs 21.2, 21.3). Megacephaly is arbitrarily defined in *Emydura* as a head width greater than or equal to 18.6% of carapace length. Increased head size results from hypertrophy of the mandibular adductor musculature and compensatory modifications of the cranium and mandible. The condition is associated with the crushing of hard food, almost always molluscs (Worrell 1945; Legler 1981, 1989b). Megacephaly provides the ability to utilise molluscs as a food source over and above the typical omnivorous opportunistic diet.

As head size increases, the secondary palate and the mandibular symphysis extend posteriorly as crushing surfaces (Fig. 21.2). These skeletal modifications shorten the effective load arm of a class III lever system and increase mechanical advantage between the posterior edges of the crushing plates. As the turtle grows in size, and gape increases, it is capable of eating larger molluscs. As individuals graduate to larger sizes of molluscs, the tomial edges of the jaw sheaths become worn and are broken frequently. This damage is never repaired and in older individuals the anterior parts of the jaw sheaths no longer occlude (Legler 1984).

Megacephaly occurs convergently in the Chelidae, Pelomedusidae, Kinosternidae, Trionychidae and Emydidae (Dalrymple 1977; Legler pers. obs.). Among Australian chelids, megacephaly is common in *Emydura* (Fig. 21.3) and occurs also in *Chelodina novaeguineae*.

Objects of an appropriate size may pass into the mouth without touching the jaws and be found in the stomach whole, undamaged and occasionally alive. Stomach flushings from *Chelodina expansa* suggest that individuals select prey of a given length (Legler pers. obs.). When a part of the prey object protrudes from the mouth, inertial movements are used to move it inward and backward. The jaws of *Chelodina* are weak.

The oesophagus is normally regarded only as a tube of transmission in chelonians. However, large intrinsic glands are present in the submucosa of the cardiac oesophagus in all Australian chelids studied so far (Hoffmann 1890; Legler pers. obs.). The glands are present in various forms and sizes in *Chelus fimbriatus*, in several emydids and in both families of marine turtles (Hoffmann 1890). They seem to be homologous with the deep oesophageal glands of mammals (Bloom & Fawcett 1968).

At maximal development in *Emydura* the glands swell the oesophagus to the diameter of the neck and compress its lumen to a narrow vertical slit, though eating continues during this period. The oesophageal enlargement is a cylinder tapered at each end with visible and palpable longitudinal lobes. It lies immediately dorsal to the trachea. Most of the enlargement lies anterior to the bifurcation of the trachea and all of it lies within the confines of the shell (Fig. 21.4).

In *Emydura*, *Elseya latisternum* and *Elseya dentata* the glandular tissue forms three longitudinal lobes — a dorsal lobe and a lateral lobe on each side (Fig. 21.4A, B). The trachea usually indents the ventral oesophageal wall between the two lateral lobes. The internal surface of each lobe bears a longitudinal series of approximately 25 clusters of pores. Most observations have been made on eastern *Emydura*. The lateral lobes are subdivided in some genera. There are five lobes in *Chelodina longicollis* and seven in *Chelodina rugosa* and *Pseudemydura umbrina*.

The glands are of the branched tubular type and drain to longitudinal collecting ducts which parallel the pores (Fig. 21.4B, C). Unstratified columnar epithelium lines all parts of the system and is the only layer in which the glands are convoluted. In more peripheral parts of the system, the underlying stratified epithelium seems to be non-secretory. The columnar cells have a distinct nucleus and secretory granules. The secretory granules accept an Azocarmine stain and appear to be eosinophilic. At full development the glands stretch the *tunica muscularis* of the oesophagus virtually beyond recognition as smooth muscle (Fig. 21.4B). The secretion is brownish, odourless, tasteless and has no noticeable effect on humans. Other turtles will eat the glandular tissue and appear not to react to it in any unusual way (Legler pers. obs.). Specimens held for several days in captivity develop white, comma-shaped secretory plugs which can be squeezed from the orifices.

The glands are sexually dimorphic and seasonal in their development in the few species studied. Glandular hypertrophy has been observed only in adult males. Homologues of the gland are evident in females and immature stages but only by microscopic examination. Development of esophageal glands complements the gonadal cycle. They are largest at the beginning of the breeding season when testes are smallest and wane to minimal size by January when testes are largest and most active.

Locomotion

Aquatic turtles must leave the water to nest. Usually this involves only a short round trip from water to land, and aquatic turtles are rarely seen on land. Terrestrial locomotion in Australian chelids resembles that of most aquatic cryptodires, and is a slow, deliberate trotlike gait in which the contralateral front and hind limbs propel, while the other two recover for the next stroke (Walker 1973, 1979; Zug 1971).

Thermoregulation

Australian chelids thermoregulate primarily by basking, either whilst floating at the waters's surface, or on solid substrata. During aquatic basking, turtles float near to the surface for extended intervals, with the snout and sometimes the top of the carapace exposed and the rest of the body submerged (Chessman 1987). The limbs are usually spread and a slow, paddling action is common (Fig. 17.5). The turtles are presumably taking advantage of direct exposure to solar radiation in addition to conductive uptake of heat from the warm surface layers of the water.

Basking out of water is a common activity among shortnecked species of *Emydura* and *Elseya*, but rarely observed in the

Chelodina (Webb 1978). During aerial basking, the turtles climb from the water onto the shore, exposed banks, logs and tree roots to expose their bodies to the sun (Chessman 1987). Typically the legs are spread and the head and neck are extended upward. In the latter stages of basking, tears may be wiped over the head with the forelimbs, or the animal may dip its forefeet into the water then wipe them over the head (Webb 1978). The head, neck and limbs may be withdrawn periodically beneath the carapace and the animal may gape.

These behaviours have led to the suggestion that the turtles experience discomfort during the latter stages of basking, but persist with the activity so as to raise body core temperatures even though temperatures of the extremities may be uncomfortable. Elevated core temperatures are probably important for rapid and effective digestion, especially in omnivorous species, though other functions of basking have been suggested (Neill & Allen 1954; Boyer 1965; Pritchard & Greenhood 1968; Chessman 1987).

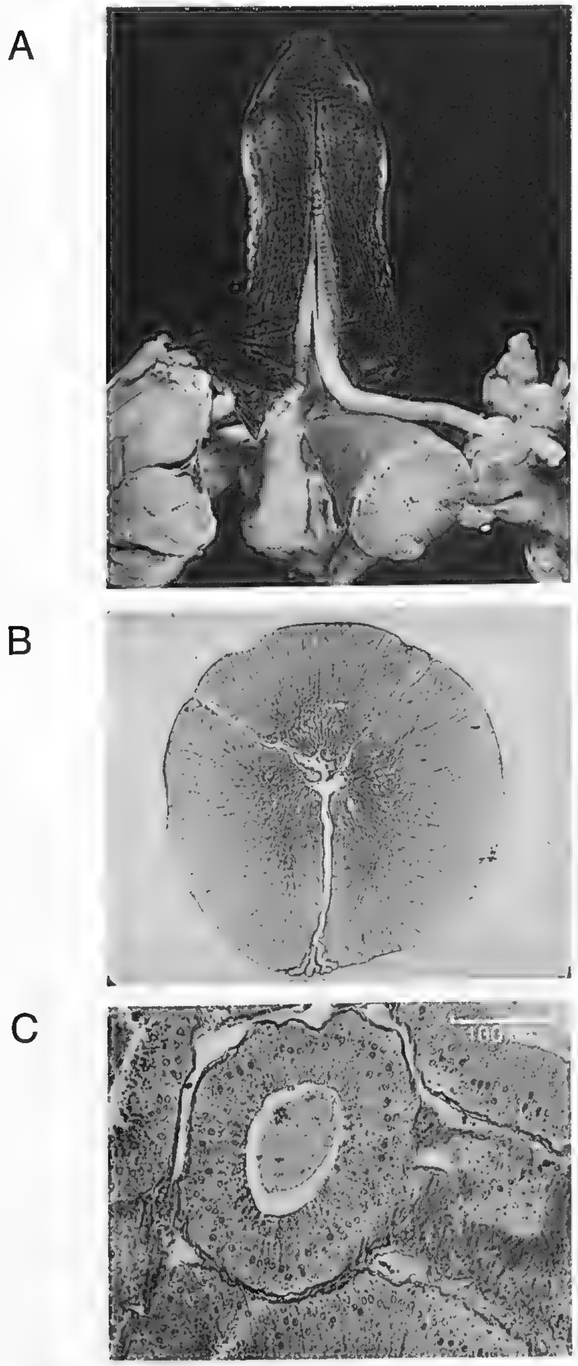

Figure 21.4 Fully hypertrophied oesophageal glands of a male *Emydura*, from the Macleay drainage basin, New South Wales. Diameter of glands 18 mm. A, dissected neck region, showing transverse section of the exposed oesophagus. Pale tissues on either side are muscles of the axillary region; B, transverse section through oesophagus, showing the single dorsal lobe, two lateral lobes and compressed oesophageal lumen. Collecting ducts from the glands converge on the lumen at the apex of each lobe. The stretched *tunica muscularis* and *tunica externa* are barely visible on the oesophageal periphery. H&E stain; C, transverse section of a single secretory tube. H&E stain. [Photos by J. Legler]

Respiration

All Australian chelids have functional lungs of similar eight-lobed structure, that are much like those of generalised cryptodires (see Chapter 16). All can rely indefinitely on the lungs for respiratory function where air breathing is possible. Observations of captive shortnecked chelids (except *Rheodytes*) show a rapid ventilation of lungs during the first few seconds at the surface, as evidenced by the rise and fall of the body in the water. Muscular activity associated with this behaviour has not been analyzed, but movements of both inguinal pocket and anterior limbs have been noted (Legler pers. obs).

All chelids can also augment pulmonary respiration with gaseous exchanges through accessory respiratory structures. These consist of the buccal and pharyngeal mucosae and the cloacal bursae. Buccopharyngeal respiration is considered in Chapter 16.

Cloacal bursae have a vascular lining and the degree of respiratory exchange that can take place is chiefly a surface phenomenon. Surface area is increased by modifications of the lining. The simplest bursae in Australian chelids have a rugose lining (*Chelodina* of both groups (Fig. 21.5A), *Pseudemydura*, and some *Emydura*). Most *Emydura* and *Elseya latisternum* have a rugose lining with elongate papillae only near the orifice. The bursae of *Elseya dentata* are completely lined with elongated ribbonlike papillae, each of which may bifurcate several times. Shortneck alpha has a dense aggregation of flattened papillae near the bursal orifices and is structurally intermediate between *Elseya dentata* and the genera which are only partly papillose.

Cloacal bursae reach a quintessence of development in *Rheodytes* (Fig. 21.5). The volume of a relaxed bursal sac equals that of a lung (measured by filling with water) and the entire bursa is lined with highly vascular, cylindrical papillae which have multiple branches (Fig. 21.5B). The papillae are richly vascularised with small, spirally arranged blood vessels and capillaries (Fig. 21.5C). Bursae are lined with non-ciliated, pseudostratified columnar epithelium. The apices of these cells stain densely with Alcian blue, but no specialised mucus cells occur. There are large numbers of eosinophilic granulocytes and lymphoid nodules.

Nielsen & Legler (unpub. data) present approximate figures for internal surface area of cloacal bursae in terms of increase in surface area over a theoretical smooth area. A value of 2.5 (for example, *Chelodina expansa*) means that the topography of the mucosal lining increases the surface area by 2.5 times that of a smooth area. Surface increase values for Australian chelids range from 1.4 to 16.1. In *Chelodina* (both groups), *Pseudemydura*, *Emydura* and the *Elseya latisternum* group, the figures vary from 1.4 to 6.2, but average between 3.5 and 4. The upper range is represented by the *Elseya dentata* group (10.0) and by *Rheodytes* (16.1).

In general, the physical diffusional barrier decreases as surface area increases. At its extreme, in *Rheodytes* this barrier consists of the endothelium of a blood capillary and as few as two epithelial cells. Papillae contain smooth muscle, suggesting that flow of blood into a papilla can be regulated. This smooth muscle contracts on fixation, and greatly reduces the length of the principal papillae. The bursal wall has an intrinsic *tunica muscularis* of at least two layers, in which contractile units are orientated almost perpendicular to one another.

All Australian chelids can acquire oxygen, and probably dispose of carbon dioxide, via the cloacal bursae. Captive *Rheodytes* seldom breathe air and we have never observed heads at the surface in the wild. It has been demonstrated that captive animals diving voluntarily can obtain all of their necessary oxygen from the bursae (Gatten & Legler unpub. data). *Rheodytes* has

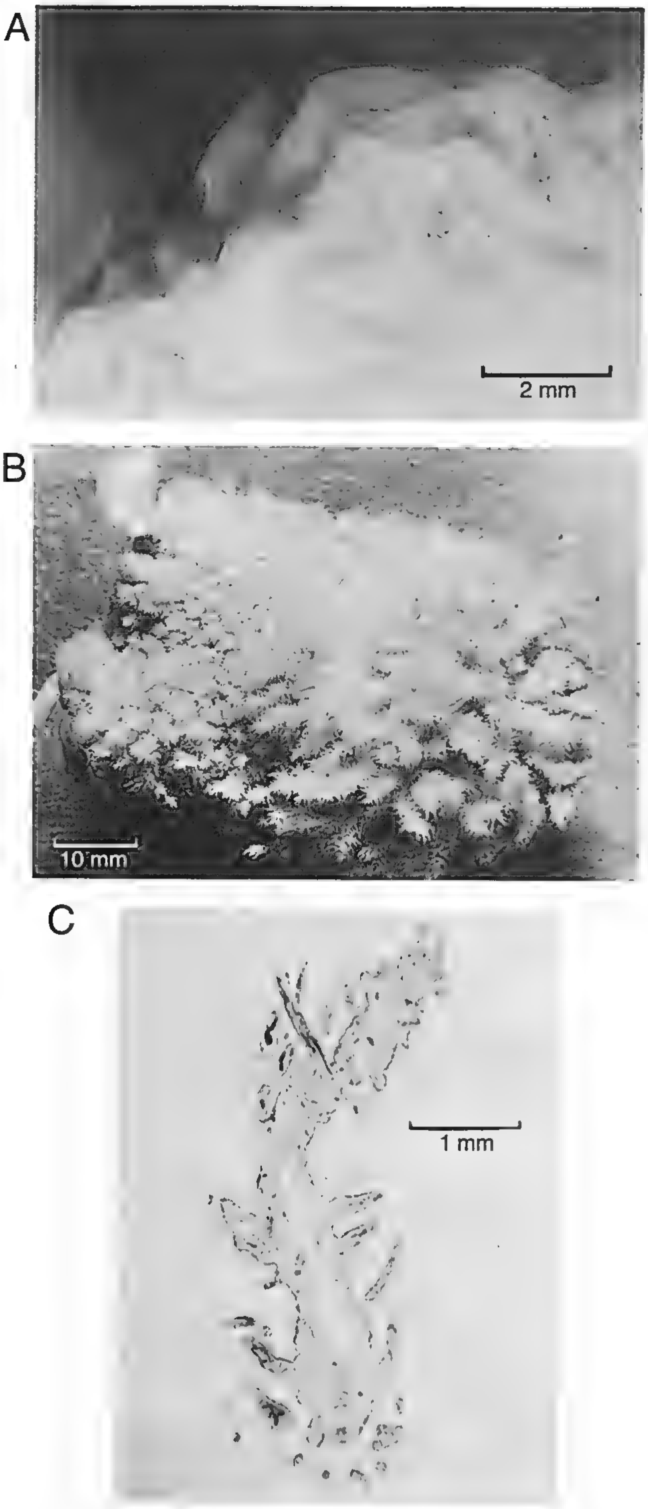

Figure 21.5 Structure of cloacal bursa lining. **A**, *Chelodina expansa*, showing series of simple rugosities in the lining; **B**, the lining of *Rheodytes leukops* is covered with branched papillae. The longest of these were ≈15 mm before fixation; **C**, longitudinal section through a single branched papilla of *Rheodytes leukops*. The central lumen, and blackened lumina in the bases of the branches are vascular. Blackened capillary networks are discernible just beneath the epithelial covering of the papilla. Smooth muscle occurs in the main walls of the central stem. [Photos by J. Legler]

seemingly achieved the greatest emancipation from air breathing of any aquatic chelonian.

Excretion and Osmoregulation

Burbidge (1967) compared the physiology of two chelids in south-western Australia. *Chelodina steindachneri* occurs in temporary water in severe desert, and *Chelodina oblonga* spends most of the year in permanent fresh water. The former is apparently adapted to a desert environment; it has a lower desiccation rate, increased ability to store water using cloacal bursae and an enlarged urinary bladder. It has the ability to convert ammonia to urates more effectively than *C. oblonga*, is able to maintain blood volume during dehydration, and has a higher critical thermal maximum.

Sense Organs and Nervous System

Australian chelids are well-endowed with a variety of integumentary organs on the head and neck, which are thought to function as mechanoreceptors (see Chapter 16). The nictitating membrane is absent or vestigial in all Australian chelids. Its absence is probably a derived condition (Legler & Cann 1980; Legler & Bruno unpub. data; Legler pers. obs.). Most Australian chelids have a translucent to transparent lower eyelid, through which the turtle's eye is visible. Brief mention of eyelid translucency was made by Walls (1942) and Gadow (1901).

Eyelid translucency occurs to a variable extent throughout the order Chelonia but tends to be greater in taxa that lack a nictitating membrane. The lower eyelids of young *Chelodina* of both groups and various shortnecked chelids can be virtually transparent. The transparency lessens with age but usually at least some detail of the eyeball can be discerned. Certainly perception of light is proportional to translucency, and probably an image can be formed in instances of transparency without opening the eye. Translucent eyelids may therefore serve in lieu of nictitating membranes. Captive chelids close their eyes when they sleep and usually wake when there is movement in front of the aquarium. Integumentary appendages and transparent eyelids are probably adaptations for dark and turbid aquatic environments.

Some chelids can achieve a high degree of stereoptic vision. Members of both groups of *Chelodina* and *Hydromedusa* provide the best examples but there is some stereopsis in *Rheodytes* and other shortnecks. In longnecks, stereopsis facilitates an accurate strike at moving prey.

Secretory Organs

Australian chelids all have well-developed musk glands (see Chapter 16). Captives accustomed to handling usually secrete only under traumatic circumstances. Members of the *Chelodina longicollis* group are perhaps the most odiferous turtles in the world. Each gland may store as much as 2.5 ml of yellowish secretion. This can be squirted for a few centimetres, but usually it is just smeared on the surface of the turtle. While the odour of widely diffused musk is interesting and distinctive, concentrated musk is unique and powerful. It makes some persons nauseous, and may irritate the mucous membranes of the eyes, nose, and pharynx (Legler pers. obs.). Eisner *et al.* (1978) isolated the several compounds from the musk of *Chelodina longicollis*, including oleic acid, linoleic acid, palmitoleic acid, palmitic acid, stearic acid, citronellic acid and beta-ionone.

The function of musk is unknown. Kool (1981) was unable to demonstrate that the musk of *Chelodina longicollis* deterred various native predators. Dorrian & Ehmann (1988) have presented data that suggest that some predators are repulsed by musk from *C. longicollis*. They tested various sympatric freshwater fishes (eels, catfish, murray cod, and lungfish) and freshwater crocodiles with normal food and food to which musk had been applied. Musk-tainted food was avoided by eels and crocodiles.

Dorrian & Ehmann (1988) observed that some *C. longicollis* hatchlings turned on their backs in the presence of eels and also that some orientated the bright orange and black plastron towards a fish while floating at the surface. This sparse information suggests a possible warning colouration/noxious taste combination in young *C. longicollis*.

Table 21.1 Egg size and weight (mean ± one standard deviation and sample size) for the eight genera or generic groups (indicated by parentheses) of Australian chelid turtles. Length and breadth are simply the largest and smallest dimensions of each egg.

Genera	Length (mm)		Breadth (mm)		Weight (g)	
	Mean ± SD	N	Mean ± SD	N	Mean ± SD	N
Chelodina (expansa)	39.16 ± 3.40	304	27.51 ± 2.41	304	17.08 ± 3.46	169
Chelodina (longicollis)	30.87 ± 2.88	282	20.00 ± 1.86	282	6.65 ± 1.47	57
Elseya (dentata)	50.21 ± 2.14	72	28.84 ± 1.75	72	24.49 ± 4.22	39
Elseya (latisternum)	33.06 ± 2.76	300	21.55 ± 1.55	300	9.41 ± 1.84	194
Shortneck Alpha	34.20 ± 1.26	120	22.40 ± 0.68	120	10.10 ± 0.72	119
Rheodytes	29.37 ± 1.51	234	21.04 ± 0.80	234	7.40 ± 0.89	208
Emydura	34.06 ± 3.06	1278	19.96 ± 1.65	1279	8.66 ± 2.29	489
Pseudemydura	36.64 ± 1.43	8	19.70 ± 0.51	8	8.47 ± 0.35	3

Reproduction and Development

Egg volume (ml) and egg weight (g) are roughly equal (Legler pers. obs.). Weight is a valuable descriptor for egg size but unfortunately is not available uniformly in studies of turtle eggs. However, the volume can be estimated with reasonable accuracy from egg measurements, using the formula for an elliptical spheroid, where:

$$V\ (\text{ml}) = \frac{4}{3}(\pi B^2 A) \quad \text{where } A = \frac{1}{2}\text{ length and } B = \frac{1}{2}\text{ breadth}$$

Most of the comparative data are presented by Ewert (1979). Egg volume varies substantially within and between Australian chelid species (Table 21.1). The largest eggs are those of *Elseya dentata* and *Chelodina expansa*, which range from 20 to 26 ml, and 12 to 20 ml, respectively. The smallest Australian chelid eggs are those of *Emydura* in several southeast coastal drainage basins (3.75 to 5.3 ml) and of *Chelodina longicollis* (4.0 to 6.7 ml).

Egg shape can be expressed simply as W/L. The eggs of most chelonians are ellipsoidal spheroids (0.5 to 0.7). The eggs of some populations of *Chelodina rugosa* are closest to spherical (0.809 to 0.858) of the Australian Chelidae.

Table 21.2 Selected data on carapace length and weight of hatchling Australian chelid turtles. Mean, one standard deviation and sample size (N) are given for each datum. All hatchlings were measured and weighed between 3 and 14 days of age, which avoided anomalous measurements caused by shell distortion immediately after hatching and precluded most early growth.

Species	Length (mm)		Weight (g)	
	Mean ± SD	N	Mean ± SD	N
Chelonia expansa	35.3 ± 4.9	3	8.6 ± 1.1	4
Chelodina longicollis	30.0 ± 1.7	87	4.6 ± 0.5	83
Elseya dentata	46.8 ± 0.8	21	14.8 ± 0.9	21
Elseya latisternum	31.8 ± 2.1	32	5.1 ± 1.0	8
Shortneck Alpha	34.8	4	–	–
Rheodytes leukops	29.3 ± 1.6	20	4.3 ± 0.5	24
Emydura victoriae	32.6 ± 0.7	15	5.1 ± 0.3	15
Emydura australis	32.7 ± 1.7	22	5.6 ± 0.6	35
Emydura krefftii	29.8 ± 2.4	66	4.1 ± 0.7	60
Emydura macleay	26.6 ± 3.0	48	3.6 ± 0.8	46
Emydura macquarii	30.1 ± 0.6	10	5.4 ± 0.6	7

Hatchling sizes and weights for seven Australian chelid genera are summarised in Table 21.2. There is a general direct correlation of hatchling size with egg size in all turtles (see Ewert 1979 for comparative data).

Incubation times in the laboratory for six genera are summarised in Table 21.3. The longest incubation times are those of those of *Elseya dentata* and *Chelodina expansa*. Legler (1985) demonstrated that incubation time at a given temperature (30°C) is inversely related to southern latitude in wide ranging taxa (*Emydura* sp. and *Elseya latisternum*). Ewert (1985) presents the most comprehensive comparative data on incubation times at controlled temperature. Australian chelids studied to date lack temperature dependent sex determination (Bull, Legler & Vogt 1985; Georges 1988a; Thompson 1988; Palmer-Allen, Beynon & Georges 1991).

NATURAL HISTORY

Life History

Two broad reproductive patterns can be identified among the Australian Chelidae. Species of the temperate zone commonly nest in spring and hatch in summer, while patterns of tropical zone chelids can be more variable.

The most common reproductive pattern among Australian temperate zone chelids is one of spring nesting and summer hatching. This pattern is exhibited by *Emydura krefftii* (Georges 1983), *E. macquarii* (Chessman 1978), *Elseya latisternum* (Legler 1985), *Rheodytes leukops* (Legler & Cann 1980), shortneck alpha (Cann unpub. data) and *Chelodina longicollis* (Parmenter 1985). Variations on this theme occur with latitude and altitude. In the more southern populations, ovarian development and mating activity ceases in winter. The nesting period may begin as early as August (Georges 1982a) in warmer areas and as late as November in colder areas (Vestjens 1969). For each of the above species, multiple clutching is common throughout their ranges (Legler 1981), with the exception of populations of *Chelodina longicollis* located close to the altitudinal limit of their range (Vestjens 1969).

The western swamp turtle, *Pseudemydura umbrina*, must contend with both cold winter temperatures and summer drought near Perth, Western Australia. It inhabits ephemeral clay swamps which are dry for six to nine months of the year, depending upon rainfall (Burbidge 1981). The turtles spend the dry summer period in refugia beneath leaf litter, under fallen branches or in holes in the ground. Ovarian development begins while the turtles are aestivating, and continues throughout winter and spring (Kuchling & DeJose 1989). Ovulation is apparently stimulated by the spring flush in food availability, in the short period when temperatures and availability of free-standing water allow the accumulation of reserves for breeding and aestivation. The turtles copulate when

Table 21.3 Incubation time (in days) to pipping for genera or generic groups (indicated by parentheses) of Australian chelid turtles, at controlled laboratory temperatures. Data derived from Legler (1985) and Ewert (1985) for *C. longicollis* and *E. latisternum* at 25°. N represents number of eggs for *Chelodina expansa* and number of clutches for all other taxa.

Genera	Incubation temperature (°C)	Mean ± SD (days)	N
Chelodina (*expansa*)	30°	126 ± 2.0	3
	28°	150 ± 17.4	26
	25°	163 ± 16.8	22
Chelodina (*longicollis*)	30°	69 ± 4.7	8
	28°	65 ± 0.0	1
	25°	81 ± 0.0	3
Elseya (*dentata*)	30°	77 ± 0.0	2
	28°	85 ± 0.0	1
Elseya (*latisternum*)	30°	59 ± 4.8	15
	28°	56 ± 0.4	2
	25°	75 ± 0.0	3
Emydura	30°	46.6 ± 4.4	54
	28°	51.8 ± 0.9	6
	25°	72.8 ± 1.6	9
Shortneck Alpha	–	56	–
Rheodytes	30°	46 ± 2.2	10

active during winter and spring, and females nest during the early summer, not long before they must aestivate once more. Hatchlings emerge in the late autumn and early winter some 180 days after laying, an event timed to coincide with the winter season rains (Burbidge 1981).

Even greater variation from the typical temperate zone pattern is shown by *Chelodina expansa*, which nests in the autumn and winter (Goode & Russell 1968; Georges 1984; Legler 1985). After an exceptionally long incubation period, the hatchlings emerge in the following autumn. Little development of the eggs can be expected in winter, and overwintering of eggs no doubt contributes substantially to the incubation period of the species. However, eggs of *C. expansa* laid in the autumn still hatch some months after those of *Emydura macquarii* and *C. longicollis* laid in the following spring (Goode 1967). There may be some form of delayed or retarded development in *C. expansa* (Goode & Russell 1968).

The reproductive pattern of *C. expansa* is a curious one for the temperate zones, and more in keeping with the tropical strategy of coping with the seasonal cycles of wet and dry rather than the temperate cycles of hot and cold (Georges 1984; Legler 1985). It may well be that *C. expansa* originated in tropical Australia and that it is a recent arrival in the temperate zones, after a rapid spread through the Murray-Darling system. At the same time, the species may have retained many of the features of a tropical reproductive strategy (Legler 1985).

The need for flexibility in the reproductive patterns of tropical zone chelids is evident in the complex nesting habits of the northern longnecked turtle, *Chelodina rugosa* (Kennett, Christian & Pritchard 1993a; Kennett, Georges & Palmer-Allen 1993b). It is found in the extensive network of floodplains covering thousands of square kilometres (Finlayson, Bailey, Freeland & Fleming 1988), over which rapidly fluctuating water levels limit the availability of relatively dry ground suitable for nesting. In the dry season, the turtles survive by burying in the muddy bottom of the receding waterbody and aestivating underground (Grigg, Johansen, Harlow, Beard & Taplin 1986; Covacevich, Couper, McDonald & Trigger 1990a). If *C. rugosa* has similar preferences to *C. longicollis*, *C. expansa* and other freshwater species for relatively dry nest sites, only a short period would be available for nesting, after the wet season waters have receded but before aestivation becomes necessary.

In itself, this is not an insurmountable problem, as the reproductive cycle could be timed so that nesting coincides with suitable conditions, brief though they might be. Pseudemydura umbrina is faced with constraints of similar severity. However, although the wet-dry rainfall cycle occurs reliably each year, there is considerable annual variability in the timing of the onset, the duration, and the intensity of the wet and dry seasons (Taylor & Tulloch 1985). The combination of the short period suitable for nesting and extreme unpredictability as to when that period will occur would make it very difficult for *C. rugosa* to persist in the floodplains if its nesting requirements are similar to those of other freshwater turtles.

Instead, *C. rugosa* appears to lay its eggs under water or in a saturated soils (Kennett *et al.* 1993a). Development is arrested presumably because of the hypoxic conditions resulting from immersion (Kennett *et al.* 1993b). By nesting underwater, inability to predict the timing of the wet-dry transition is obviated and a more protracted nesting period is made possible. When the ground eventually dries and oxygen reaches the eggs, conditions presumably become suitable for incubation and development proceeds. The incubation period is such that the eggs hatch in time for the onset of the torrential rains of the wet season that follows.

Chelodina novaeguineae also occupies ephemeral waterbodies of the wet-dry tropics, but moves overland to more permanent waters when the floodplain recedes. If permanent water is not available, it will aestivate beneath litter, in burrows constructed by other animals or in flood crevasses and channels (Covacevich *et al.* 1990a; Kennett, Georges, Thomas & Georges 1992). In the Northern Territory, the species nests from April to July (Kennett *et al.* 1992). Apparently breeding is opportunistic, and a protracted nesting season is possible only for turtles successful in finding permanent or semi-permanent water to carry them through the dry season. Such opportunistic nesting has been suggested also for its close relative, *Chelodina steindachneri* (Kuchling 1988).

Elseya dentata occupies permanent water and nests in the early dry season of the Northern Territory and in the winter months in its Queensland range. There are insufficient data on the reproductive biology of this species and many others to speculate on the adaptive significance of the timing of egg laying and hatching.

Ecology

Recent studies have done much to increase knowledge of the diets of Australian freshwater turtles. Species of the genus *Emydura* are typically omnivorous. A broad range of food types is eaten, such as filamentous algae, periphyton, sponges, aquatic macrophytes and macro-invertebrates, terrestial insects which fall or are blown onto the water, and carrion (Legler 1976; Georges 1982b; Chessman 1986). Highly mobile species such as fish appear to be unavailable to these species except as carrion. The diet of *Emydura* provides much scope for opportunism, and may vary considerably from place to place and with season in response to local differences in the availability of food resources (Chessman 1986). Small juveniles of *Emydura krefftii* (Fraser Island) are principally carnivorous, and become omnivorous as they age (Georges 1982b). The diet of *Emydura macquarii* in the Murray Valley shifts from periphyton to greater reliance on plant material and carrion as the turtles age (Chessman 1986). Variation in diet with size and age can be explained in terms of energetic efficiency and the fact that more robust foods become available to them, as the turtles grow in size and strength.

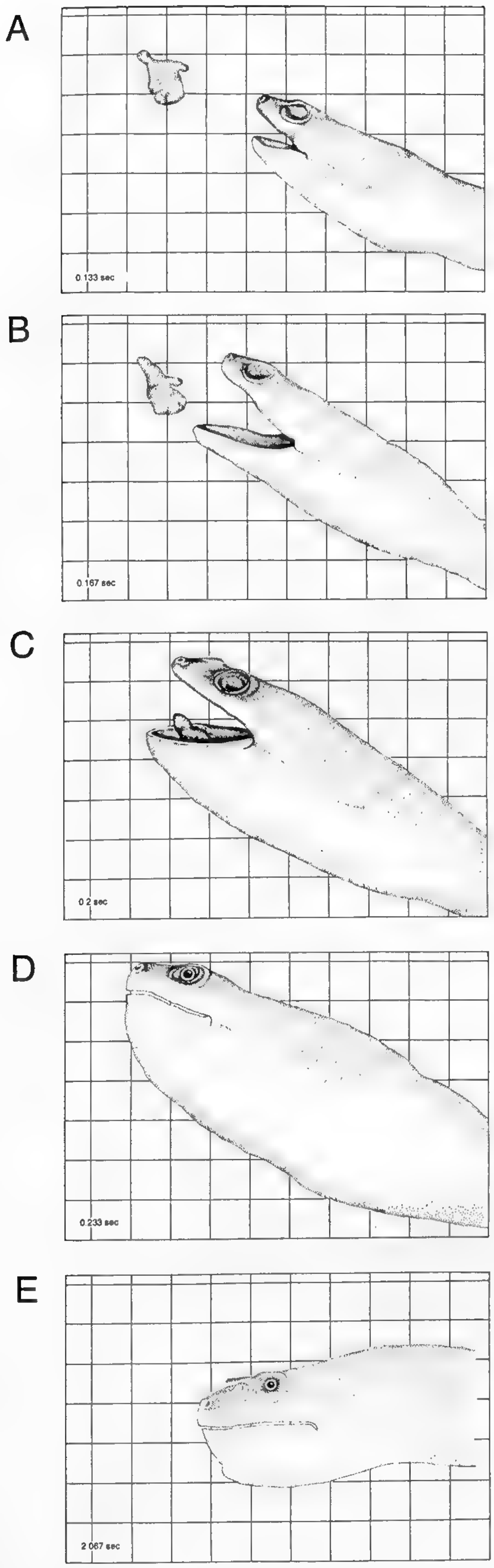

Figure 21.6 The strike of *Chelodina expansa*. In this experiment, numerals show the time (seconds) elapsed since the bait was dropped into the water. **A**, mouth opening rapidly, hyoid apparatus drawn slightly ventrad, and rapid forward thrust continues, eyes closed; **B**, increasing volume of mouth produces significant negative pressure and food moves toward mouth, hyoid still not fully abducted, eyes closed; **C**, rapid forward strike terminates and extreme hyoid abduction begins, food now in buccal cavity, eyes closed and seemingly retracted; **D**, strike continues to apogee, mouth closes and hyoid maximally abducted, neck retraction follows immediately, food now in pharynx, eyes open; **E**, head tilted back to original position during rapid withdrawal, mouth closed and hyoid expansion maintained, food in oesophagus and swallowing movements evident. (From video by J. Legler) [T. Wright]

Chelodina longicollis has a diverse and opportunistic diet that differs little in composition from that of available prey (Parmenter 1976; Chessman 1978; Georges *et al.* 1986). The shortnecked *Pseudemydura umbrina* and *Rheodytes leukops* are carnivorous. *Pseudemydura* will only take live prey, including aquatic crustacea and insects, small tadpoles and an aquatic earthworm *Eodrilus cornigravei* (Burbidge 1981). *Rheodytes leukops* feeds upon insect larvae and freshwater sponges (Legler & Cann 1980). These species lack the specialised morphological adaptations of *Chelodina* and other longnecked chelid turtles (Parmenter 1976; Legler 1978; Pritchard 1984) necessary for securing rapid prey.

Most shortnecked chelids secure their food by active foraging, which consists of slow prowling on the bottom. Neustophagia has been noted (Legler 1976). Food is ingested by inertial feeding movements combined with some suck and gape feeding. Sensory cues in locating edible items seem to be tactile, visual and olfactory. Typical olfactory inspection involves pressing the snout against the object with the neck extended and the head cocked slightly forward. Foraging turtles react to and alter course for movements detected at a distance. Chelids rarely actively pursue prey under water. The jaws of shortnecks are sufficiently powerful to hold objects firmly in the mouth while tearing at them with the foreclaws.

The longnecked chelids combine foraging with a sit-and-wait ambush feeding strategy. All longnecks are capable of executing an accurate strike at a prey target, which may be moving, and engulfing it by suck and gape ingestion (Fig. 21.6). Members of the *Chelodina expansa* group rely more on ambush feeding than members of the *C. longicollis* group. *Chelodina expansa* is sometimes found buried in silt with only the tip of the snout visible (Legler & Cann pers. obs.). It is not known whether this is simple concealment or a part of sit-and-wait predation.

Before striking, *C. expansa* remains virtually motionless and is usually firmly supported on the bottom or in a tangle of underwater brush (Legler 1978). The head and flexed neck are gradually oriented toward the prey. The strike is sudden and explosive and recovery to the flexed-neck position follows immediately. As the head nears the target, the mouth opens rapidly and the hyoid apparatus is depressed, creating an increased volume and negative pressure. The prey target is brought into the mouth with a rush of water. The mouth quickly closes and at least some excess water is expelled by hyoid movements before swallowing begins.

The mode of feeding and associated apparatus preclude chelid turtles from feeding out of water, but within these constraints, dependence on water varies considerably among species. Some require permanent water and typically leave it only to bask or nest (*Emydura* spp.). Others occupy seasonally ephemeral waters and survive dry periods by migrating overland to permanent water refugia (*Chelodina longicollis*, *Elseya latisternum*), by aestivating beneath the muddy bottoms of their once watery abodes (*Chelodina rugosa*) (Fig. 17.4) or beneath litter in surrounding terrestrial habitats (*Chelodina novaeguineae*, *C. longicollis*).

Six species of freshwater turtle occur in the Fitzroy-Dawson drainage of Queensland (Legler & Cann 1980) (Fig. 21.7). *Rheodytes leukops* prefers fast flowing water and riffle, where it can be found in microsympatry with *Emydura krefftii* and *Elseya dentata*. *Rheodytes leukops* is numerically dominant in riffle. In the deep, slow flowing pools of the main channel, *Emydura krefftii* is numerically dominant, but found together with *Elseya dentata*, *Chelodina expansa* and the occasional *Rheodytes leukops*. *Elseya latisternum* is abundant only in small tributaries off the main channel, and *Chelodina longicollis* is restricted to backwaters. These habitat differences, together with variation in diet, presumably allow these species to co-exist in the same drainage.

In the Murray valley, *Emydura macquarri* and *Chelodina expansa* live in deep, slow flowing stretches of the main river channel and in deep river backwaters and oxbows adjacent to the river

Figure 21.7 Diversity of Australian Chelidae expressed as number of genera in particular regions. Highest diversity occurs in the Fitzroy and Mary drainages of Queensland (four shortnecked, two longnecked genera). Three shortnecked and two longnecked genera occur in the Burnett drainage.
[W. Mumford]

(Chessman 1988). *Emydura macquarii* dominates in lentic environments. The third species, *Chelodina longicollis*, is the most common species in oxbow lakes, anabranches and ephemeral ponds, rain pools and swamps.

In the tropics, species in the genera *Emydura* and *Elseya* occupy permanent water only, as their abilities to aestivate or migrate overland are limited. *Emydura victoriae*, *Emydura* sp. aff. *victoriae* (formerly *Emydura australis*), and *Elseya dentata* are riverine species, but their distribution within a drainage may be very patchy. In the dry season, *Emydura victoriae* prefers smaller waterholes and tends to congregate in smaller tributaries than *Elseya dentata*, which predominates in the main channel and larger waterholes (Coventry & Tanner 1973; Georges & Kennett 1989). In the Daly River, which flows continuously in all months, turtle diversity reaches a peak at Policeman's Crossing where the large pools are shared by *Elseya dentata*, *Emydura victoriae* (red face), *Emydura* sp. aff. *victoriae* (yellow face) and *Chelodina rugosa* (Kennett & Georges 1989). A third species, *Emydura* sp. aff. *subglobosa* occurs in the upper reaches of the Daly drainage, above the escarpment. Further to the east in Arnhem Land, *Elseya latisternum* and a species of *Chelodina* with close affinities with the lowland *Chelodina rugosa* occur in sandstone billabongs and washpools above the escarpment.

Many species inhabiting ephemeral waters aestivate during dry periods (*Pseudemydura umbrina*, *Chelodina rugosa*, *C. steindachneri*, *C. novaeguineae*) while others rely upon migration to more permanent water during dry spells. *Chelodina longicollis* is capable of terrestrial aestivation (Chessman 1983b), but unlike *P. umbrina* and *C. rugosa*, it occupies ephemeral environments that may dry unpredictably for several consecutive years (Chessman 1978; Kennett & Georges 1990). Physiological studies indicate that prolonged terrestrial aestivation is unlikely in this species (Chessman 1978).

Behaviour

Basking is a major component of daily activity for *Emydura* sp. and *Elseya latisternum*, whereas *Chelodina expansa* and *Chelodina longicollis* bask only occasionally (Webb 1978). The function of basking in turtles has been debated by Neill & Allen (1954), Boyer (1965), Pritchard & Greenhood (1968) and Chessman (1978). Aerial basking appears to facilitate scute shedding and general epidermal sloughing in aquatic turtles. All *Emydura* shed whole scutes in the manner described by Moll & Legler (1971) for tropical *Pseudemys*.

Shedding of whole scutes has not been observed in adults of either group of *Chelodina*, in the *Elseya dentata* group, or in *Rheodytes*. In *Elseya latisternum* and in shortneck alpha, scutes are shed in fragments or as a result of wear. In *Rheodytes*, the scutes are not as thick as those of other chelids and the outer layer of the scute sloughs away as a pasty substance when the shell is touched.

There seems to be a close association with the almost completely aquatic mode of life, the absence of basking and scute shedding and the occurrence of autogrooming in *Chelodina expansa* and *Rheodytes*. Grooming is common in captive *Rheodytes* and *Chelodina expansa* and serves to remove the cornified layer of the soft skin wherever the head can reach (Legler 1978 pers. obs.).

The mating sequences of *Emydura macquarii*, *Elseya latisternum* and *Chelodina longicollis* have been described by Murphy & Lamoreaux (1978). In *Emydura macquarii* and *Elseya latisternum*, males approach females with a series of head-bobs, which the females reciprocate. The males then engage in cloacal touching, attempt to align their barbels with those of the females, and begin extensive stroking of the females' barbels, snout and orbital region with the forefeet and claws (Fig. 21.8). The female is then mounted from the rear. This sequence has been confirmed for *Emydura krefftii* (Banks 1987a).

Goode (1965) described the nesting behaviour of *Emydura macquarii*. The cavity is dug with the hind limbs and enlarged through the slow process of inserting one leg then the other into the hole. Dirt is extracted with a cupped foot, while the alternate limb bears the animal's weight. The soil is placed to either side and behind the animal. Once the flask-shaped nest chamber is complete the eggs are laid. After each egg is deposited, the hind leg is inserted into the hole to arrange it in position (Fig. 17.1). When laying is completed, the nest cavity is covered. The hind legs are extended until almost at right angles to the spine, the feet are orientated in a backward direction and brought together through an arc, carrying with them the soil from the excavated cavity. This action is repeated until the nest cavity is filled. The turtle then raises itself on all four legs and then drops its shell hard on the ground to compact the soil in the filled nest. This tamping of the soil has been observed also in *Chelodina longicollis* (Vestjens 1969), *C. oblonga* (Clay 1981) and *C. expansa* (Georges pers. obs.).

In the Murray Valley, *Emydura macquarii* tends to nest more frequently in lighter soils, whereas *Chelodina longicollis* and *C. expansa* will nest in any type of soil (Goode & Russell 1968). The latter two species apply copious quantities of cloacal fluid to the soil when constructing their nests (McCooey 1887; Goode & Russell 1968) and *C. longicollis* may 'puddle' its eggs in the mud formed by the cloacal fluids and clay soils. Rain is not necessary for nesting, as *Chelodina novaeguineae* has been observed nesting in the heaviest of clays in the absence of recent rain during the dry season in the Northern Territory, with the aid of cloacal fluids (Georges & Kennett unpub. data; Curtis 1928).

Head-bobbing has been observed in both groups of *Chelodina* (Legler pers. obs.) and is probably a form of communication. Some captives develop the habit and will perform various sequences of rapid head-bobbing in response to a person passing the aquarium or to bobbing motions made with human fingers. Amateur turtle fanciers are very familiar with such behaviour and have observed it in a variety of chelids, chiefly longnecks, but it has never been described or analysed.

Typical defence behaviour out of water consists of tucking in the head and tilting the shell toward the source of danger before turning the body, minimising the exposure of soft parts and maximising exposure of the shell. Defensive snapping and biting are common in shortnecks. Both of the *Elseya* groups, *Emydura*, and shortneck alpha can be savage and can inflict painful wounds. *Rheodytes* seldom bites under any circumstances and, in our own experience, neither group of *Chelodina* bites defensively.

Members of the *Chelodina expansa* group often lash the head and neck from side to side in a behaviour that resembles a strike.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

The distribution of Australian chelids is limited by the availability of permanent water or predictably seasonal water. The correlates of this geographic distribution are natural drainage systems. Australia is a relatively dry continent. Total effluent is 345 × 10^6 megalitres. By comparison, single rivers in other parts of the world discharge almost as much water, for example, 281 × 10^6 megalitres for the Danube River. Most of Australia's fresh water habitats are in a series of small coastal drainage systems at the periphery of the continent. The Murray-Darling system is the largest external drainage (Anon. 1967; Leeper 1970). Total external drainage is about 47% (by rough estimate) of continental area. The rest is dry by comparison and drainage is internal; water drains to internal basins and/or evaporates. This internal drainage area defines 'The Centre' for purposes of turtles. Turtles occur only in the easternmost part of this internal drainage system, the Cooper's Creek catchment or Lake Eyre drainage. If the Cooper's Creek drainage is included with all other drainage systems in which turtles are known to occur, the rough estimate is maximally 51% of the Australian land mass. Actually, the figure would be much lower because the upper reaches of many small, well-watered drainage systems are dry much of the time, especially in the north. The *Chelodina expansa* group has the largest distribution of any Australian chelid genus, occurring in most of the external drainage systems and approximately 45% of the continent.

Chelodina longicollis occurs farther south than any other Australian chelid. There are breeding populations at or near the southern tip of Victoria (39°S) and records for King and Flinders Islands in the Bass Strait (Cogger 1979; Iverson 1992). A species of *Emydura* is known from the Miocene of Tasmania (Gaffney 1981, 1991), but no chelid species occur there now. *Emydura macquarii* and *Chelodina expansa* occur in the lower Murray-Darling system at approximately 37°S. *Emydura* (near *signata*) and *Elseya* (near *latisternum*) occur at elevations of about 1000 m on the New England Tableland, equivalent to 34°30'S when corrected for altitude (Legler 1975). Although the extreme southern limits of distribution for Australian chelids may constitute 'harsh' conditions in human or agricultural terms, nowhere do chelids experience what could be termed a severe winter.

Chelids occur commonly on islands near the coasts of Australia and New Guinea, such as for example, Fraser Island, Daru and Stradbroke islands, and islands in the Torres Strait. There is an old record of '*Chelodina longicollis*' on Roti, off the south-western tip of Timor (de Rooij 1915) which has recently been confirmed by Anders Rhodin (pers. comm.) and is currently under study. Thus far there is no evidence that chelids have a natural distribution on oceanic islands but it is possible that they have been introduced in many places, including those mentioned above.

The Fitzroy and Mary drainages of Queensland each support six species of chelids in broad geographic sympatry — two species each of *Chelodina* and *Elseya*, *Emydura* and either *Rheodytes* or shortneck alpha (Fig. 21.8).

Affinities within the Chelidae

Burbidge, Kirsch & Main (1974) made the first attempt to develop a phylogeny for the Australian Chelidae. They undertook a phenetic analysis of morphological and serological data and identified three divergent groups, equally related to each other. These are the species of *Chelodina*, the species of *Emydura/Elseya*, to which Legler & Cann (1980) later added *Rheodytes leukops*, and *Pseudemydura umbrina*. This trichotomy is supported by other studies of morphology (Goode 1967; Gaffney 1977; Legler & Cann 1980), total protein electrophoresis (Frair 1980), karyotypes (Bull & Legler 1980) and behaviour (Webb 1978). In his studies of skeletal morphology, Gaffney (1977) refined and extended this phylogeny to incorporate South American forms. From the perspective of Australian forms,

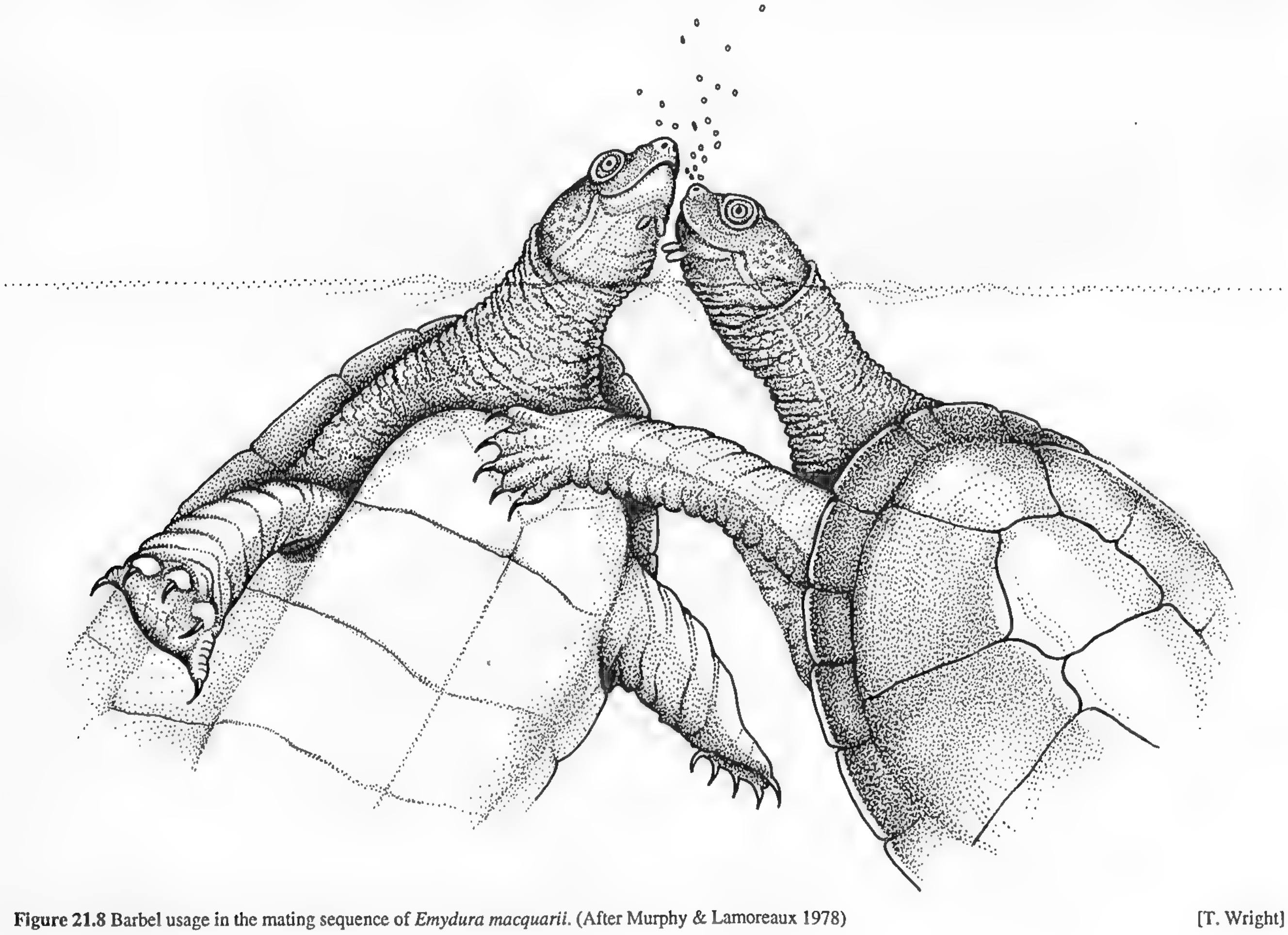

Figure 21.8 Barbel usage in the mating sequence of *Emydura macquarii*. (After Murphy & Lamoreaux 1978) [T. Wright]

Gaffney's phylogeny differed from that of Burbidge *et al.* (1974) in that the divergence of *Pseudemydura umbrina* pre-dated the divergence of *Emydura* and *Elseya* from *Chelodina.*

As chelid turtles are conservative in many morphological features, Georges & Adams (1992) used allozyme electrophoresis as an alternative to traditional morphological approaches to the systematics of the Australian chelids. They added many more species to the phylogenetic tree, some of which are yet to be described. The most striking departure from the phylogeny accepted at the time was the paraphyletic nature of the genus *Elseya.* The closest common ancestor of the living species of *Elseya* has the species of *Emydura* among its descendents. One approach to resolving this paraphyly is to synonymise *Elseya* with *Emydura,* the latter name having precedence, as suggested by McDowell (1983). McDowell's suggestion built upon previous support for the synonymy of the two genera from Gaffney (1977, 1979) and Frair (1980). Unfortunately, *Rheodytes* and shortneck alpha were not available for study by McDowell. These two monotypic genera could not be placed by the electrophoretic analyses of Georges & Adams (1992), but several of their analyses placed one or both of these species within the clade containing *Elseya* and *Emydura.* Synonymy of *Elseya* and *Emydura* may have to include the distinctive *Rheodytes* and shortneck alpha, a far less acceptable proposition when genera are erected largely on morphological criteria. Georges & Adams (1992) therefore recommended the preferred option of Legler (1981), who proposed to split the genus *Elseya* into two genera (*Elseya dentata* plus related species, and *Elseya latisternum* plus related species), and of Legler & Cann (1980) who considered that morphological similarities between species in *Elseya, Emydura* and *Rheodytes* were sufficient to indicate a common ancestry, but not to warrant lumping of any of the three genera.

Whether or not the Australian and South American chelid faunas each represent monophyletic assemblages is subject to dispute. It is not clear whether the *Elseya–Emydura–Rheodytes, Pseudemydura, Chelodina* trichotomy arose in Australia independently of lineages in South America. On the basis of a cladistic analysis of skeletal structure, Gaffney (1977) considered the longnecked South American genera *Hydromedusa* and *Chelus* to be the closest relatives of the Australian longnecked *Chelodina.* However, a subsequent analysis by Pritchard (1984) suggested that the similarities in head and neck structure of the South American and Australian longnecked turtles are the result of parallel evolution, in response to a common piscivorous diet. Attempts to relate *Pseudemydura umbrina* to other Australian chelids have failed (Legler 1981), possibly because the monotypic genus has no close relatives in Australia. Gaffney & Meylan (1988) considered *Pseudemydura* so divergent that they suggested placing it in a monotypic subfamily. *Pseudemydura* shares many morphological features with the South American genus *Platemys,* species of which may be the closest living relative of *Pseudemydura* (Legler 1981).

In a non-cladistic analysis using mensural morphological characters, soft anatomy, behaviour and life history, Cann & Legler (1993) place the Australian shortnecked chelids in three distinct groups (*cf.* Legler 1981, 1984, 1989a; Legler & Cann 1980). These are: *Pseudemydura,* which is not closely related to any Australian chelid, and may more closely related to a South American shortneck; *Emydura;* and the '*Elseya* complex', containing the *Elseya dentata* group, the *Elseya latisternum* group, *Rheodytes,* and shortneck alpha.

A multidiscriminate analysis of 39 morphological characters for the *Elseya* complex, including shortneck alpha and *Rheodytes,* showed the four genera of this group clustered almost equidistantly from each other without overlap in a three-dimensional plot, but distantly from all other Australian chelids. Thus the four genera are probably of common origin, and although they differ substantially from each other, are seemingly more closely related to each other than any is to *Emydura.*

Cann & Legler (1993) substantially corroborate the hypotheses of Georges & Adams (1992) on phylogeny and relationships. One of us (JL) however, questions the placement of *Chelodina oblonga* and the genus *Emydura,* and prefers to regard *Emydura* as more distantly related to all members of the *Elseya* complex and to regard *Chelodina oblonga* as a derivative of a *C. rugosa*-like ancestral stock that gave rise to other extant members of the genus. This approach to the genus *Chelodina* has a precedent in the division of *Chelodina,* by Burbidge *et al.* (1974), into the *longicollis* group, the *expansa* group, and a third group comprising *C. oblonga.*

Fossil Record

There are reports of fossil chelid turtles from Europe, North Africa and India, but the diagnoses of these fossils as chelids have been disputed (Williams 1953, 1954b). There is no well-accepted evidence that fossil chelids occur ouside the range of extant taxa (Pritchard 1979b; Pritchard & Trebbau 1984; see also Chapter 18). As such, chelid turtles are the only reptile group with clear Gondwanan origins.

22. FAMILY CARETTOCHELYIDAE

Arthur Georges & John C. Wombey

DEFINITION AND GENERAL DESCRIPTION

The family Carettochelyidae is represented by a single extant genus and species *Carettochelys insculpta*, found only in northern Australia and southern New Guinea. *Carettochelys* is distinguished from other Australian freshwater turtles by the absence of epidermal scutes overlying the shell, which is covered instead with a continuous skin. The limbs are paddle-shaped, like those of sea turtles, and each bears two claws. The nostrils are at the anterior end of a prominent fleshy proboscis (Pl. 3.9), and give rise to the name pig-nosed turtle.

Although initially placed in the suborder Pleurodira, the side-necked turtles (Boulenger 1889, *Carettochelys* is now included in the superfamily Trionychoidea of the suborder Cryptodira (Ogilby 1907; Wermuth & Mertens 1961). It is the only extant freshwater cryptodire.

HISTORY OF DISCOVERY

Carettochelys was first described in 1886 by Dr E.P. Ramsay, from an incomplete specimen collected on the Strickland River, a tributary of the Fly River in Papua New Guinea (Waite 1905). The collectors, Walter Froggatt and Jas H. Shaw, were part of a Geographical Society of Australasia expedition. More complete specimens from this region have been described since (Waite 1905; Walther 1922).

This peculiar species generated great interest in Europe, and was often sought specifically by explorers and travellers visiting New Guinea *Carettochelys* (Boulenger 1914; de Rooij 1915, 1922; Schultze-Westrum 1963; Wermuth 1963; Cann 1974).

The existence of *Carettochelys* in northern Australia was not widely known until 1970 when a specimen from the Daly River was reported in the scientific literature (Cogger 1970; Peters 1970). Evidence of breeding populations dates back to 1918 when eggs from the East Alligator River were lodged with the Victorian Museum by P. Cahill (Georges, Choquenot, Coventry & Wellings 1989), but the presence of Aboriginal rock paintings of *Carettochelys* (Cann 1980; Dupe 1980), dating back more than 7000 years (Chaloupka pers. comm.), indicates that the species has been a long-term resident of northern Australia.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Carettochelys is a heavy-bodied turtle, attaining about 55 cm in length (Cann 1978) and up to 22.5 kg in weight (Groombridge 1982). Its colour ranges from rich grey to grey-brown above and white, cream or yellowish below (Cogger 1992). The jaws are cream and a pale streak is present behind the eye. The carapace is elevated and rounded anteriorly, flattened laterally and has a strong median keel posteriorly. The shell is covered with a continuous skin, and epidermal scutes are absent. The fleshy, truncated, pig-like snout projects forward and downwards, its anterior and lateral surfaces are covered with tubercles and it is well-furrowed (Waite 1905; Pl. 3.9). The paddle-shaped forelimbs bear narrow crescentic scales on the rounded anterior edge. Only the first two digits are clawed and the remaining digits are strongly webbed to the tips (Ramsay 1886). The hindlegs are similar but shorter. Crescentic scales form a single line along the dorsal surface of the tail and decrease in size towards the tip. Prominent folds of skin extend laterally on each side from the undersurface of the tail across the thigh region and down the hind limbs (Pritchard 1979a).

On emergence, hatchlings have well-formed, strong limbs, but the plastron and carapace are extremely soft (Georges & Rose in press). Loose flaps of skin along the periphery of the shell harden to form a serrated margin after about one week. Hatchlings have a tuberculate median keel. The poorly defined polygonal outline around each of these tubercles may be homologous with the scute seams of other turtles (Pritchard 1979a). These tubercles are lost as the turtle grows. Mature males have a larger tail than females of the same size.

Skeletal System

The morphology of the species was described by Ramsay (1886), Waite (1905) and Walther (1922). The large skull bears five to seven shields, the anterior and median pairs of which are fused (see Waite 1905 for further details). A characteristic, strong,

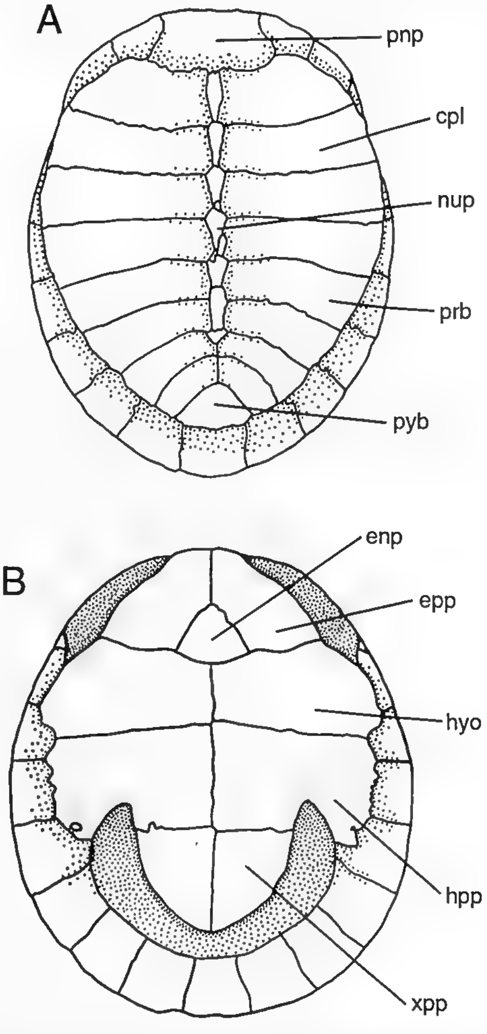

Figure 22.1 Elements of the shell of *Carettochelys insculpta* . **A**, carapace; **B**, plastron. **cpl**, costal plate; **enp**, entoplastron; **epp**, epiplastron; **hpp**, hypoplastron; **hyo**, hyoplastron; **nup**, neural plate; **pnp**, preneural plate; **prb**, peripheral bone; **pyb**, pygal bone; **xpp**, xiphyplastron. [J. Courtenay]

lateral excavation of the robust lower jaw accommodates the insertion of the *pars superficialis* of the *m. adductor mandibulae externus* (Meylan 1988). The vertebrae are broad and the cervico-dorsal joint is double (Williams 1950). The nuchal bone of all carettochelyids has paired ventral processes just anterior to the prezygopophyses of the first thoracic vertebra, which simplifies identification of isolated nuchals in the fossil record (Meylan 1988).

The ten peripheral bones on each side of the shell are complete and well developed (Fig. 22.1A). The number of neural plates and their relationship to the costals is variable (Waite 1905; Longman 1913). The plastron is complete and lacks a median fontanelle. There are nine plastral elements (Fig. 22.1B). Several of these are not rigidly ossified together, but have cartilaginous connections which allow a certain amount of flexibility (Pritchard 1979a). The plates of the carapace, plastron and skull are covered with small, round rugosities or wavy irregular raised lines between shallow sculptures (hence *insculpta* = engraved), though these are clearly evident only in preserved specimens.

Reproduction

The eggs of *Carettochelys* are white, hard-shelled and almost round (Ramsay 1886), with a mean diameter of 38.7 ± 1.3 mm and a mean weight of 33.7 ± 3.5 g (Daly River; Webb, Choquenot & Whitehead 1986). The shells are extremely hard compared to those of other chelonians, and are 0.39 ± 0.05 mm in thickness (Webb *et al.* 1986). The distinct shell membrane (0.067 ± 0.014 mm) is composed of four or five individual layers. The ultra-structure of the eggshell and membranes have been described in detail by Erben (1970). They account for about 16% of egg weight, and yolk and albumen each comprise about half of the remaining 84% (Webb *et al.* 1986).

Clutch sizes range from 7 to 19 in northern Australia (Webb *et al.* 1986; Georges 1987). Bimodal distributions of nesting dates provide strong evidence of multiple clutching, a conclusion supported by examination of reproductive tracts of three specimens dissected during the nesting season at Kikori, Papua New Guinea (Georges & Rose in press). There are no data to support a relationship between clutch size and adult body size, as is often the case in chelonians (Moll 1979), so it is not known how annual reproductive potential varies with size or age.

Embryology and Development

After 64 to 74 days at 30°C the embryos enter a period of diapause or aestivation within the egg (Webb *et al.* 1986). At onset of aestivation, metabolic rate decreases precipitously and embryonic growth ceases. Yolk is used during aestivation at a rate likely to exhaust supplies after about 59 days at 28° to 30°C. Incubation periods for 30 natural nests from the Kikori River of Papua New Guinea ranged from 86 to 102 days, at an average nest temperature of 31.6°C (Georges & Rose in press), suggesting that aestivation occurs in the field within this estimated limit of 59 days. Hatching can be stimulated experimentally by reducing oxygen availability, suggesting that in the field the stimulus is either the first rains of the season or flooding (Webb *et al.* 1986) (Fig. 22.2). The period of aestivation presumably ensures that hatching is timed to coincide with favourable environmental conditions. It may also be of adaptive value to hatch synchronously within nests, as development rates may vary considerably because of thermal gradients within nests (Georges 1992), or between nests, to satiate predators.

The hatchling sex ratio is influenced by incubation temperature both under constant laboratory conditions (Webb *et al.* 1986) and under fluctuating conditions in the field (Georges 1992). Embryos incubated at a constant 28° to 30°C become males whereas those incubated at 32°C become females (Webb *et al.* 1986). The laboratory threshold for sex determination lies somewhere between 30° and 32°C.

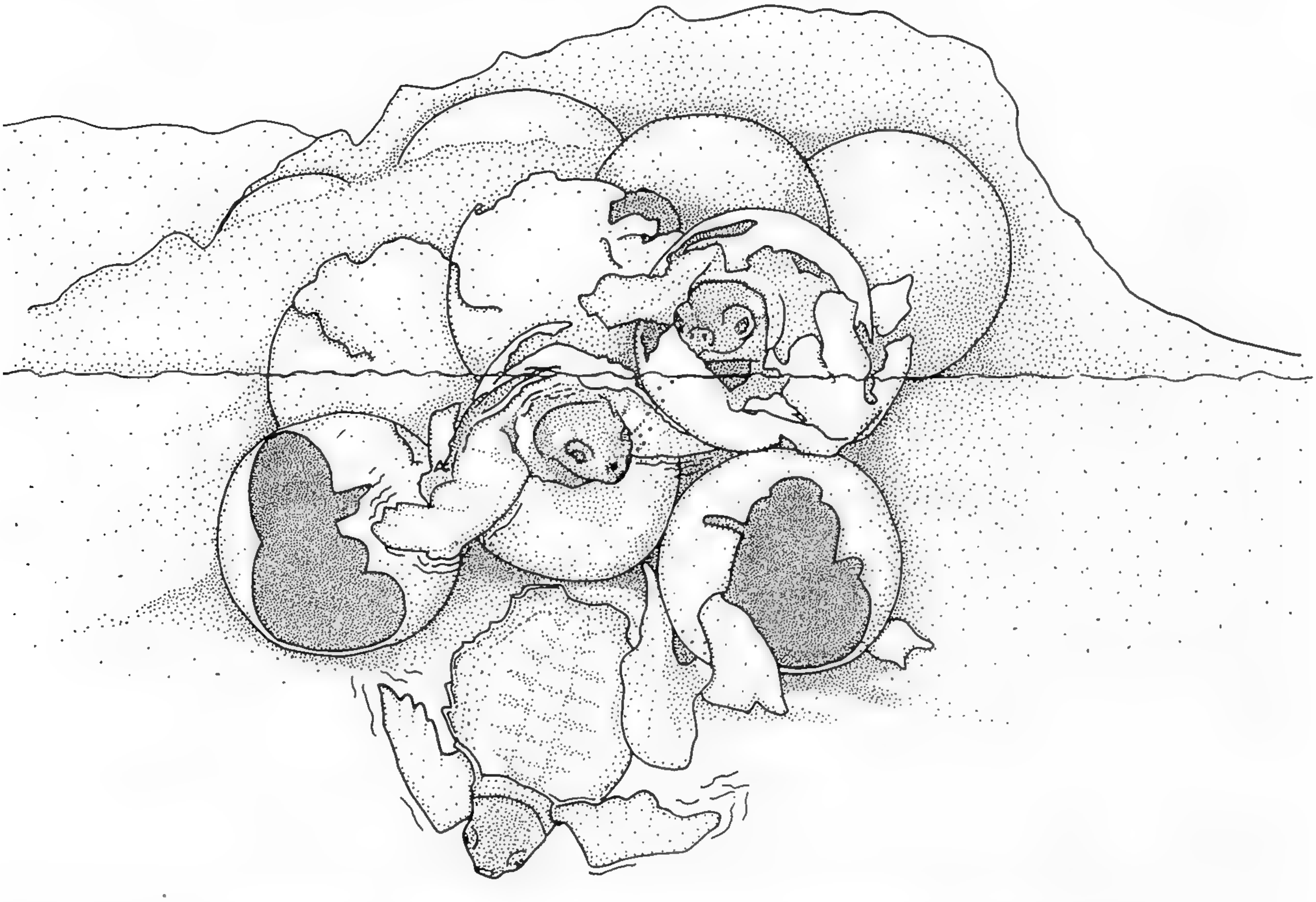

Figure 22.2 Nest site and emergent hatchlings of *Carettochelys insculpta*. Reduction of oxygen by rising floodwaters probably stimulates the eggs to hatch. (After ABC 1988) [J. Courtenay]

NATURAL HISTORY

Life History

Carettochelys was long considered one of the rarest turtles in the world (Groombridge 1982), but it is not certain whether this reputation reflects its remote distribution or its low population densities (Pritchard 1979a). Georges & Kennett (1989) found *Carettochelys* to be widespread between the tidal reaches and the head-waters of the South Alligator River, and that high densities of 33.8 ± 11.2 turtles/ha may be present in the upper reaches during the dry season. Although its distribution in Australia may be patchy, and in these terms it is rare, the species may be common locally in both Australia and Papua New Guinea (Brongersma 1958; Slater 1961; Cann 1974; Press 1986).

Little is known of the population dynamics of *C. insculpta*. Nests are subject to predation by monitor lizards and man (Cann 1974; Pernetta & Burgin 1980; Groombridge 1982; Press 1986; Georges & Kennett 1988). However, data on rates of recruitment to the breeding population or on survivorship of adult and subadult turtles are lacking, and the age at sexual maturity is unknown. Adult sex ratios are skewed in favour of females, a common trait in species with temperature dependent sex determination.

The nesting season in Australia extends between mid-August and early October in the Daly River and from mid-July to early November in the East and South Alligator rivers (Georges & Kennett 1989). *Carettochelys insculpta* nests upon sandy banks adjacent to water in the middle reaches and mouths of rivers, on sandy shores of islands in river deltas, and on coastal beaches. It prefers clear, fine sand adjacent to water, but also nests in mud and loams (Slater 1961; Rhodin & Rhodin 1977; Cann 1978; Pernetta & Burgin 1980; Webb *et al.* 1986; Georges & Kennett 1989).

Ecology

Carettochelys is known from the clear, shallow, continuously flowing waters of the Daly drainage (Cogger 1970; Cann 1972; Webb *et al.* 1986) and from billabongs and plunge pools of the South and East Alligator rivers (Legler 1980, 1982; Press 1986; Georges & Kennett 1989). There are no substantiated reports of *Carettochelys* from estuarine areas (Press 1986; Georges & Kennett 1989), unlike those for estuaries in Papua New Guinea (Groombridge 1982). The preferred substratum in the billabongs of the Alligator River region is sand and gravel, covered with a thin layer of fine silt and litter. Fallen trees and branches, undercut banks, exposed tree roots, and local accumulations of litter provide a diverse range of underwater cover for turtles. The banks of the billabongs are covered in a dense broadleafed forest, including the important turtle food, *Ficus racemosa.* The wet season habitat of *Carettochelys* in Australia is unknown.

Carettochelys is omnivorous. In the dry season, it feeds predominantly upon the fruits, seeds and leaves of a wide variety of riparian vegetation, including *Ficus racemosa*, *Syzygium forte* and *Pandanus aquaticus*, and mangroves (*Sonneratia* species) in both Australia and New Guinea. Aquatic plants, such as the eelweed *Valisneria* sp., the water nymph *Najas tenuifolia* and algae, are also eaten when available. Molluscs, crustaceans, fishes, and mammals are eaten, the last of these presumably taken as carrion (Cogger 1970; Schodde, Mason & Wolfe 1972; Georges & Kennett 1989; Georges & Rose in press). The wide range of foods eaten provides great scope for opportunism, and the diet varies greatly between localities, according to the foods available.

Economic Significance

Carettochelys insculpta is highly prized as a food by the indigenous peoples within its range in New Guinea. In Australia, where turtles are regularly eaten by Aborigines, *Carettochelys* is favoured by some for its size and flavour (Schultze-Westrum 1963; Cann 1980; Press 1986). Georges & Kennett (1989) reported an annual take of 19 turtles by two Aboriginal families at Nourlangie Camp. Their traditional and current methods of capture were described by Georges & Kennett (1988). There are no reports of harvesting of the eggs of *Carettochelys* in Australia, unlike the situation in Papua New Guinea (Pernetta & Burgin 1980).

Carettochelys insculpta is listed by the IUCN (1991) as a threatened species in need of specific conservation measures. In Australia, *Carettochelys* benefits from State and Federal legislation prohibiting the exploitation of native fauna by all but Aboriginal peoples. However, such legislation does not protect the species from habitat destruction or modification. Within the Alligator rivers region of Kakadu National Park, feral water buffalo, *Bubalus bubalis*, can trample the sand banks and destroy nests (Georges & Kennett 1989). As a result, the species may have become much more restricted in its Australian distribution since the introduction of water buffalo (A. Carr in Pritchard 1979b). Water buffalo also forage on young plants and damage the bank structure of billabongs, thus destroying the riparian vegetation on which the turtles depend in the dry season for food. While this may initially benefit *Carettochelys* by increasing underwater cover afforded by fallen trees, branches and litter, it can only have long-term deleterious effects on the turtle populations. An intensive buffalo control program is now in place in the Park.

The catchment of the Daly River is largely unprotected and control of even the river banks and important riparian vegetation is largely in private hands. Urgent attention should be given to protecting the section of the Daly River corridor between Policeman's Crossing and the junction of the King River, and to protecting the riparian vegetation throughout the Daly drainage.

It is important to know more of the distribution, ecology and seasonal movements of *Carettochelys* in Australia in order to better assess the value of the two known major populations in the Daly River and the three Alligator rivers and their innumerable branches. Such information is also needed to assess the possible impact of proposed or potential development within catchments, and to judge the adequacy of existing reserves for protecting the species.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

In northern Australia, *Carettochelys* occurs in the Daly (Cogger 1970; Cann 1972; Webb *et al.* 1986; Georges 1987), South Alligator (Schodde *et al.* 1972; Legler 1980, 1982; Georges & Kennett 1989), East Alligator (Georges *et al.* 1989) and Victoria drainages (Cogger 1992; Roberts pers. comm.). There are also anecdotal reports of the species from the Darwin, Adelaide, McKinlay and Roper rivers of the Northern Territory (Cann 1972; Bywater pers. comm.) and the Wenlock River on the west coast of Cape York Peninsula (K. Day pers. comm. in Webb *et al.* 1986).

Although a resident of Australia for many thousands of years, the absence of a fossil record in Australia, the lack of subspecific differentiation between the Australian and New Guinean populations, and the highly aquatic nature and estuarine tendencies of this species suggest that it is a relatively recent immigrant to Australia from New Guinea (Cogger & Heatwole 1981).

Carettochelys has been recorded from all the major rivers of Papua New Guinea east to the Vailala and from several of the southern flowing rivers of Irian Jaya (Georges & Rose in press).

Affinities with other Groups

Carettochelys has no close living relatives, and the debate over its affinities has been protracted (Walther 1922; Frair 1985; Meylan 1988). Current wisdom has it that the closest living relatives of the family are among the soft-shelled turtles of the family Trionychidae (Chen, Mao & Ling 1980; Frair 1983, 1985). The relationship of the Carettochelyidae to other extant chelonian families is shown in Figure 18.2.

Fossil Record

The family Carettochelyidae was widespread in the Tertiary, its distribution covering much of Laurasia by the Eocene (Meylan 1988). It was a diverse family with six genera in two subfamilies. *Allaeochelys*, *Carettochelys* and *Chorlakkichelys* form the Carettochelyinae; *Anosteira*, *Pseudanosteira* and *Kizylkumemys* form the Anosteirinae (Meylan 1988).

The fossil record from the Australasian region is confined to a single fragment of the nuchal bone and an associated external mould (Glaessner 1942). The fossil was collected from marine beds at the mouth of Mariana Creek, Vailala River, Papua New Guinea, and was dated as upper Miocene. A fossil fragment of plastron from the post-Miocene of Western Australia attributed to *Carettochelys* by Gorter & Nicoll (1978), on the basis of surface sculpturing, is apparently misidentified (Gaffney 1981).

23. GENERAL DESCRIPTION AND DEFINITION OF THE ORDER SQUAMATA

Harold G. Cogger

The Squamata are members of the diapsid subclass Lepidosauromorpha, a group whose only living descendants are the lizards, amphisbaenians, snakes and tuataras. The lizards, amphisbaenians and snakes together constitute the Order Squamata (or Superorder Squamata, according to Estes 1983).

Because the Squamata include approximately 95% of living reptiles, the phylogenetic position of this group within the Lepidosauromorpha, its component taxa, and their diagnostic features, have been the subject of numerous reviews (Estes & Pregill 1988; Kluge 1989).

The three suborders of the Squamata include the Sauria (lizards) and the Serpentes (snakes), which are represented in Australia by diverse faunas of nearly 500 species, and 250 species, respectively. The third suborder, the Amphisbaenia, comprises a small group of worm lizards and related species which do not occur in Australia.

The earliest known squamate fossils date from the late Permian and early Triassic, approximately 230 million years ago. These early fossils were already clearly lizard-like in their preserved features. Carroll (1988a) points out that lizards (the first squamates) do not appear to have originated as a result of '...a significant shift in behavioral patterns or the evolution of major new structural elements, but rather may be seen as resulting from the gradual accumulation of improvements in feeding, locomotion, and sensory apparatus.' Carroll (1988b) includes among these changes the emargination of the lower temporal fenestra and the development of a joint between the upper end of the quadrate and the squamosal. This mobility of the quadrate is termed streptostyly, and provides the opportunity to increase the force of the *m. pterygoideus*, the largest of the jaw-closing muscles, by moving the effective jaw joint from the lower to the upper end of the quadrate. Improvements in the hearing apparatus involved an enlarged tympanum, and the development of epiphysial joint structures resulted in determinate growth of the affected long bones. Also unique to the squamates is the possession of paired intromittent or copulatory organs in the males, termed 'hemipenes'. The squamates lack abdominal ribs, or gastralia, and the vertebral centra are usually procoelous (concave anteriorly, convex posteriorly).

In Australia, squamates constitute about 97% of some 750 species of Australian reptiles. The Australian members of these two groups may be distinguished by the following key:

Key to the suborders of the order Squamata

1 (a) Limbs usually present, but even if absent some remnants of pectoral and pelvic girdles remain; non-regenerated tail in limbless forms at least 50% of snout–vent length; maxilla united to, and forming an integral part of, the cranium; external ear-opening usually present; parietals not extending to ventral side of braincase; brain not enclosed by bone anteriorly .... Sauria (sometimes Lacertilia)

(b) Limbs always absent; tail at most 35% of snout–vent length; maxilla free and attached to the cranium only by tendons and muscles; external ear-opening always absent; parietal bones extending to ventral surface of braincase; brain entirely enclosed by bone .... Serpentes (sometimes Ophidia)

Though the first lizards appeared in the Triassic, forms which are clearly associated with what we think of as modern lizards did not appear until the Cretaceous, about 130 million years ago. These lizards, like modern forms, were generally small and probably preyed mostly on arthropods.

Modern lizards occupy most of the world's terrestrial environments. They are most abundant in the tropics, but extend to the Arctic Circle in the north and to the southernmost islands of Australia, New Zealand and South America. Except for the marine iguana of the Galapagos Islands, all other members of the group are restricted to terrestrial or freshwater habitats.

Most lizards have well-developed limbs; the head is normally held high off the ground, and they are agile predators. However many have evolved adaptations which depart from the typical lizard body form and which allow them to exploit specialised habitats or lifestyles. Many burrowing forms have reduced limbs. The mandibles are fused anteriorly at the symphysis, and typically an external ear opening and some tympanic bones are present. The ear-opening and tympanum have been lost many times in lizard evolution.

Autotomy, a feature of many lizards, and one which is absent in snakes, is the ability to break off voluntarily all or part of the tail, to distract predators or during territorial fights. This is achieved at special fracture planes in some or all of the caudal vertebrae. When the tail is broken off, muscle spasms often make the lost section of tail wriggle violently for several minutes, distracting a predator from the escaping owner. Typically a tail lost by autotomy regrows from the point of fracture, usually within a few months, but lacks the bony caudal vertebrae of the original tail. Rather, the new section of tail is supported by a cartilaginous rod lacking fracture planes.

Lizards present a vast range of behaviours. As ectotherms, much of their daily cycle of behaviour is concerned with thermoregulation. This enables them to maintain body temperatures at a level which optimises metabolic processes while maintaining optimum locomotor ability, to feed, escape predators, or avoid potentially lethal environmental conditions. Both diurnal and nocturnal species thermoregulate, although their temperature requirements may differ greatly. Further, many species have evolved complex social and sexual behaviours, often associated with sexual differences in size and colour, and sometimes involving territoriality between males and/or females.

While most lizards lay eggs, various forms of livebearing (viviparity) have evolved in different groups. Parental care of nests, eggs or young is rare.

Snakes evolved from a lizard ancestor at some time during the Cretaceous, although animals that are unequivocally snakes are not known from the fossil record until relatively late in the Cretaceous, about 100–120 million years ago, and the characteristic cranial features of snakes were in place by this time. These features included even greater emargination of the lower temporal fenestra and increased mobility of the quadrate, while the lower and upper jaw elements were becoming highly mobile in the fashion of modern snakes. These features, together with limblessness, suggest that early snakes, like their modern descendants, were active predators which swallowed their prey whole.

It has long been accepted as given that snakes evolved from a fossorial (burrowing) lizard-like ancestor (Senn & Northcutt 1973), because snakes share a number of features with extant burrowing lizards. These include elongation of the body, limb girdle reduction, the loss of limbs, middle and outer ear structures, and movable eyelids, and the development of a fixed spectacle. This view has come under increasing challenge (Carroll 1988b).

Moreover, modern snakes appear to be most closely related to varanoid lizards, with which they share a highly mobile forked tongue, high mobility of the quadrate and jaw elements, and the highly developed role of the vomeronasal (Jacobson's) organ in sensory perception. However, this hypothesised relationship is also under challenge (Rieppel 1983).

Snakes are characterised, as mentioned above, by the loss of limbs and limb girdles (although vestiges of the pelvic girdle are rear limbs are found in some groups of primitive snakes) and the loss of outer and middle ear structures. There are no movable eyelids, the eye being covered by a fixed, transparent scale. The tongue is long, forked and highly mobile, collecting particles from its immediate environment which the tongue tip transfers to the vomero-nasal organ for sensory identification. The shape and position of the viscera reflect the elongate body form; the left lung is usually absent, or is much smaller than the right lung. In many species, but especially in aquatic, diving snakes, the trachea may also be highly vascularised to form a forward extension of the lung. The elongate body is also accompanied by a marked increase in the number of vertebrae and associated ribs. The vertebrae have additional bony projections (compared with lizards) to which the muscles of the back are attached, giving greater control and power in limbless locomotion. Like other squamates the male intromittent organs are paired.

The skull of snakes is generally highly kinetic in the mobile, loose attachment to each other of many of the bony elements. The great relative mobility, especially of the jaws and bones of the palate, including the two halves of the lower jaw, permits most snakes to swallow food items with diameter greater than the predator's head. In particular, the quadrate bone is more mobile than that of lizards, allowing the mouth to open very widely. All snakes swallow their prey whole, and the needle-like and backwardly-directed teeth constrain the prey while it is forced back into the throat by the alternate forward motion of the jaws on either side.

Unlike lizards, the parietal and frontal bones have grown downwards to fuse with the parabasisphenoid and so create a solid bony casing for the forebrain. This ensures that the brain is not damaged when the snake swallows large or struggling prey.

CLASSIFICATION OF THE SAURIA

Currently some 17 families of extant lizards are recognised (Savage 1992). These are believed to be derived from three major evolutionary lines. All date from about the end of the Mesozoic, and are usually treated as distinct infraorders: the Iguania, Gekkota, Scincomorpha, and Anguinomorpha. The last two are often placed together as a single assemblage. Estes (1983) and Greer (1989) provide further discussion of these and other groupings.

The Iguania includes one Australian family, the Agamidae (dragons). Both families in the Gekkota, the Gekkonidae (geckos) and Pygopodidae (snake-lizards), are found in Australia. The close relationship of the snake-lizards with the Australian diplodactyline geckos has been recognised by Kluge (1987), who placed them together in the family Pygopodidae, and is discussed further in Chapter 28. The Scincomorpha is represented in Australia by the Scincidae (skinks), of which we have the most diverse fauna in the world, while the Anguinomorpha is represented by the Varanidae (monitor lizards or goannas). The five lizard families represented in Australia may be distinguished using the following key:

Key to the families of suborder Sauria

1 (a) Limbs normally present, though often very small; if limbs are entirely absent, then the eyes are very small and lie within a slit-like opening and there is a single large frontonasal scale (Fig. 23.1A) 2

(b) No obvious or normal limbs, though a scaly flap or 'fin' may be present on each side of the vent in some species; all with round, snake-like, lidless eyes; one or two pairs of frontonasal scales (Fig. 23.1B) (snake-lizards) (Pl. 4.9–4.12) .... Pygopodidae

2(a) Eyes with or without movable lids; if eyelids are absent then the pupil in daylight is not a narrow, vertical slit and the scales on the dorsum are imbricate (overlapping) 3

(b) Eyes snake-like, without movable lids; pupil in daylight a narrow, vertical slit; scales on the dorsum small, juxtaposed (not overlapping) (geckos) (Pls. 4.1–4.8) .... Gekkonidae

3 (a) Top of head covered with very small, irregular scales, usually 10 or more between the eyes (Fig. 23.1C) . 4

(b) Top of head covered with large, regular and usually symmetrical, shield-like scales, usually fewer than 8 between the eyes (Fig. 23.1D) (skinks) (Pl. 6) .... Scincidae

4 (a) Tongue long, slender, sheathed at its base and deeply forked like that of a snake (Fig. 23.1E); tongue frequently flicked in and out when lizard is alert (goannas or monitor lizards) (Pl. 5.10–5.13) .. Varanidae[1]

(b) Tongue broad, flat, not sheathed at its base and with only a slight notch in front (Fig. 23.1F); tongue not normally protruded except for eating and drinking.(dragon lizards) (Pl. 5.1–5.9) .... Agamidae

[1] Single genus *Varanus*

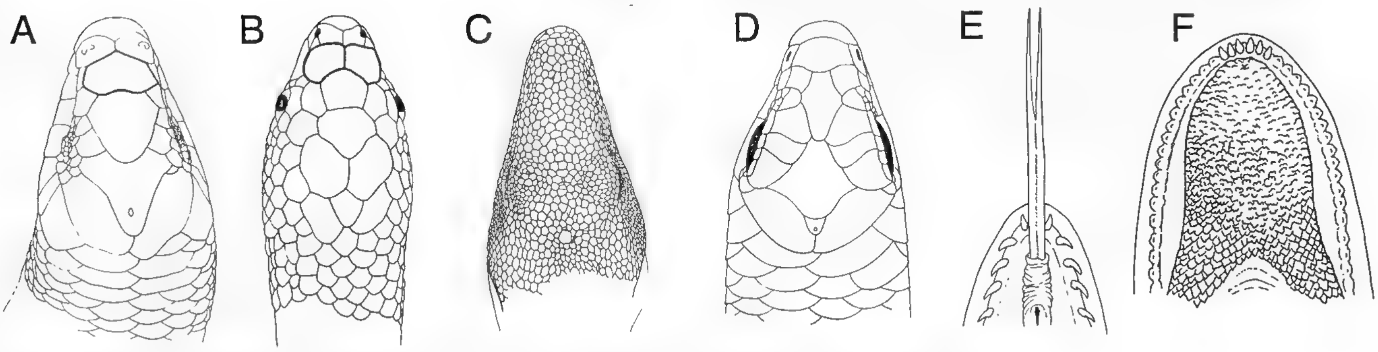

Figure 23.1 Key characters for families of the suborder Sauria. Pertinent features of elements A–F are noted in the adjacent key. [H.G. Cogger]

Key to the genera of family Gekkonidae

1 (a) Subdigital scales granular, without any enlarged terminal scales, tubercles or lamellae (Fig. 23.2A) 2

(b) Subdigital scales with at least enlarged terminal scales or one or more enlarged tubercles or transverse lamellae (Fig. 23.2B) 3

2 (a) Rostral and mental shields rounded (Fig. 23.2C); labials much larger than adjacent scales, or, if subequal, tail not much longer than broad, strongly depressed 3

(b) Rostral and mental shields projecting, beak-like (Fig. 23.2D); labials and adjacent scales subequal; tail long and slender .... *Rhynchoedura*

3 (a) Tail ending in a globular knob (Fig. 23.2E); several scales between rostral and nostril (Fig. 23.2F)..*Nephrurus*

(b) Tail long and slender, not ending in a knob; rostral contacting nostril or separated from it by only one scale .... *Lucasium*[1]

4 (a) Digits lying flat, entirely on the substrate when viewed laterally (Fig. 23.2G); terminal claws, if present, small and lying in a groove between distal lamellae (Fig. 23.2H) or arising from the upper surface of a large digital expansion (Fig. 23.2I) 5

(b) Digits angular when viewed laterally (Fig. 23.2J); feet bird-like, their terminal claws conspicuous and free (Fig. 23.2K) 12

5 (a) At least some digits with claws 6

(b) All digits without claws .... *Crenadactylus*

6 (a) A distal pair of enlarged plates on the lower surface of each digit, quite distinct from and discontinuous with the remaining subdigital lamellae or tubercles (Fig. 23.2L) 7

(b) The enlarged subdigital lamellae in a continuous series (Fig. 23.2M) 9

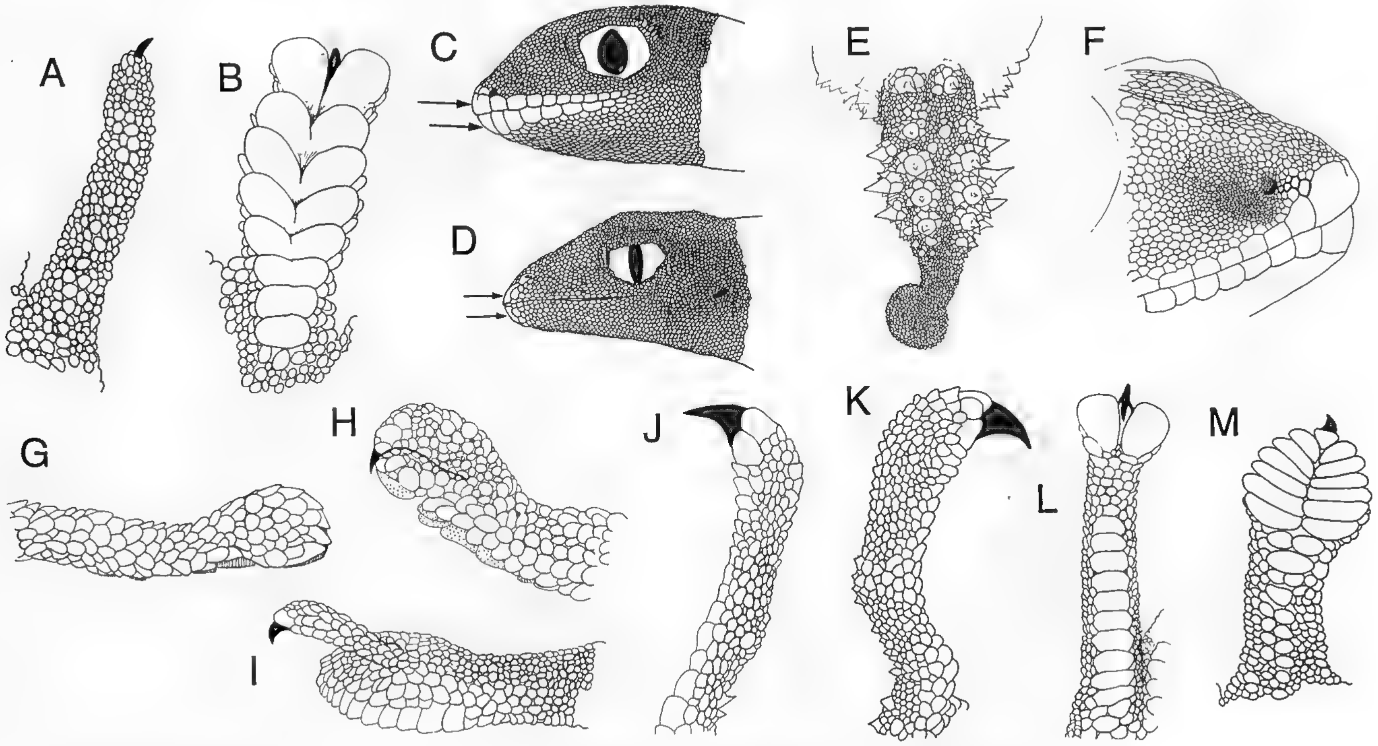

Figure 23.2 Key characters for genera of the family Gekkonidae. Pertinent features of elements A–M are noted in the key above. [H.G. Cogger]

7 (a) Distal subdigital lamellae (excluding enlarged apical plates) single (Fig. 23.2L) 8

(b) At least some distal subdigital lamellae (excluding enlarged apical plates) paired (Fig. 23.2B) (Pl. 4.4) .... *Oedura*

8 (a) Scales above distal expansions of digits significantly larger than scales above basal parts of digits (Fig. 23.3A) .... *Christinus*[2]

(b) Scales above distal expansions of digits more or less equal in size to those above basal parts of digits (Fig. 23.3B) (Pl. 4.5) .... *Diplodactylus*[3]

9 (a) Claws of digits free, arising from the upper surface of the digital expansion well within the border of the expansion (Fig. 23.2I) 10

(b) Claws of digits arising from the edge of the digital expansion (Fig. 23.3C) 11

10 (a) Inner toe of each foot clawless (Pl. 4.6) .... *Gehyra*

(b) Inner toe of each foot clawed .... *Hemidactylus*

11 (a) Claws of digits small, sessile and retractile in the distal median groove (Fig. 23.3C) (Pl. 4.3) .... *Pseudothecadactylus*[4]

(b) Claws of digits large, not retractile in a distal median groove (Fig. 23.3D) .... *Lepidodactylus*

12 (a) Postmentals greatly enlarged (Fig. 23.3E); tail long and slender, without large spines 13

(b) Postmentals and adjacent gulars subequal (Fig. 23.3F); tail swollen, or broad and flattened, or covered in large spines 15

13 (a) Claw between three scales (Fig. 23.3G); two rows of lateral scales on digits (Fig. 23.3H) .... *Heteronotia*

(b) Claw between two scales, the lower deeply notched (Fig. 23.3I); three rows of lateral scales on digits (Fig. 23.3J) 14

14 (a) A lateral skin fold from axilla to groin .... *Cyrtodactylus*

(b) No lateral skin fold from axilla to groin (Pl. 4.2) .... *Nactus*

15 (a) Claw between two or three scales, body not laterally compressed 16

(b) Claw between five scales (Fig. 23.3K); body laterally compressed .... *Carphodactylus*

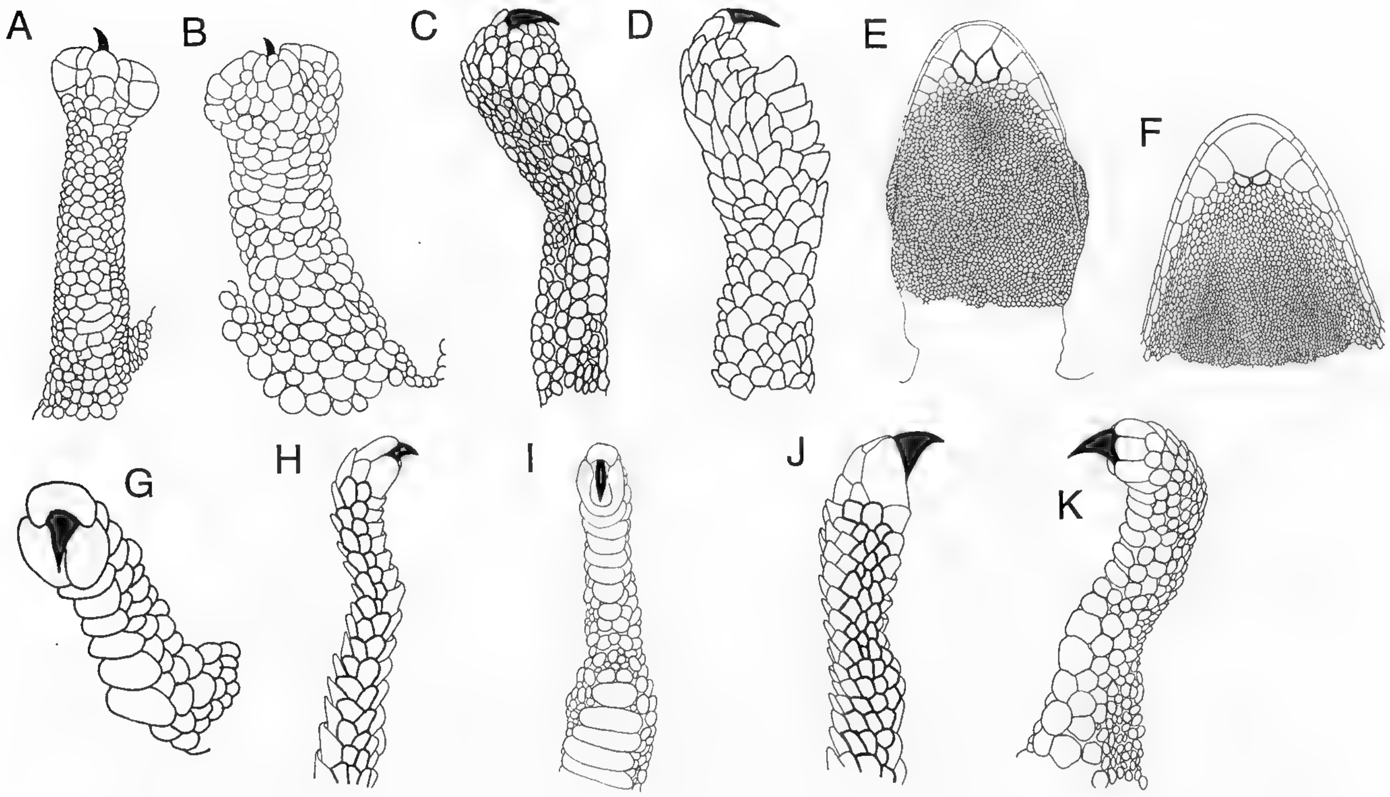

Figure 23.3 Key characters for genera of the family Gekkonidae. Pertinent features of elements A–K are noted in the key above. [H.G. Cogger]

16 (a) Claw between two scales, the lower deeply notched; digits compressed with three or more rows of lateral scales; tail long, with large spines, or strongly depressed, leaf-shaped, and more than twice as broad as thick (Pl. 4.7, 4.8) .... *Phyllurus*

(b) Claw typically between two scales, but lower scale may be deeply grooved or even divided; digits with two rows of lateral scales; tail without spines, less than twice as broad as thick .... *Underwoodisaurus*[5]

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[1] sometimes regarded as a member of genus *Diplodactylus*

[2] includes the Australian representatives of *Phyllodactylus*

[3] sometimes divided into two or more distinct genera

[4] sometimes regarded as a synonym of the otherwise New Caledonian genus *Rhacodactylus*

[5] sometimes treated as a synonym of *Nephrurus*

Key to the genera of family Pygopodidae

1 (a) Head covered with enlarged, symmetrical shields (Fig. 23.4A) 2

(b) Head covered with small, irregular shields (Fig. 23.4B) (Pl. 4.10) .... *Lialis*

2 (a) Ventral scales smooth 3

(b) Ventral scales keeled .... *Pletholax*

3 (a) Preanal pores present (Fig. 23.4C) 4

(b) Preanal pores absent 5

4 (a) Eight or more preanal pores (Pl. 4.12) .... *Pygopus*

(b) Four preanal pores .... *Paradelma*

5 (a) Parietal scales present (Fig. 23.4D) 6

(b) Parietal scales absent (Fig. 23.4E) (Pl. 4.11) .... *Aprasia*

6 (a) Anterior nasals in contact (Fig. 23.4F), or fewer than 20 mid-body scale rows 7

(b) Anterior pair of nasals separated by rostral (Fig. 23.4G), and 20 mid-body scale rows .... *Aclys*

7 (a) External ear-opening present and obvious; more than eight scales along a line across the top of the head joining the angle of the mouth on each side (Fig. 23.4H) (Pl. 4.9) .... *Delma*

(b) External ear-opening very small and hidden by overlying temporal scales; fewer than eight scales along a line across the top of the head joining the angle of the mouth on each side (Fig. 23.4I) .... *Ophidiocephalus*

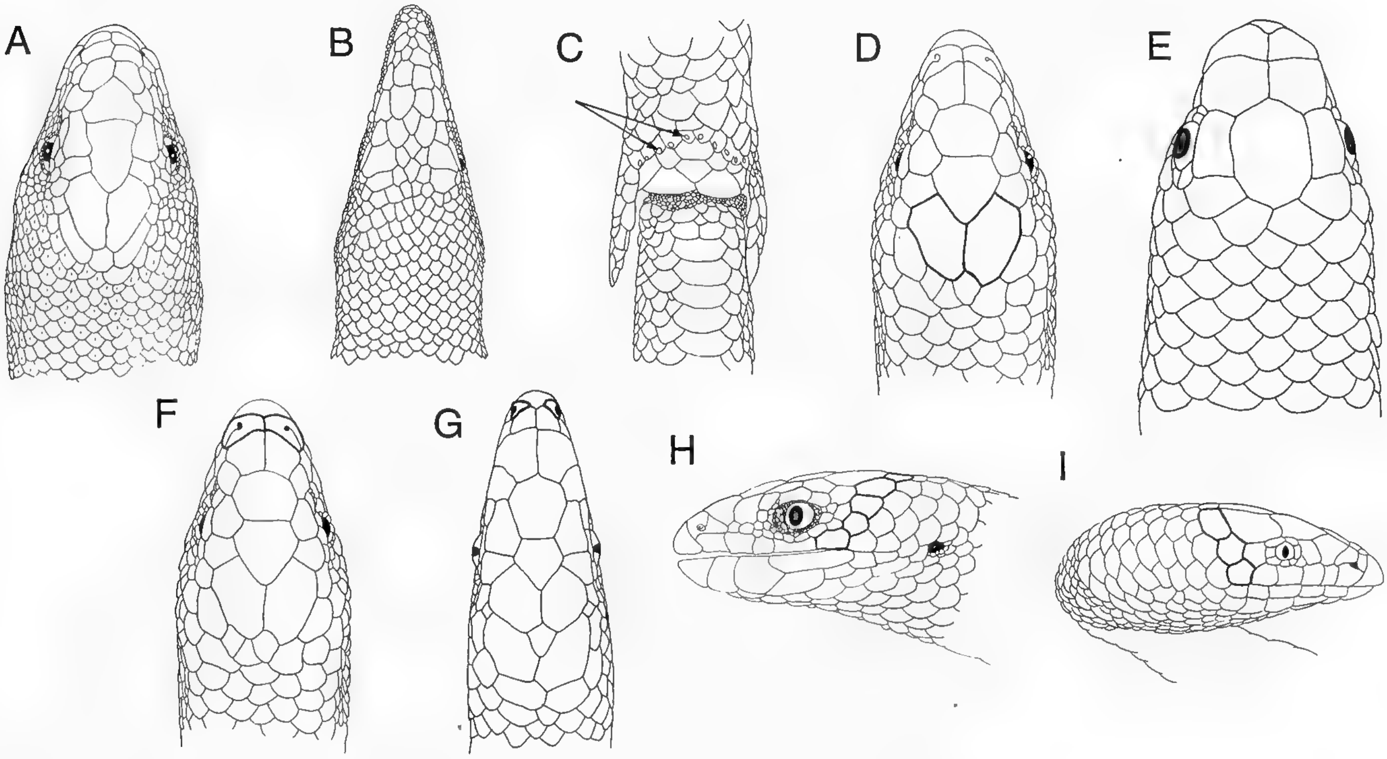

Figure 23.4 Key characters for genera of the family Pygopodidae. Pertinent features of elements A–I are noted in the key above. [H.G. Cogger]

Key to the genera of family Agamidae

1 (a) Body without very large conical spines or a spiny nuchal hump 2

(b) Body covered above with large conical spines, each much larger than the eye; nape with a large spiny hump (Fig. 23.5A) (Pl. 5.6) .... *Moloch*

2 (a) No large, loose, erectile fold of skin around the neck 3

(b) A large, loose, erectile fold of skin, or 'frill', almost completely encircling the neck (Fig. 23.5B) (Pl. 5.9) .... *Chlamydosaurus*

3 (a) Tail shorter than head+body (snout–vent length) .... *Cryptagama*

(b) Tail longer than head+body (snout–vent length) 4

4 (a) Femoral and/or preanal pores absent 5

(b) Femoral and/or preanal pores present (Fig. 23.5C), at least in males 6

5 (a) Transverse gular fold absent; tail about one and one quarter times as long as body; tip of tail rounded, not tapering to a point .... *Chelosania*

(b) Transverse gular fold present (Fig. 23.5D); tail at least twice as long as head and body; tip of tail tapering to a point .... *Hypsilurus*

6 (a) Tail at most slightly laterally compressed, without a strongly differentiated dorsal keel 7

(b) Tail strongly compressed with a strongly differentiated dorsal keel (Pl. 5.3) .... *Physignathus*

7 (a) Nil to two femoral pores present on either side 8

(b) Three or more femoral pores on either side 9

8 (a) Femoral pores present or absent; keeled scales of snout irregularly aligned; tail tapers to a point (Pl. 5.5) .... *Diporiphora*

(b) Femoral pores absent; a median row of slightly enlarged keeled scales on the snout; tail ends abruptly, without a long taper .... *Caimanops*

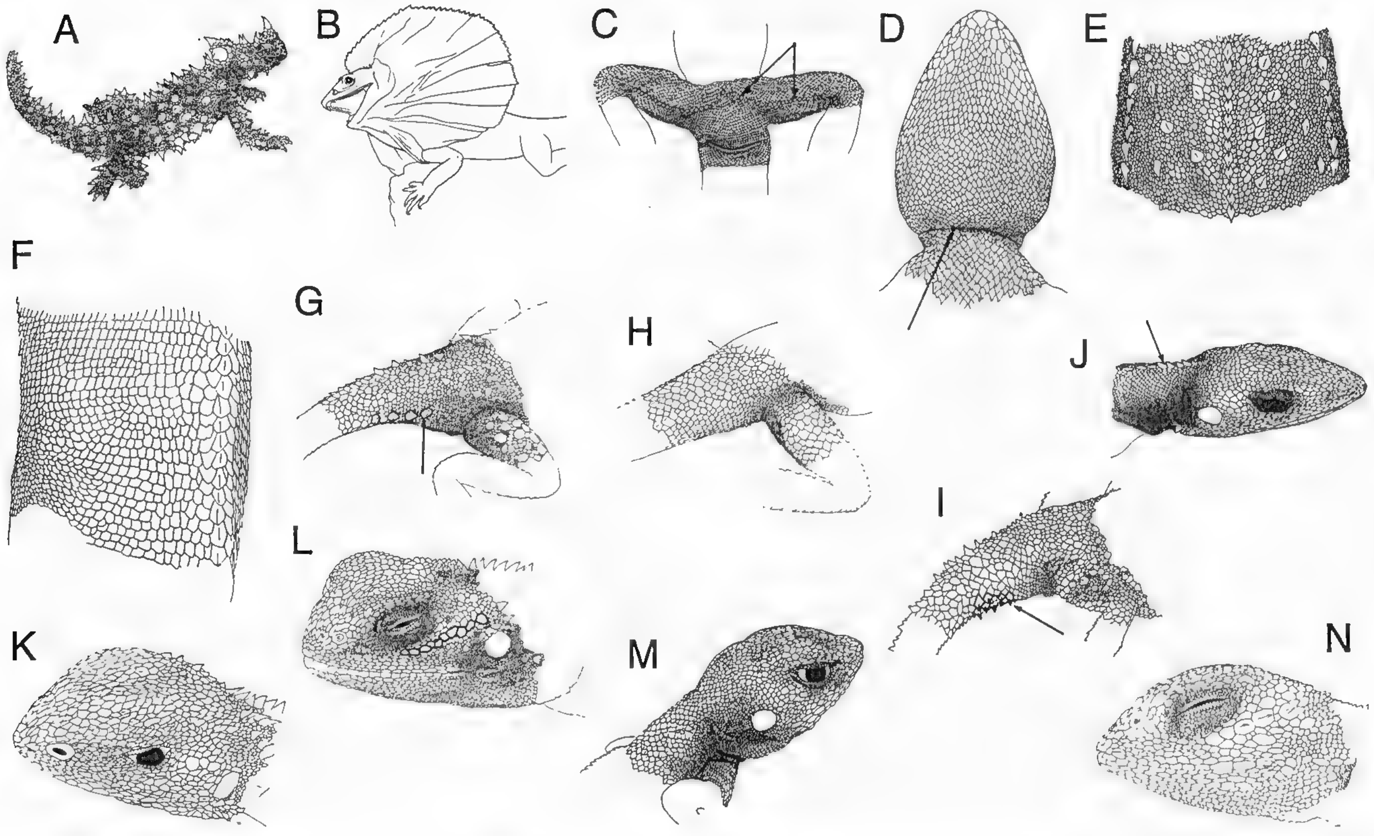

Figure 23.5 Key characters for genera of the family Agamidae. Pertinent features of elements A–N are noted in the adjacent key and above. [H.G. Cogger]

9(a) Nuchal crest and/or series of enlarged, keeled vertebral scales (Fig. 23.5E) present or absent; if latter, present along at least anterior two-thirds of body; enlarged, strongly keeled or spinose scales are present elsewhere on dorsum 10

(b) A distinct nuchal crest present (Fig. 23.5J), continuous with a series of enlarged, keeled scales forming a distinct vertebral series along at least the anterior two-thirds of the body; enlarged dorsal scales (excluding vertebrals) never strongly keeled or spinose (Fig. 23.5F) (Pl. 5.2) .... *Lophognathus*

10 (a) Spinose scales on sides of base of tail present or absent, but in a single linear row (Fig. 23.5H) if present ...11

(b) Sides of base of tail with a series of irregularly scattered spinose scales (Fig. 23.5I) (Pl. 5.8) .... *Pogona*

11 (a) No row of enlarged scales from below eye to above ear (Fig. 23.5K); dorsal scales of body heterogeneous, with distinctive vertebral and paravertebral rows of enlarged, keeled or spinose scales 12

(b) A row of enlarged scales from below the eye to above the ear (Fig. 23.5L); dorsal scales of body more or less homogeneous with at most a few slightly enlarged scattered tubercles .... *Ctenophorus*

12 (a) Tympanum exposed, the external ear-opening prominent (Fig. 23.5M); no enlarged spinose scales along each side of the base of the tail (Fig. 23.5H) .... *Amphibolurus*

(b) External ear-opening either absent (Fig. 23.5N), with the tympanic region covered by skin, or, if present, a series of enlarged spinose scales along each side of the base of the tail (Fig. 23.5G) (Pl. 5.1) .... *Tympanocryptis*

Key to the genera of family Scincidae

1 (a) Parietal shields (if unfragmented) nowhere in contact, being separated behind by the interparietal (Fig. 23.6A) 2

(b) Parietal shields in contact behind the interparietal (Fig. 23.6B) 5

2 (a) Third and fourth toes subequal or the third slightly longer than the fourth (Fig. 23.6C) 3

(b) Fourth toe markedly longer than the third (Fig. 23.6D) (Pl. 6.5) .... *Egernia*

3 (a) Tail short, at most about 60% of snout–vent length 4

(b) Tail long, from nearly as long as to longer than snout–vent length .... *Cyclodomorphus*

4 (a) Tail moderate to long, tapering (Fig. 23.6E); dorsal scales moderate, smooth; head shields smooth, entire, symmetrical (Fig. 23.6F); subdigital lamellae undivided (Fig. 23.6G) (Pl. 6.3, 6.4) .... *Tiliqua*

(b) Tail short, depressed, blunt-ended (Fig. 23.6H); dorsal scales grossly enlarged, strongly rugose; head shields broken up, only vaguely symmetrical (Fig. 23.6I); subdigital lamellae divided, at least basally (Fig. 23.6J) (Pl. 6.1, 6.2) .... *Trachydosaurus*

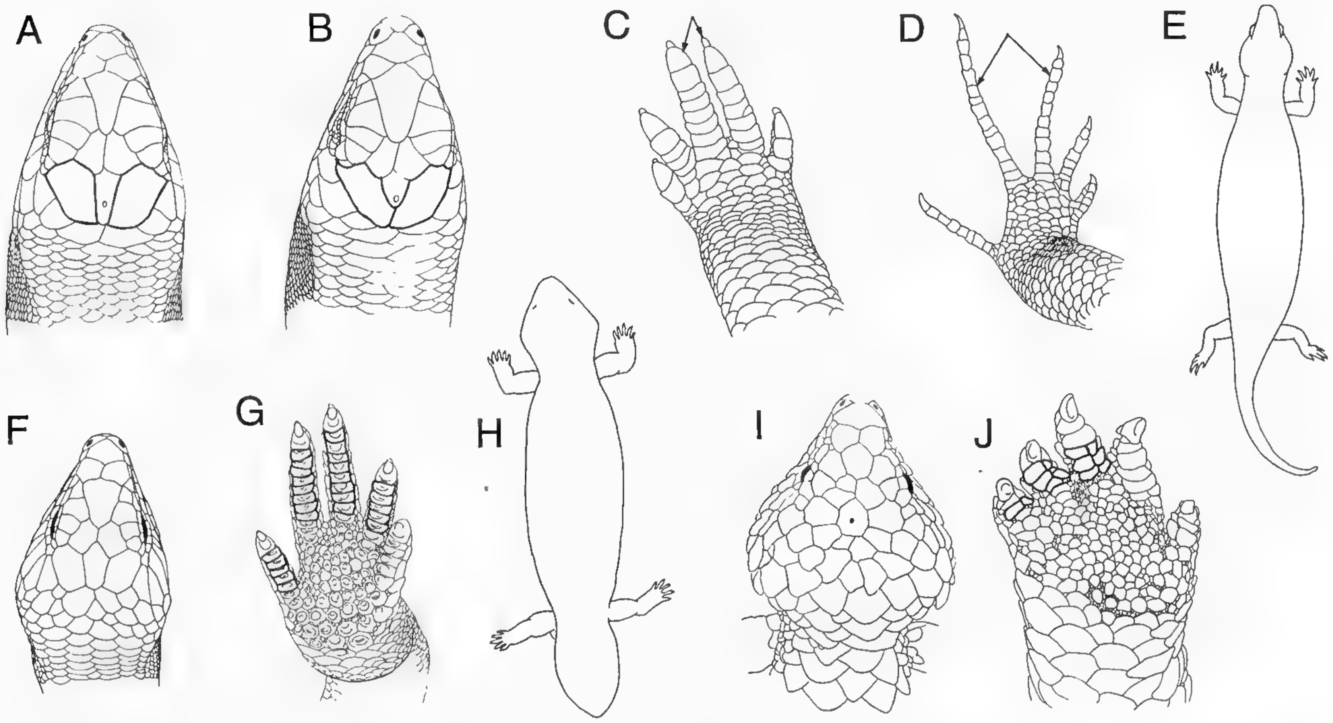

Figure 23.6 Key characters for genera of the family Scincidae. Pertinent features of elements A–J are noted in the keys above. [H.G. Cogger]

5 (a) Lower eyelid with a transparent disc and either movable (Fig. 23.7A) or fused (Fig. 23.7B) to form a permanent spectacle 6

(b) Lower eyelid movable, scaly (Fig. 23.7C) or with an opaque disc 21

6 (a) Lower eyelid movable, or partly (open slit along upper edge) or totally fused to form a permanent spectacle; if the lower eyelid is fused the prefrontals are small and widely separated (Fig. 23.7D) or absent (Fig. 23.7E) 7

(b) Lower eyelid fused to form a permanent spectacle; prefrontals large (Fig. 23.7F), in contact or narrowly separated 17

7 (a) Supranasals present, or nasals divided (Fig. 23.7G) 8

(b) Supranasals absent and nasals undivided (Fig. 23.7H) 9

8 (a) Frontoparietals paired (Fig. 23.7I) or single (Fig. 23.7J); fewer than 30 lamellae under fourth toe; anterior auricular lobules present (Fig. 23.7K) .... *Pseudemoia*

(b) Frontoparietals united to form a single shield (Fig. 23.7J); more than 30 lamellae under fourth toe; anterior auricular lobules absent (Fig. 23.7L) .... *Emoia*

9 (a) Limbs well developed, meeting or overlapping when adpressed (Fig. 23.7M), or else separated by one or two scale lengths; ear-opening prominent 10

(b) Limbs short, separated by at least several scale lengths when adpressed (Fig. 23.7N); ear-opening small to minute, or hidden 14

10 (a) Fingers four; ear-opening with one or more obvious lobules (Fig. 23.7K) 11

(b) Fingers five, or if four, ear-opening without lobules 12

11 (a) Ten or more scales along the top of the fourth toe (Fig. 23.7O) (Pl. 6.7) .... *Carlia*

(b) Fewer than ten scales along the top of the fourth toe (Fig. 23.7P) .... *Lygisaurus*

12 (a) Nasals usually widely separated (Fig. 23.7Q) 13

(b) Nasals usually narrowly separated (Fig. 23.7R) .... *Pseudemoia*

13 (a) Frontoparietals fused (Fig. 23.7J) .... *Lampropholis*

(b) Frontoparietals paired (Fig. 23.7I) .... *Saproscincus*

14 (a) Nasals small to moderate, usually separated (Fig. 23.7Q) 15

(b) Nasals enlarged, usually in contact medially (Fig. 23.7S) (Pl. 6.12) .... *Lerista*

15 (a) Forelimbs with two to five fingers, but if four fingers present then hindlimb with at most four toes 16

(b) Forelimbs with four fingers and hindlimbs with five toes .... *Eroticoscincus*

16 (a) Two to five fingers, two to five toes; ear-opening hidden in specimens with five fingers and five toes .... *Hemiergis*

(b) Five fingers and five toes; ear-opening minute, punctiform, but distinct .... *Nannoscincus*

17 (a) Fingers and toes five 18

(b) Fingers four, toes five .... *Menetia*

18 (a) Frontoparietal single (Fig. 23.7J) or paired (Fig. 23.7I), but always distinct from the interparietal (Fig. 23.7T); ear-opening absent, or smaller than eye if present 19

(b) Frontoparietal and interparietal fused to form a single shield (Fig. 23.7U); ear-opening approximately same size as eye 20

19 (a) Frontoparietals paired (Fig. 23.7I) .... *Proablepharus*

(b) Frontoparietals fused to form a single shield (Fig. 23.7J) .... *Notoscincus*

20 (a) Upper eyelid with three or four scales much larger than granules surrounding remainder of eye (Fig. 23.7V); frontal and prefrontals subequal (Fig. 23.7W) (Pl. 6.8) .... *Cryptoblepharus*

(b) Eye more or less surrounded by a circle of uniformly small granules (Fig. 23.7X); frontal much larger than prefrontals (Fig. 23.8A) (Pl. 6.10) .... *Morethia*

21 (a) Supranasals absent and nasals undivided (Fig. 23.7H) 22

(b) Supranasals present (Fig. 23.7G), although sometimes partially fused with nasals .... *Eugongylus*

22 (a) Dorsal scales moderate, smooth or with a faint median keel 23

(b) Dorsal scales very small, each with a sharp keel .... *Gnypetoscincus*

23 (a) Five fingers and five toes 24

(b) Fewer than five fingers and toes 28

24 (a) Ear lobules absent (Fig. 23.7L); pattern usually transversely aligned or of irregularly scattered spots and variegations 25

(b) Conspicuous ear lobules present (Fig. 23.7K); pattern usually of dorsal and/or lateral longitudinal stripes (Pl. 6.11) .... *Ctenotus*

25 (a) Dorsal and upper caudal scales smooth 26

(b) Scales on the rump and the base of the tail, and sometimes on the remaining dorsals, with distinct median 'humps' or low keels forming a series of continuous longitudinal ridges .... *Eremiascincus*

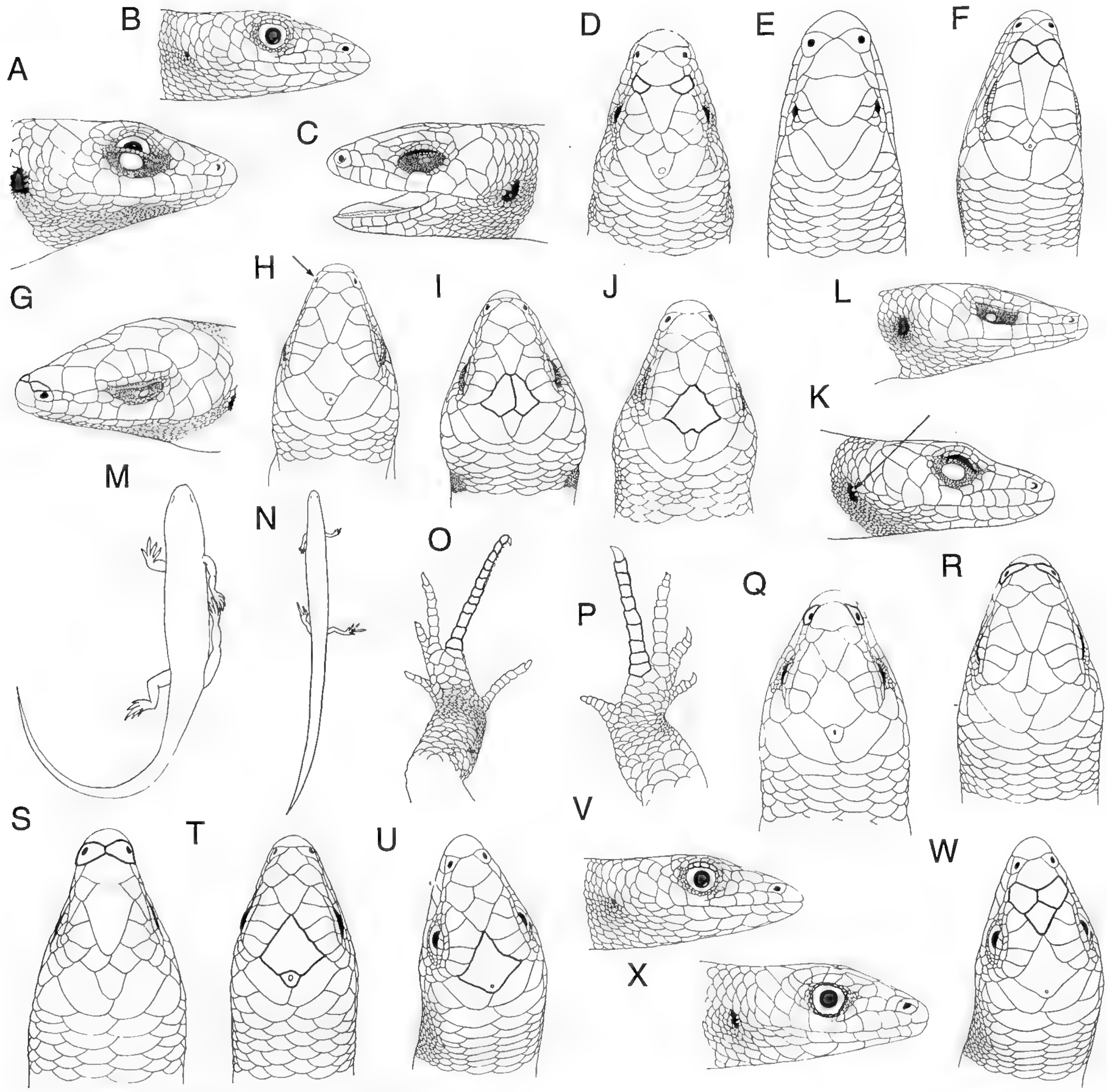

Figure 23.7 Key characters for genera of the family Scincidae. Pertinent features of elements **A–X** are noted in keys above and on the adjacent page. [H.G. Cogger]

26 (a) Hindlimb short to moderate, its length contained at least 2.5 times in the snout–vent length 27
(b) Hindlimb long, its length contained less than 2.5 times in the snout–vent length .... *Eulamprus*

27 (a) Fourth toe lamellae fewer than 16; a single loreal scale (Fig. 23.8B) .... *Calyptotis*
(b) Fourth toe lamellae usually more than 16 but, if fewer, then two or more loreal scales are present (Fig. 23.8C) (Pl. 6.8) .... *Glaphyromorphus*

28 (a) If limbs tridactyl, mid-body scales in 23 or more rows 29
(b) Limbs tridactyl; mid-body scales in fewer than 23 rows .... *Saiphos*

29 (a) With or without limbs; limbed forms with only one or two digits on each limb; limbless forms without prefrontals (Fig. 23.7E) or with prefrontals at most moderately developed and widely separated (Fig. 23.7D); five or six supralabials 30
(b) With or without limbs; limbed forms with three digits on each limb; limbless forms with large prefrontals, contacting (Fig. 23.7F) or only narrowly separated; 6 supralabials .... *Coeranoscincus*

30 (a) Either six supralabials and two to four supraoculars or five supralabials and two supraoculars (Pl. 6.13) .... *Anomalopus*
(b) Five supralabials and three supraoculars .... *Ophioscincus*

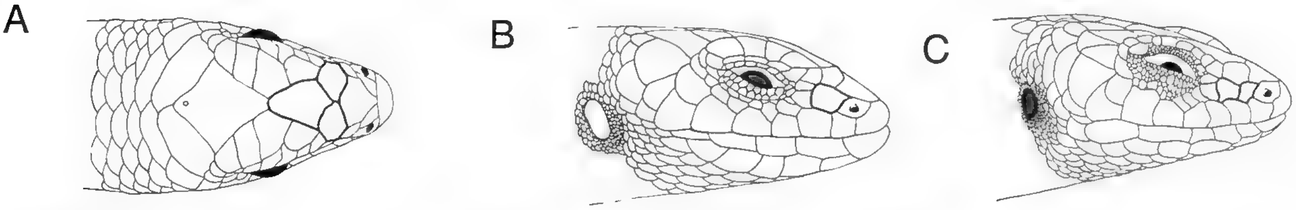

Figure 23.8 Key characters of the genera of the family Scincidae. Pertinent features of elements A-C are noted in the key above [H.G. Cogger]

CLASSIFICATION OF THE SERPENTES

Currently about 10 families of extant snakes are recognised (Savage 1992), and these are considered to be derived from three separate evolutionary stocks represented by the infraorders Scolecophidia, Henophidia and Caenophidia (Parker & Grandison 1977).

The Scolecophidia includes one Australian family, the Typhlopidae (blind or worm snakes). Only the Boidae (pythons) represent the Henophidia in Australia. The remaining Australian snake families, the Acrochordidae (file snakes), the Colubridae (colubrids) and front-fixed fang snakes, here grouped as 'Elapidae', are included in the Caenophidia. In this volume, the major groups within the 'Elapidae' are themselves given family status — the terrestrial elapids (Elapidae), the Laticaudidae (sea kraits) and the Hydrophiidae (sea snakes). These changing classifications are discussed under each of these families. These seven Australian families may be distinguished using the following key.

Key to the families of suborder Serpentes

1 (a) Tail more or less cylindrical, not flattened and paddle-shaped (Fig. 23.9A) 2
(b) Tail strongly vertically compressed and paddle-shaped (Fig. 23.9B) 6

2 (b) No enlarged ventral scales, the scales on the belly more or less equal in size to those on the back and sides 3
(b) A single row of enlarged ventral scales which are at least three times as wide as those on the back and sides 4

3 (a) More than 80 mid-body scale rows; body scales rough, strongly keeled; eyes well developed (file snakes) .... Acrochordidae
(b) Fewer than 40 mid-body scale rows; body scales smooth; eyes vestigial, consisting of dark spots beneath scales of head (blind snakes) (Pl. 7.2) .... Typhlopidae[1]

4 (a) Fewer than 30 mid-body scale rows 5
(b) More than 30 mid-body scale rows (pythons) .... Boidae

5 (a) One or more loreal scales present (Fig. 23.9C), or, if absent, 23 or more mid-body scale rows and a divided anal shield (colubrid snakes) .... Colubridae
(b) No loreal scales (Fig. 23.9D); anal single if mid-body scales are in 23 or more rows (elapid snakes) ..... Elapidae

6 (a) Ventral scales large, at least three times as wide as the adjacent body scales (Fig. 23.9E); nasals separated by internasals (Fig. 23.9F) (sea kraits) (Pl. 7.11, 7.12) ... Laticaudidae[2]

(b) Ventral scales small or large; if large (two to three times as wide as the adjacent body scales) then the nasals are in contact (Fig. 23.9G) (sea snakes) ... Hydrophiidae

[1] Single genus *Rhamphotyphlops*

[2] Single genus *Laticauda*

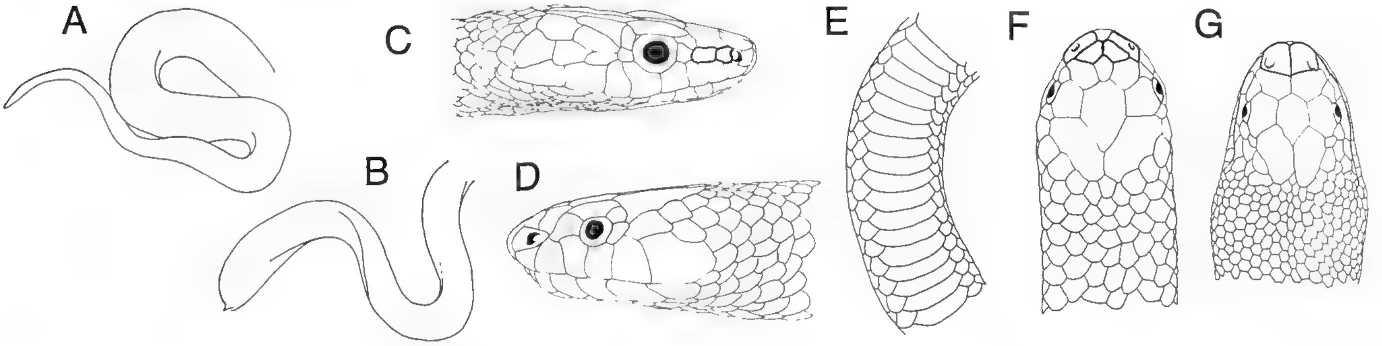

Figure 23.9 Key characters of the families of the suborder Serpentes. Pertinent features of elements A-G are noted in the key on the adjacent page and above. [H.G. Cogger]

Key to the genera of family Boidae

1 (a) Mental groove bordered by scales which are more or less equal in size to the other gular scales (Fig. 23.10A) ... 2

(b) Mental groove bordered by granular scales (Fig. 23.10B) (Pl. 7.3, 7.4) ... *Chondropython*

2 (a) Premaxilla with teeth (Fig. 23.10C) ... 3

(b) Premaxilla without teeth (Pl. 7.1) ... *Aspidites*

3 (a) Scales, at least on rear of body, with one or two apical pits (Pl. 7.5) ... *Liasis*

(b) Most scales, including those on rear of body, without apical pits ... *Morelia*

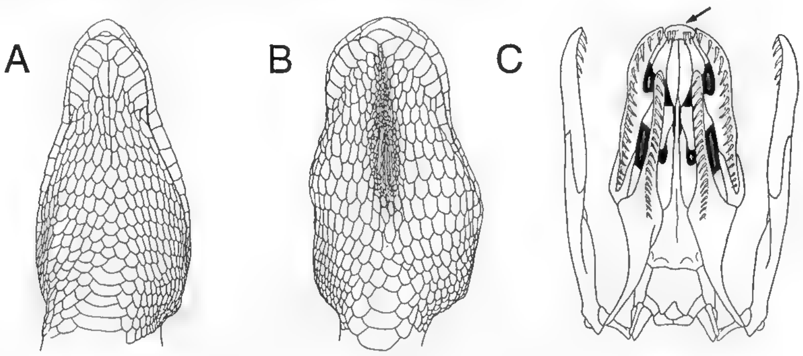

Figure 23.10 Key characters of the genera of the family Boidae. Pertinent features of elements A-C are noted in the key above. [H.G. Cogger]

Key to the genera of family Colubridae

1 (a) Scales strongly keeled ... 2

(b) Scales smooth or feebly keeled ... 3

2 (a) 23 or more mid-body scale rows ... *Cerberus*

(b) 15 or 17 mid-body scale rows ... *Tropidonophis*

3 (a) More than 15 mid-body scale rows ... 4

(b) 13 (occasionally 15) mid-body scale rows ... *Dendrelaphis*

4 (a) Anal scale single (Fig. 23.11A) ... 5

(b) Anal scale divided (Fig. 23.11B) ... 6

5 (a) 17 mid-body scale rows ... *Stegonotus*

(b) 19 or more mid-body scale rows (Pl. 8.1) ... *Boiga*

6 (a) Nasals not in contact (Fig. 23.11C) 7

(b) Nasals in contact (Fig. 23.11D) .... *Enhydris*

7 (a) Loreal scale present (Fig. 23.11E); scales feebly keeled (Pl. 8.2) .... *Myron*

(b) Loreal scale absent (Fig. 23.11F); scales smooth (Pl. 8.3) .... *Fordonia*

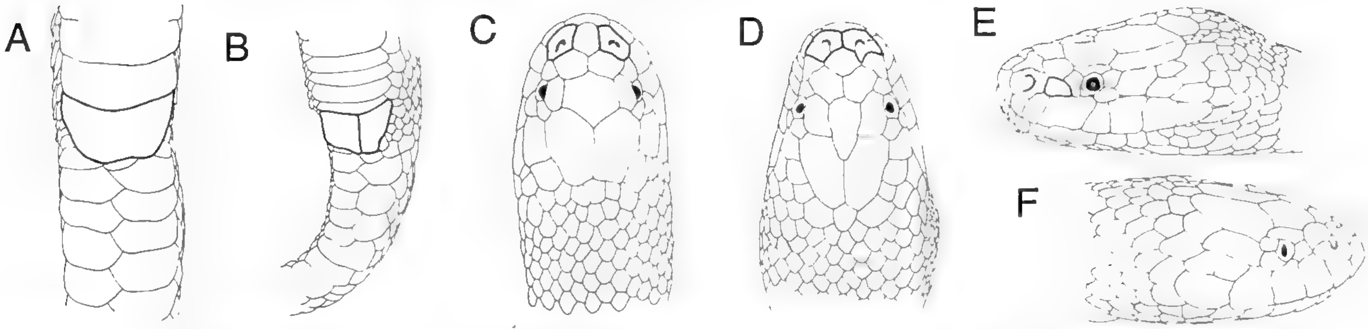

Figure 23.11 Key characters for genera of the family Colubridae. Pertinent features of elements **A–F** are noted in the key above and on the previous page. [H.G. Cogger]

Key to the genera of family Elapidae

1 (a) No suboculars (Fig. 23.12A); no specialised curved soft spine on the tip of the tail (Fig. 23.12B) 2

(b) Suboculars (Fig. 23.12C); a curved soft spine on the tip of the tail (Fig. 23.12D) (8.9) .... *Acanthophis*

2 (a) All subcaudals normally undivided 3

(b) At least some subcaudals divided 13

3 (a) Dorsal scales smooth 4

(b) Dorsal scales strongly keeled .... *Tropidechis*

4 (a) Anal scale normally single (Fig. 23.12E) 5

(b) Anal scale normally divided (Fig. 23.12F) .... *Hemiaspis*

5 (a) Scales in 13–21 rows at mid-body; if in 19 or more rows, ventrals more than 140 or head not jet-black above contrasting with brown body colour 6

(b) Scales in 19 rows at mid-body; ventrals fewer than 140 or head jet-black above contrasting with paler brown body colouring .... *Echiopsis*

6 (a) Frontal shield longer than broad; where frontal is only slightly longer than broad, lower anterior temporal shield is shorter than frontal (Fig. 23.12G) 7

(b) Frontal shield not, or scarcely, longer than broad; lower anterior temporal about as long as or longer than the frontal (Fig. 23.12H) (8.7) .... *Notechis*

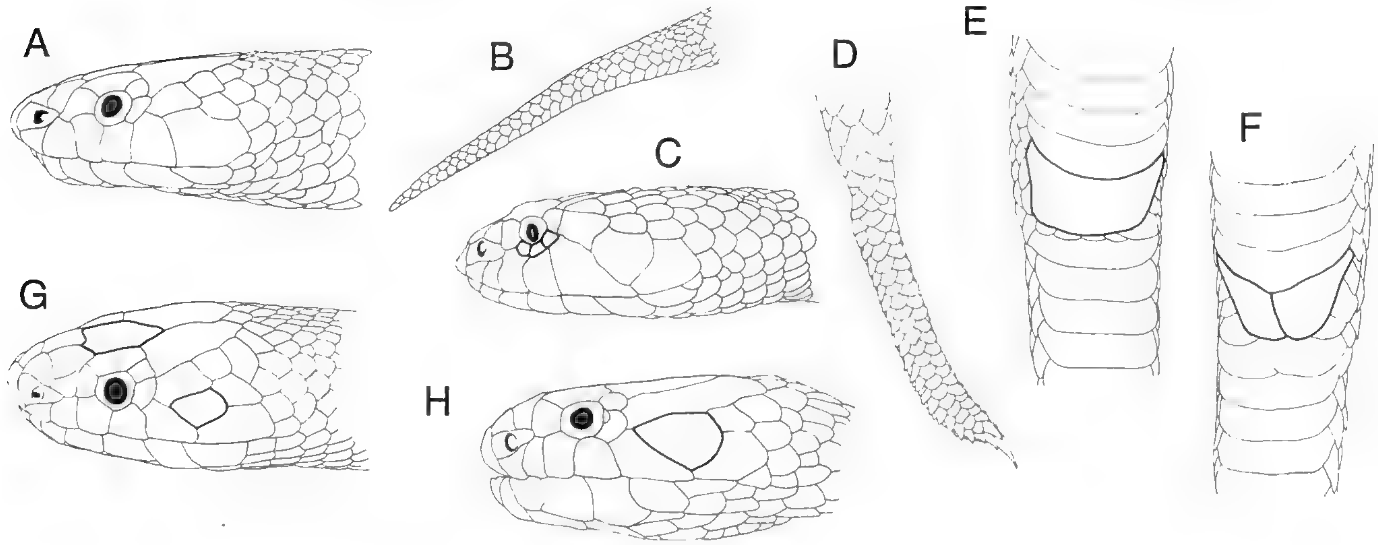

Figure 23.12 Key characters for genera of the family Elapidae. Pertinent features of elements **A–H** are noted in the key above and on the adjacent page. [H.G. Cogger]

7 (a) Scales in 15–21 rows at mid-body; ventrals not keeled or notched; if 19 or more, ventrals fewer than 190 8

(b) Scales in 19–21 rows at mid-body; ventrals keeled or notched; ventrals 190 or more .... *Hoplocephalus*

8 (a) Three or more solid maxillary teeth following the fang (Fig. 23.13A); belly without a series of crescent-shaped, transverse, black bars 9

(b) No maxillary teeth following the fang (Fig. 23.13B); belly with a median series of crescent-shaped, transverse, black bars (Fig. 23.13C) .... *Elapognathus*

9 (a) Frontal less than one and a half times as broad as the supraocular (Fig. 23.13D) 10

(b) Frontal more than one and a half times as broad as the supraocular (Fig. 23.13E) 11

10 (a) Lateral scales adjoining ventrals not noticeably enlarged (Fig. 23.13F) .... *Drysdalia*

(b) Lateral scales adjoining ventrals noticeably enlarged (Fig. 23.13G) .... *Austrelaps*

11 (a) Scales in 15–21 rows at mid-body; upper labials uniformly pale, without darker bars 12

(b) Scales in 17 rows at mid-body; upper labials strongly barred .... *Denisonia*

12 (a) Scales in 15 rows at mid-body; head and body usually uniformly coloured above, or sides of body and face a paler pink in one species (*R. nigrostriatus*) .... *Rhinoplocephalus*

(b) Scales in 15–21 rows at mid-body; head with a dark, contrasting hood or with strongly contrasting darker spots and streaks .... *Suta*

13 (a) Anal scale normally divided; 21, or usually fewer, mid-body scale rows 14

(b) Anal scale normally single; 21 or more mid-body scale rows .... *Oxyuranus*

14 (a) Subcaudals 35 or more 15

(b) Subcaudals fewer than 35 19

15 (a) Nasal and preocular scales in contact (Fig. 23.13H) 16

(b) Nasal and preocular scales widely separated (Fig. 23.13I) (Pl. 8.11) .... *Furina*

16 (a) Scales in 17 or more rows at mid-body 17

(b) Scales in 15 rows at mid-body 18

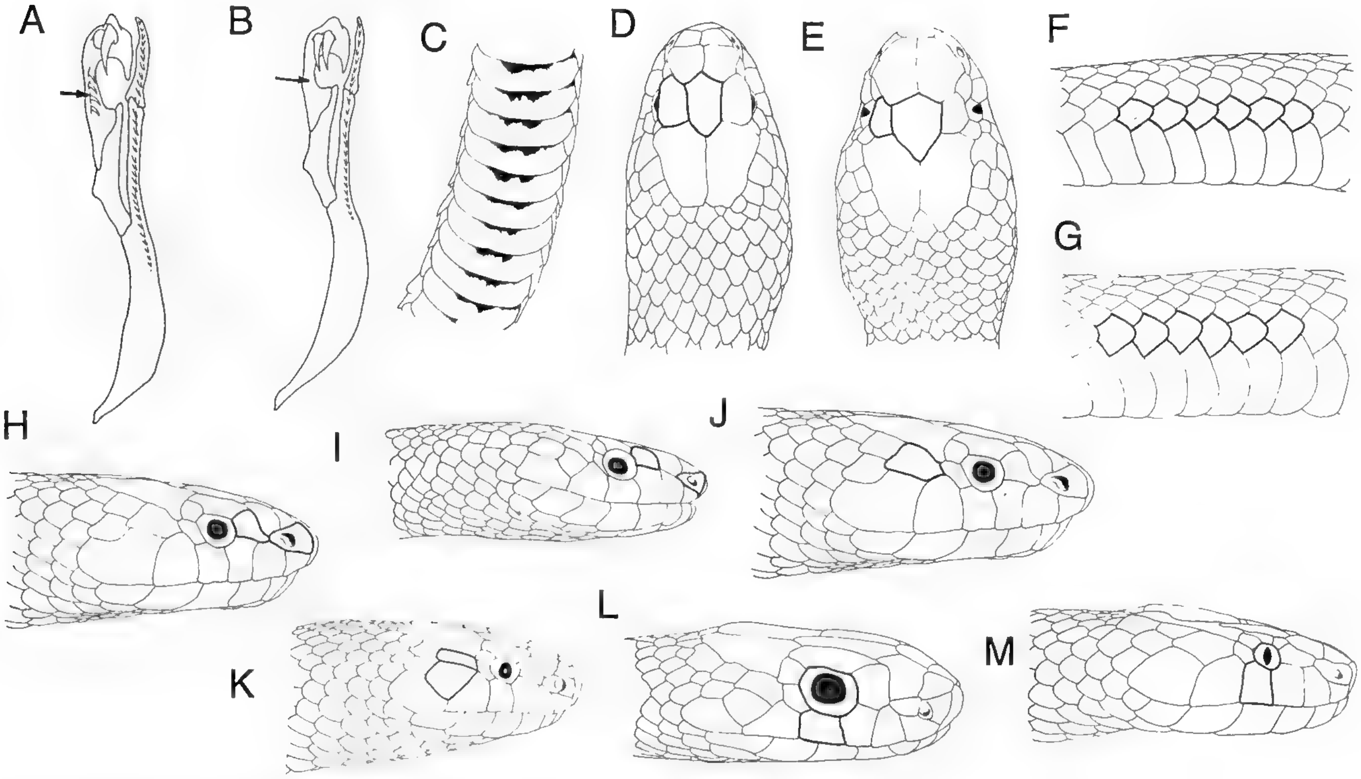

Figure 23.13 Key characters for genera of the family Elapidae. Pertinent features of elements A–M are noted in the key above and overleaf. [H.G. Cogger]

17 (a) Nearly always a single temporal scale between the fifth upper labial and the parietal scale (Fig. 23.13J); usually all subcaudals divided or at most a few anterior ones undivided (Pl. 8.8) .... *Pseudonaja*

(b) Nearly always two temporal scales between the fifth upper labial and the parietal scale (Fig. 23.13K); usually at least anterior 20% of subcaudals undivided, remainder divided .... *Pseudechis*

18 (a) Diameter of eye markedly greater than its distance from the mouth (Fig. 23.13L) (Pl. 8.6, 8.12) *Demansia*

(b) Diameter of eye about equal to or less than its distance from the mouth (Fig. 23.13M) .... *Cacophis*

19 (a) Colour pattern not consisting of alternate black and white bands 20

(b) Colour pattern consisting of black and white bands from head to tail (Pl. 8.4) .... *Vermicella*

20 (a) Body with or without cross-bands; if not banded, the ventral surface is immaculate white or cream (Pl. 8.5) .... *Simoselaps*

(b) Body without cross-bands; ventral surface coloured and/or patterned .... *Cacophis*

Key to the genera of family Hydrophiidae

1 (a) Ventrals large, at least three times as wide as the adjacent body scales (Fig. 23.14A) 2

(b) Ventrals small, at most scarcely more than twice as wide as the adjacent body scales (Fig. 23.14B) 5

2 (a) Six or more supralabials (Fig. 23.14C) 3

(b) Three supralabials (Fig. 23.14D) .... *Emydocephalus*

3 (a) Posterior chin shields not reduced and separated by a mental groove (Fig. 23.14E); portion of rostral scale bearing median valve-like fold continuous with remainder of scale (Fig. 23.14F) 4

(b) Posterior chin shields usually reduced and separated by one or more scales (Fig. 23.14G) and/or portion of rostral scale bearing median valve-like fold sometimes separated from remainder of scale by a suture (Fig. 23.14H) (Pl. 7.7, 7.8) .... *Aipysurus*

4 (a) No preocular scale (Fig. 23.14I); rostral with a median lobe at its anterior-most end, this lobe fitting into a median notch in the mental and completely dividing the lingual fossa of the rostral into separate left and right grooves (Fig. 23.14F) .... *Hydrelaps*

(b) Preocular scale present (Fig. 23.14J); rostral with a median sharp fold located within the mouth, behind the median and undivided lingual fossa, this fold formed from the posterior edge of the portion of the keratinised scale extending within the lining of the lip (Fig. 23.14K) 11

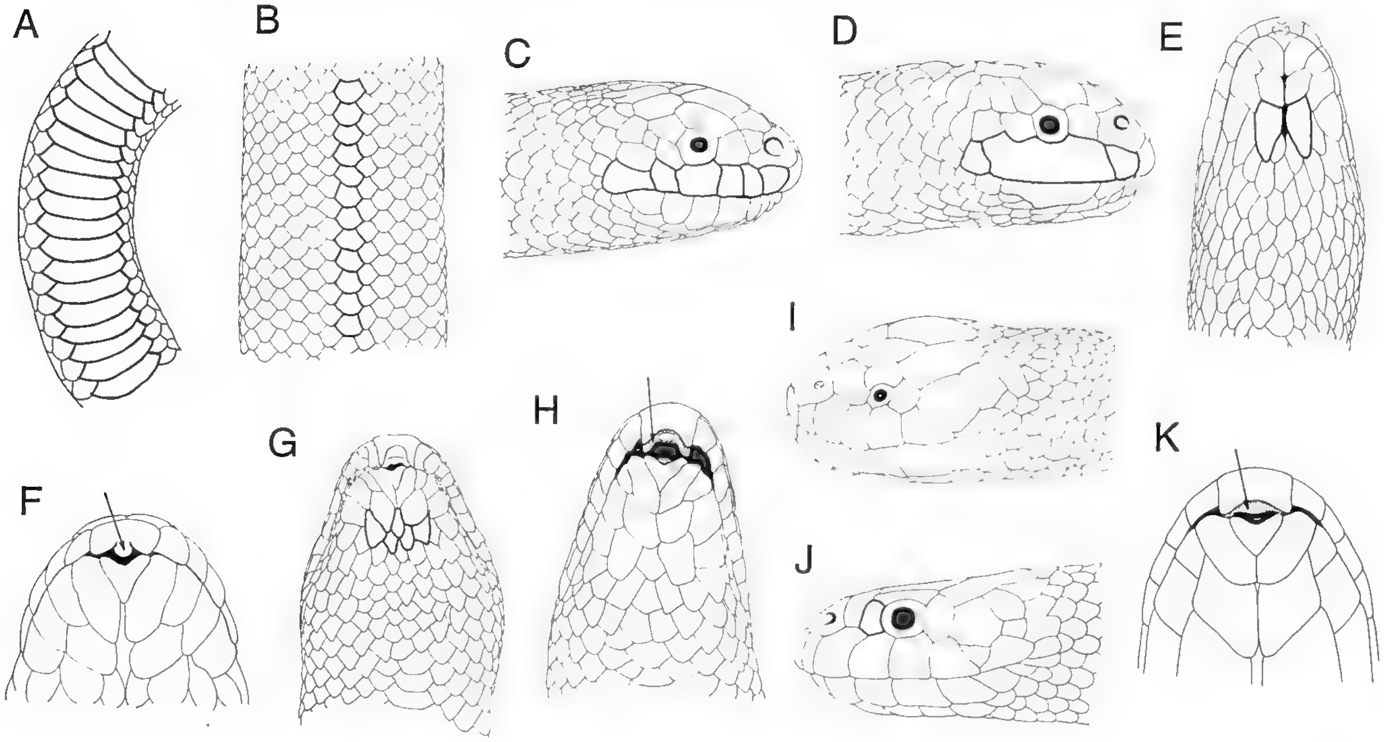

Figure 23.14 Key characters for genera of the family Hydrophiidae. Pertinent features of elements A–K are noted in the key above. [H.G. Cogger]

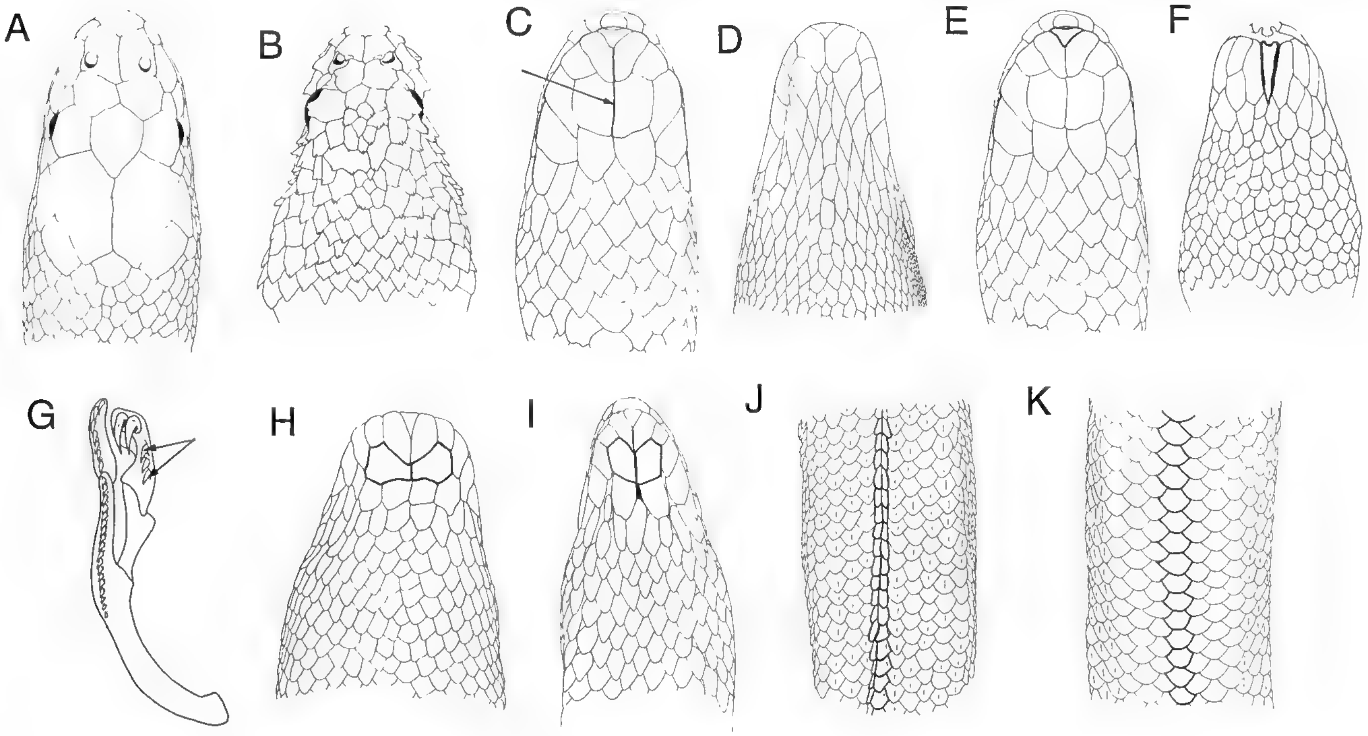

Figure 23.15 Key characters for genera of the family Hydrophiidae. Pertinent features of elements A–K are noted in the key below. [H.G. Cogger]

5 (a) Head scales enlarged, regular, symmetrical, the supraoculars without projecting tubercles or spines (Fig. 23.15A) 6

(b) Head scales broken up into small, irregular and asymmetrical scales, the supraoculars with projecting tubercles or spines (Fig. 23.15B) .... *Acalyptophis*

6 (a) A distinct mental groove (Fig. 23.15C) 7

(b) No distinct mental groove (Fig. 23.15D) .... *Pelamis*

7 (a) Mental normal, triangular, broader than long, and not partially hidden in the shallow mental groove (Fig. 23.15E) 8

(b) Mental narrow, splint- or dagger-shaped, much longer than broad, and partially hidden in the deep mental groove (Fig. 23.15F) .... *Enhydrina*

8 (a) Either fewer than four solid maxillary teeth following the fang (Fig. 23.15G) or, if four or more, anterior chin shields reduced and not, or scarcely, contacting the mental groove, from which they are separated by the elongate first infralabials (Fig. 23.15H) 9

(b) Four or more solid maxillary teeth; anterior chin shield large and mostly bordering the mental groove (Fig. 23.15I) .... *Hydrophis*

9 (a) Ventrals single or divided, but usually distinct posteriorly 10

(b) Ventrals not distinct posteriorly .... *Lapemis*

10 (a) Ventrals, except on throat, divided into pairs of foliform scales which in most specimens form a mid-ventral keel (Fig. 23.15 J) (Pl. 8.9, 8.10) .... *Astrotia*

(b) Ventrals mostly undivided, never foliform and never with a mid-ventral keel (Fig. 23.15K) .... *Disteira*

11 (a) Posterior dorsal scales smooth; scales in more than 30 rows at mid-body .... *Parahydrophis*

(b) Posterior dorsal scales with spine-like keels; scales in fewer than 30 rows at mid-body .... *Ephalophis*

24. MORPHOLOGY AND PHYSIOLOGY OF THE SQUAMATA

Philip C. Withers & James E. O'Shea

The lizards (suborder Sauria) and snakes (suborder Serpentes) comprise the order Squamata of the class Reptilia. Like other reptiles, squamates have horny epidermal scales, internal fertilisation, ectothermy and a cleidoic egg. The Squamata are distinguished from the other reptilian orders by adaptive modifications to the temporal region of the skull, and the presence of two hemipenes in the males.

The Squamata represent over 95% of all reptilian species. Of the almost 6000 species in the order, Australia has approximately 480 species of lizards and 170 species of snakes. They represent five of the 18 recognised lizard families — Agamidae (dragons), Gekkonidae (geckos), the Scincidae (skinks), Pygopodidae (legless lizards) and Varanidae (goannas) — and seven of the 11 to 14 recognised families of snakes — Acrochordidae (file snakes), Boidae (pythons), Colubridae, Elapidae, Hydrophiidae and Laticaudidae (sea snakes) and Typhlopidae (blind snakes).

EXTERNAL CHARACTERISTICS

Detailed information on the external characteristics of Australian squamates is provided by Bustard (1970b), Wilson & Knowles (1988), Gow (1989), Greer (1989), Hoser (1989) , Shine (1991a) and Cogger (1992).

Australian squamates range in size from the gekkonid lizard *Diplodactylus savagei*, with a snout-vent length of up to 46 mm and weighing only a few grams, to the perentie, *Varanus giganteus*, which has a snout-vent length of over 750 mm (Storr 1980) and weighs 17 kg (Butler 1970), and the pythons, *Morelia amethistina* and *M. oenpelliensis* which may exceed 5 m in length (Shine 1991a).

The basic body plan of squamates, which is derived from the ancestral stem reptiles, is an elongate cylinder with a well-defined head separated from the trunk by a prominent neck, and four well-developed limbs supported by pectoral and pelvic girdles. The tail tends to be slender in skinks, dragons, legless lizards and goannas, but is often bulbous or expanded laterally and compressed dorso-ventrally in geckos. Geckos and some skinks and legless lizards can autotomise and regenerate their tail. The tail often is used for fat storage and may change in diameter seasonally. A few long-tailed lizards, particularly arboreal goannas and geckos, have a prehensile tail (Bustard 1970b; Czechura 1980). In some aquatic snakes, and in dragons and goannas that swim habitually, the tail is laterally compressed and/or extended dorso-ventrally.

A covering of rough loose skin in the region of the throat may form a pendulous sac or gular pouch, a feature seen in some geckos and, most prominently, in dragons (Pl. 5.3) and goannas. In dragons, the scales of this region often are extended into mats of spines, giving rise to the common name of bearded dragons (Pl. 5.8; Throckmorton, De Bavay, Chaffey, Merrotsy & Noske 1985). In the frill necked lizard, *Chlamydosaurus kingii*, the gular skin is particularly loose and is supported by hyoid bones that allow the 'frill' to be erected when the animal is threatened (Pl. 5.9; Saville-Kent 1895; Beddard 1905). Some dragons have a central crest of rough and spinose scales along the neck or back (Pl. 5.7).

Among the Sauria, dragons, geckos, goannas and most skinks show the tetrapod condition, whereas some skinks have a reduced size and number of both digits and limbs (Mitchell 1958; Greer 1987, 1989). Almost complete limb reduction typifies legless lizards. The limb-reduced lizards have a long tail, that often exceeds the snout-vent length. Limb reduction is virtually complete in the Serpentes, although a vestigial flap may remain. Snakes differ fundamentally from the limb-reduced lizards in that their body attenuation and elongation is primarily of the trunk rather than the tail.

Usually the head is flattened dorso-ventrally and simple; notable exceptions are the spinose head of *Moloch horridus* and the nuchal crests of rainforest dragons such as *Hypsilurus boydii*. The snout is usually short, except in carnivores such as goannas, legless lizards, and pythons. Lizards usually have external ear openings. The head scales decrease in size at the edge of the ear opening, and the skin that is firmly attached to the underlying tympanic membrane usually lacks scales. In some terrestrial or burrowing skinks, the tympanic membrane is located on the external surface of the skull, and it is covered by scaly skin or occluded by the jaw musculature in some dragons. Snakes and a few legless lizards have no external ear opening. Diurnal lizards have small eyes with round or ovoid pupils, whereas nocturnal squamates tend to have large eyes with elliptical pupils. However, the nocturnal file snakes have very small eyes. The fossorial typhlopid snakes and some *Lerista* have vestigial eyes, covered by scales. The eyes and nostrils often are positioned on the dorsal surface of the head in squamates that swim.

The condition of the front and hind feet varies, from pentadactyl limbs (five digits) that terminate in keratinised claws, to the near or total absence of digits in legless lizards, snakes and some skinks. Modification of the pentadactyl condition usually is related to changes in the locomotory mode. Not even dragons or goannas that habitually swim have any webbing between their digits.

Reduction in the length of the digits in both the front and hind feet is comparatively minor in both dragons and geckos, but skinks, especially *Lerista*, display a comprehensive series of digit reductions (Mitchell 1958; Greer 1989). The length of the metatarsi is increased in dragons that stand on their rear limbs using the tail as a prop (Swanson 1976; Greer 1989). Some goannas have a similar extension of the hind foot digits, which contributes to their ability to stand and to run bipedally. The relative size of the claws is related to arboreality or digging. For example, the arboreal goanna *Varanus gilleni* has strongly curved claws (Pianka 1969a). Some arboreal dragons and skinks have similar digit and claw extension, and opposable digits.

Geckos have specialised foot pads that increase traction, in addition to claws and opposable digits. The underside of the digits of the arboreal skink, *Emoia cyanogaster*, have between two and three times as many transverse scales as do closely related terrestrial species (Williams & Peterson 1982; Greer 1989). The water dragon, *Physignathus lesueurii*, has a single row of subdigital keels rather than the typical double row of dragons (Greer 1989). Rock-climbing goannas such as *V. glebopalma* (Mitchell 1955; Swanson 1979) and arboreal species such as *V. prasinus* (Czechura 1980; Greene 1986) produce a secretion on the base of the feet that may increase traction.

The cloacal opening (vent) is a transverse ventral slit at the base of the tail, usually covered by a posteriorly projecting shield of scales. Internal fertilisation is by one of a pair of male intromittent organs, the hemipenes. When flaccid, the hemipenes lie under the skin of the ventro-lateral region of the tail in penial sacs that open into the posterior of the cloaca. Before copulation, both hemipenes are expanded and everted through the vent, but only one is used. A hemipenial groove, the *sulcus spermaticus*, transports sperm from the cloaca. The hemipenes of most lizards are simply pleated and folded, whereas those of snakes often are covered with hooks and circles of projections called calyces. Hemipenial structure can be a useful taxonomic tool.

INTEGUMENT

Squamates have a water-conserving, scaly integument with few glands. The epidermis consists of a basal germinal layer (*stratum germinativum*) and three outer layers culminating in a thick, dead, keratinised layer (Lillywhite & Maderson 1982). The scales are covered by thick epidermis, and are joined at their base to adjacent scales by a thin region of epidermis that acts as a hinge. This continuity of the scales is a seal against water loss, infection and parasitism, provides mechanical strength, and facilitates simultaneous shedding of the entire skin. The outer epidermis is periodically shed and replaced by underlying layers of cells, derived from the *stratum germinativum*. Shedding is necessary because the inelastic skin retards growth. While snakes, geckos and many legless lizards shed their skin in a single piece, dragons and goannas shed their skin in sections.

Scale morphology ranges from the minute granular scales of file snakes, geckos and legless lizards, to the smooth and overlapping scales of blind snakes, some skinks and snakes, and the elaborate, spiny scales of dragons (Fig. 24.1). Often scales are covered by a microscopic series of ridges, or pockets, that may reduce friction and prevent dirt adhesion in burrowing species, provide a water-repellant surface, or influence rates of radiative heat exchange. There is also regional specialisation of scales. Those covering the skull are often larger and more specialised than those in other regions of the body. The epidermal scales, particularly in skinks, overlay dermal scales that may be fused to the bony plates of the skull to form a robust, immobile skull. A modified scale, the spectacle, covers the eye of snakes, geckos and legless lizards. It reduces evaporative water loss in terrestrial species and provides mechanical protection in fossorial species. Most terrestrial snakes and some non-fossorial legless lizards have wide ventral body scales (gastrosteges) that span the width of the animal. Fossorial blind snakes and many totally aquatic snakes have uniformly small, ventral body scales.

Arboreal geckos have toe pads of highly modified digital lamellae, called scansors, and the prehensile tail of *Pseudothecadactylus* has a terminal pad. Foot pads have evolved independently several times within the geckos (Russell 1976, 1979). Terrestrial geckos usually lack scansorial pads. The scales on the ventral surface of the scansorial pads have an extended surface area and microscopic projections called setae (Fig. 24.2; Ernst & Ruibal 1966; Ruibal & Ernst 1965) which increase their adhesive capacity dramatically. The number of toe lamellae and their surface area has been correlated with arboreality (Collette 1961; Hecht 1952).

The colour of terrestrial reptiles can be diverse and their pigmentation complex, but less so in fossorial groups. Colouration has been related to camouflage, warning, thermoregulation, protection from ultraviolet rays, behavioural interactions and sexual dimorphism. Colouration is under physiological control (neural or endocrinal). Some legless lizards mimic the colour and sometimes the behaviour of elapid snakes (Hall 1905; Kinghorn 1924; Waite 1929; Bustard 1968c, 1970b; Greer 1989).

Although squamates generally have few glands, femoral, pre-anal and cloacal glands are often prominent. When molested, some

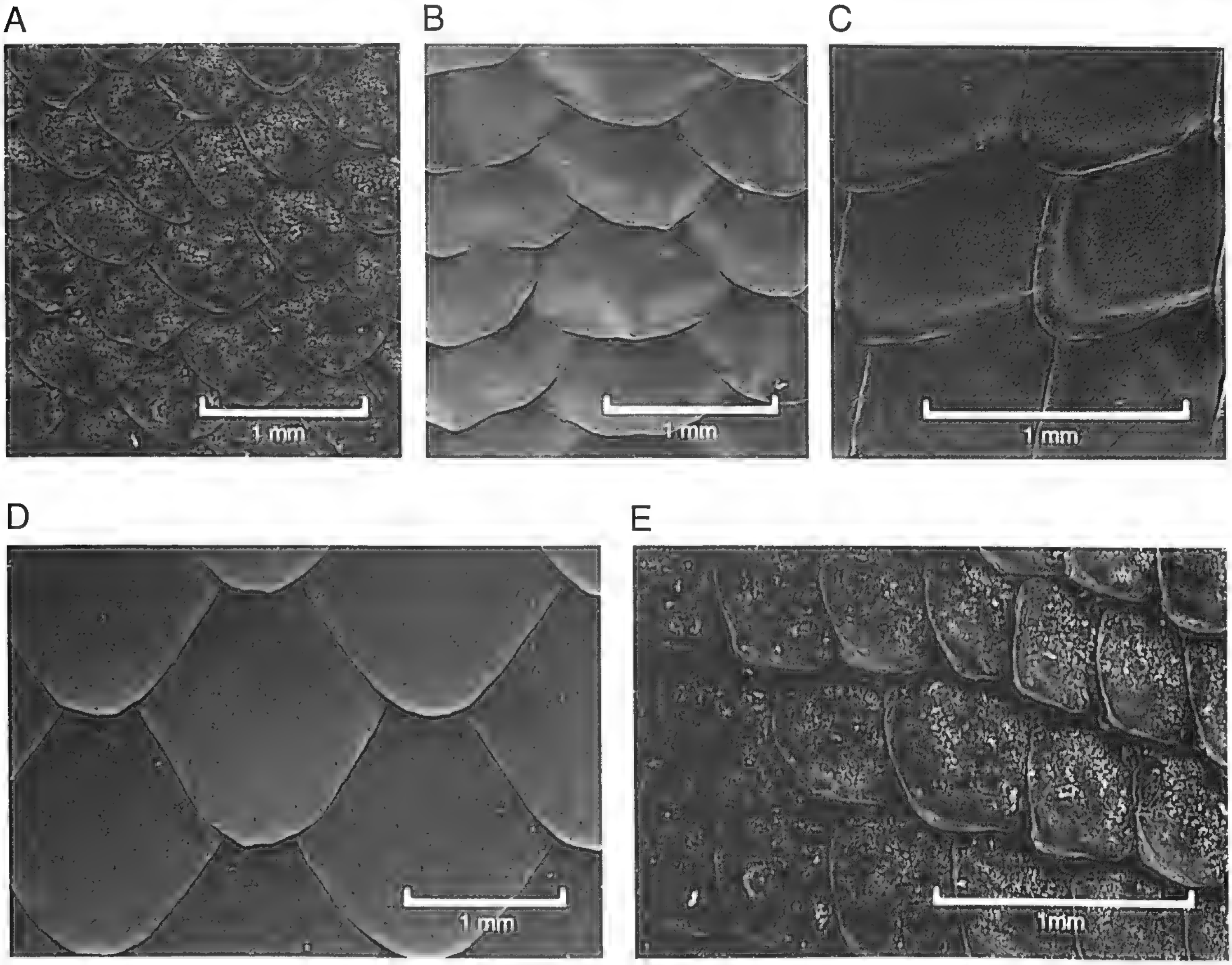

Figure 24.1 Scanning electron micrographs of integumental scales representative of squamate groups. A, Agamidae; B, Scincidae; C, Gekkonidae; D, Pygopodidae; E, Elapidae. [Photos by J. O'Shea, P. Withers & T. Stewart]

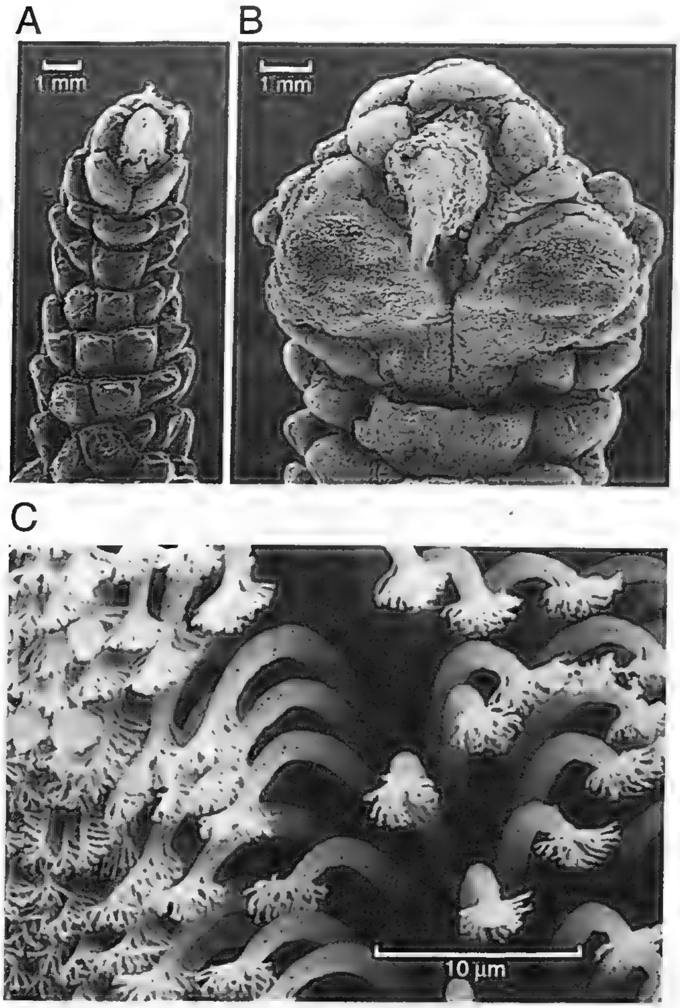

Figure 24.2 Scanning electron micrographs of the subdigital pads of geckos to show lamellar scale morphology. A, the terrestrial gecko *Rhynchoedura ornata*, shows the primitive condition in which subdigital pads are absent; B, the arboreal gecko *Diplodactylus assimilis*, showing the presence of subdigital pads; C, the numerous setae on the pads of *D. assimilis*, seen at higher magnification. [Photos by P. Withers, J. O'Shea & T. Stewart]

snakes expel a pungent cloacal secretion that may deter predators. Secretions from cloacal glands have also been related to mate attraction, particularly in female pythons which lay scent trails to attract males. The ability of blind snakes, which prey almost exclusively on termite and ant pupae, to forage within colonies without being attacked has been related to repellent cloacal secretions smeared over their body (Gehlbach, Watkins & Reno 1968). Some skinks have a postanal gland. Some terrestrial colubrids have a chain of small nucho-dorsalis glands which secrete a pheromone that irritates mucous membranes and may deter predators. A similar defensive function is performed by a sticky, noxious secretion from the tail of members of the gecko genus *Strophurus* (previously a part of *Diplodactylus*).

Femoral and pre-anal pores are found in many dragons, legless lizards and geckos. These pores are often arranged as V-shaped series or clusters anterior to the anus; for example, *Pygopus lepidopodus* has 10 preanal pores, each leading to an expanded gland (Underwood 1957). Males and females often have the same number of pores, but they are usually larger in males; females lack them in some species. These pores are the openings of papillary, follicular dermal glands (Cole 1966a). Glandular activity appears to be greatest during the breeding season, and may be under the control of androgens (Cole 1966a; Fergusson, Bradshaw & Cannon 1985). A thick, horny, yellow secretion, which often forms short plugs extending from the pore, may be a pheromone, a copulatory adhesive, or may provide a tactile cue during mating. The pores have some phylogenetic significance in amphiboluroid dragons (Greer 1989).

SKELETAL SYSTEM

The skeleton of a quadrupedal lizard (Fig. 24.3) has a moderately robust skull and a moderately long trunk. The appendicular skeleton consists of a pectoral girdle and forelimbs, and a pelvic girdle and hind limbs. The limbs are typically short and laterally orientated. The skeletal osteology of a squamate is directly related to its mode of locomotion (Romer 1956; Bellairs 1969; Porter 1972; Parker & Grandison 1977; Goin, Goin & Zug 1978; Greer 1989).

The Skull and Mandible

The squamate skull is derived from a primitive condition with two openings in the cheek or temporal region that allow for expansion of the jaw musculature and, in advanced forms, greatly increases the mobility of the lower jaw. This diapsid condition defines the subclass Lepidosauria, which consists of the orders Rhynchocephalia and Squamata. Two complete arches are found only in the Rhynchocephalia (tuatara, *Sphenodon punctatus*; Fig. 24.4A). Squamates have a modified or reduced diapsid condition. Lizards have lost the quadratojugal bone and the process of the jugal that formed the lower arch in the primitive condition (Fig. 24.4B). Snakes and some lizards have lost the upper as well as the lower arch (Fig. 24.4C), leaving the cheek region free of dermal bone and allowing great mobility of the quadrate bone which supports the lower jaw.

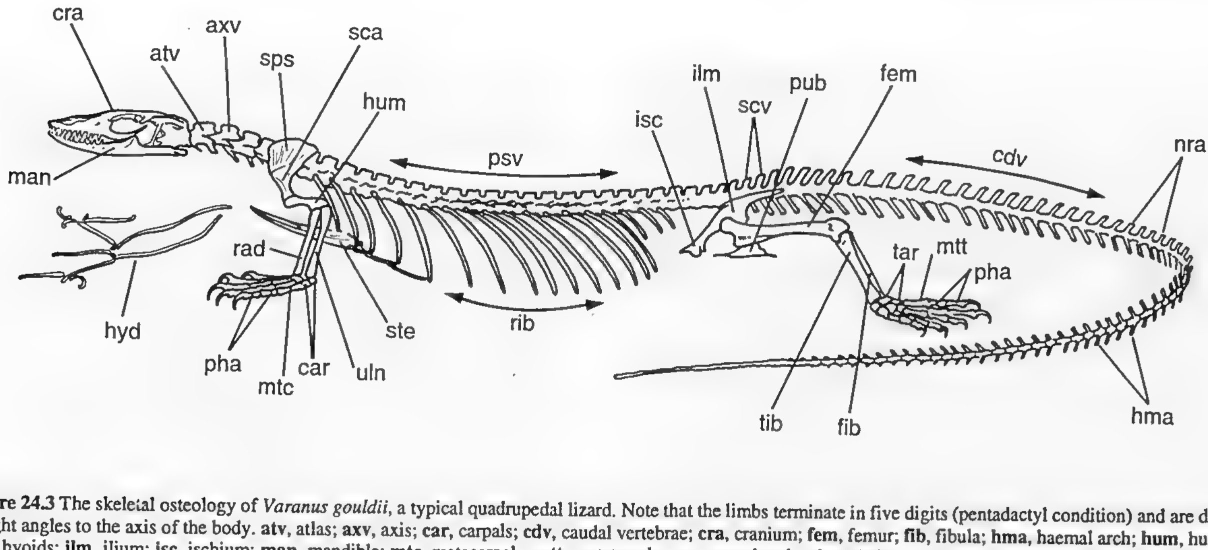

Figure 24.3 The skeletal osteology of *Varanus gouldii*, a typical quadrupedal lizard. Note that the limbs terminate in five digits (pentadactyl condition) and are directed at right angles to the axis of the body. **atv**, atlas; **axv**, axis; **car**, carpals; **cdv**, caudal vertebrae; **cra**, cranium; **fem**, femur; **fib**, fibula; **hma**, haemal arch; **hum**, humerus; **hyd**, hyoids; **ilm**, ilium; **isc**, ischium; **man**, mandible; **mtc**, metacarpals; **mtt**, metatarsals; **nra**, neural arch; **pha**, phalanges; **psv**, presacral vertebrae; **pub**, pubis; **rad**, radius; **rib**, ribs; **sca**, scapula; **scv**, sacral vertebrae; **sps**, suprascapula; **ste**, sternum; **tar**, tarsal bones; **tib**, tibia; **uln**, ulna. [M. Thompson]

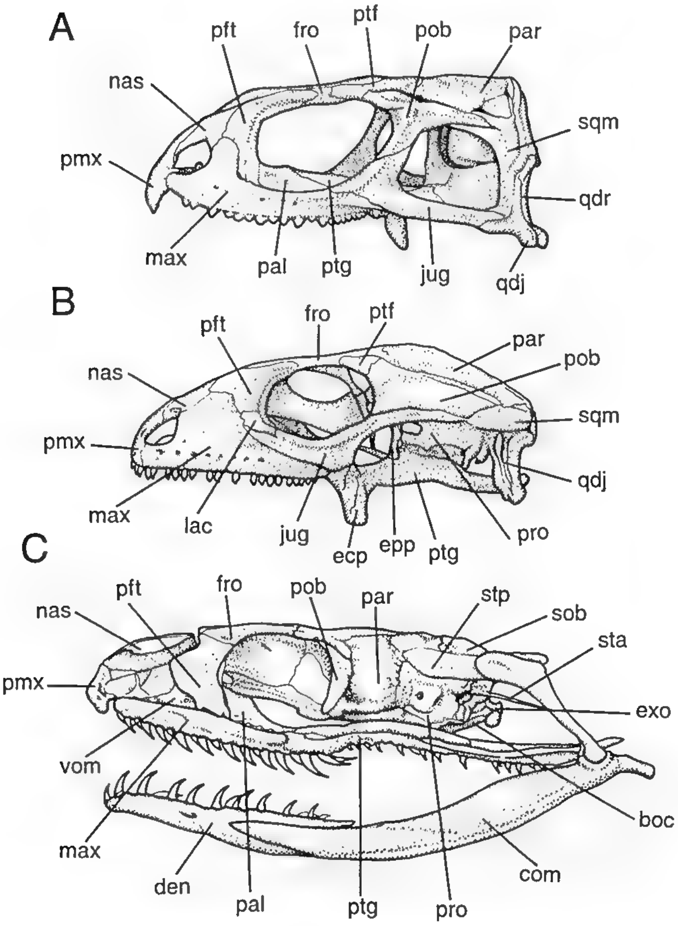

Figure 24.4 Skulls representative of the subclass Lepidosauria, showing modifications to the temporal region of the skull. A, *Sphenodon punctatus*, order Rhynchocephalia, in which the diapsid condition of two temporal openings is best seen; B, skull of a lizard, showing loss of the lower temporal bar; C, skull of a snake, in which upper and lower temporal bars have been lost. **boc**, basioccipital; **com**, compound; **den**, dentary; **ecp**, ectopterygoid; **epp**, epipterygoid; **exo**, exoccipital; **fro**, frontal; **jug**, jugal; **lac**, lachrymal; **max**, maxilla; **nas**, nasal; **pal**, palatine; **par**, parietal; **pft**, prefrontal; **pmx**, premaxilla; **pob**, postorbital; **pro**, prootic; **ptf**, postfrontal; **ptg**, pterygoid; **qdj**, quadratojugal; **qdr**, quadrate; **sob**, supraorbital; **sqm**, squamosal; **sta**, stapes; **stp**, supratemporal; **vom**, vomer. (Modified from Parker & Grandison 1977) [M. Thompson]

The brain case is caudal to the eyes. The posterior margin is formed by the fusion of four occipital bones. The supraoccipital forms the postero-dorsal portion of the brain case. The two exoccipitals form the posterior lateral margin of the neurocranium and the basioccipital forms the posterior ventral margin. The foramen magnum perforates the centre of the fused occipital bones. Raised extensions of the exoccipital bones unite at the margins of the foramen magnum, and with a similar protuberance from the basioccipital bone, form the tripartite occipital condyle, the point of articulation of the skull with the vertebral column. The roof and floor of the brain case are formed by the parietal and basisphenoid bones, respectively. The fused parietal bones form a flat plate extending anteriorly over the brain to the frontal bones. Antero-laterally the parietal joins the postorbital bones posterior to the orbits. Postero-laterally, the parietal bone is connected to the squamosal bones. In primitive or non-specialised forms, the cheek region behind and below the orbits is formed by the jugal, quadratojugal, squamosal and quadrate bones. Surrounding the orbit are the prefrontals, frontals, postfrontals and postorbitals. The snout and upper jaw are formed by the nasals, maxillae and premaxillae. The ventral portion of the skull is formed from the vomers, palatines, ectopterygoids and pterygoids, together with ventral extensions of the maxillae and premaxillae anteriorly, and the fusion of the basisphenoids with the basioccipital posteriorly. The anterior portion of the brain is poorly protected by bone in the Sauria. In contrast, the ophidian brain is enclosed by the downward growth of both the frontal and parietal bones (Fig. 24.4C).

In some squamates, reduction or loss of the temporal arches increases mobility of the quadrate bones. This and the independent movement of the pterygoids increases lower jaw mobility (streptostyly). Streptostyly increases the gape and also allows the jaws to move backwards and forwards, thus permitting extreme feeding specialisation. Many legless lizards, goannas, geckos and snakes also have highly kinetic skulls (Albright & Nelson 1959a, 1959b; Bolt & Ewer 1964; Frazzetta 1966; Gans, de Vree & Carrier 1985; Gans & de Vree 1986). Such movable joints may occur between the occipital and parietal bones (metakinesis), and parietal and frontal bones (mesokinesis). The snout and palate may also have some mobility, related to an inertial feeding strategy (for example, *Lialis*), or digging by limb-reduced fossorial forms such as *Delma*.

The internal nares and the ducts of Jacobson's organ each open into the anterior roof of the mouth. In some reptiles, the internal nares are located towards the back of the oral cavity, and separate it from the respiratory pathway. The palate is formed by the fusion of the premaxillae and the maxillae, and occasionally includes the palatines and pterygoids.

The lower jaw bones (Fig. 24.5) consist of the dentary, distinguished by the presence of teeth, the coronoid (which is usually lost), and the articular, prearticular, surangular, angular and splenial. These last five bones usually fuse to form the compound bone. The dentaries are fused anteriorly and are immobile in most of the lizards or held together loosely by elastic ligaments in most snakes and some legless lizards.

Dentition

All squamates have well-developed teeth at the edges of the premaxillae, maxillae and dentary (Fig. 24.5). Some, particularly snakes, also have teeth on the palatine and pterygoid bones. These marginal teeth are of two types, pleurodont and acrodont. The pleurodont tooth, found in all snakes and most lizards, develops on a shelf on the lingual side of the jaw and when mature fuses with the inner jaw bone margins. Acrodont teeth develop on the lingual side of the jaw but migrate to and fuse with the crest of the jaw bones and with each other to form a chisel shaped wedge. Agamids are unusual in having both tooth types (Fig. 24.5A; Greer 1989).

Pleurodont teeth are replaced regularly in a posterior to anterior sequence. Simultaneous addition of new teeth posteriorly in sub-adult individuals ensures that a diffuse and diverse dental array is always available to maintain effective biting (Cooper 1965). Acrodont teeth are not replaced over time and wear produces a cutting ridge.

The majority of skinks, legless lizards and geckos have non-specialised peg-like teeth with a vertical orientation (Fig. 24.5B–D). The large size of the molariform teeth of *Tiliqua* (Greer 1989) may be related to omnivory (Estes & Williams 1984). The pygopodid *Lialis burtonis* has many sharp, recurved teeth, like some snakes (Savitzky 1980, 1983; Patchell & Shine 1986a). The teeth of the goannas may be recurved, or laterally compressed and serrated; older non-curved rear teeth may wear to grinding, as opposed to cutting, surfaces.

Snake teeth have more positional differentiation than lizard teeth. Some are long, narrow, highly recurved and hinged to grasp and work the prey into the mouth. Aglyphous snakes have no fangs, but some teeth are modified as fangs for venom delivery in opisthoglyphous (rear-fanged) and proteroglyphous (front-fanged) snakes. The fangs often possess an open or partially closed groove running from the base to the surface for effective venom delivery (Fig. 35.8). Fangs may be permanent or replaceable. Most of Australia's snakes, including the terrestrial elapids, hydrophiids and laticaudids, are front-fanged and venomous.

Venom enters the prey by capillary action in rear-fanged snakes, such as some colubrids, which rely on multiple fangs and chewing to provide primary skin abrasion. In contrast, the comparatively

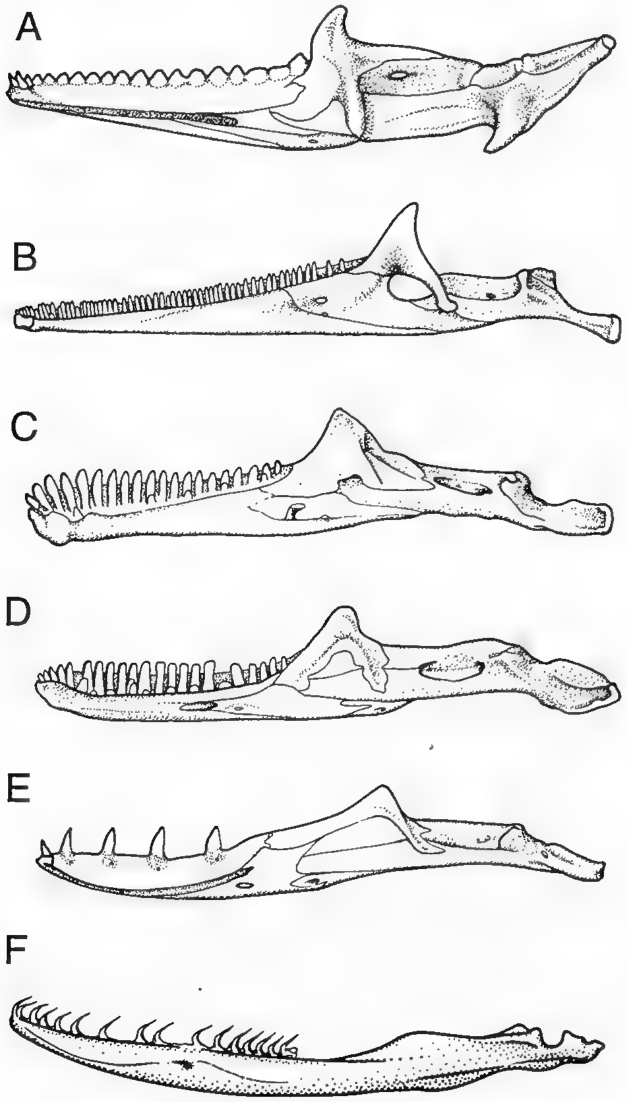

Figure 24.5 The mandible, in lingual view, from representatives of five families of lizards and one family of snakes. **A**, *Lophognathus gilberti* (Agamidae); **B**, *Carphodactylus laevis* (Gekkonidae); **C**, *Pygopus lepidopodus* (Pygopodidae); **D**, *Egernia saxatilis* (Scincidae); **E**, *Varanus timorensis* (Varanidae); **F**, *Pseudonaja affinis* (Elapidae). (Modified after Greer 1989) [M. Thompson]

long fangs of front-fanged snakes are capable of hypodermically injecting large quantities of neurotoxic venom deep into prey.

Vertebral Column

The vertebral column protects the spinal cord, supports the trunk and limbs, and provides leverage for locomotory muscles. Vertebrae show regional specialisation in number and morphology. This is most pronounced in short-bodied lizards such as *Moloch horridus* and least in limb-reduced, attenuated forms, particularly snakes.

Typical vertebrae have a solid bony centrum (Fig. 24.6A). Lateral plates from the dorsal surface of the centrum fuse to enclose the spinal cord and form a neural arch. Similar ventral extensions may enclose the blood vessels of the tail and form haemal arches. In all snakes and lizards, except some geckos, vertebrae articulate by procoelous ball-and-socket joints formed by the interaction of the concave anterior surface of one vertebra with the convex posterior surface of the preceding vertebra. The amphicoelous vertebrae of some geckos are concave at both ends. Each vertebra is supported by two pairs of articulating zygapophyses that prevent rotation of the vertebral column. Each postzygapophysis extends posteriorly and laterally from the posterior of each neural arch, where its ventro-lateral surface articulates with the dorso-medial surface of the prezygapophysis of the adjacent vertebra (Fig. 24.6A). Snakes and some legless lizards have two additional pairs of zygosphenes which extend anteriorly from the base of each neural arch to articulate with specialised postero-lateral zygantra of the preceding vertebra (Fig. 24.6B).

The neck usually has no more than eight cervical vertebrae. The first and second (atlas and axis respectively) support the skull and allow its movement. The other cervical vertebrae usually bear ribs that increase progressively in length posteriorly, although none reach the sternum. Thoracic vertebrae have ribs which reach the sternum (except in snakes). Lumbar vertebrae have no ribs, or short ribs that do not reach the sternum. Frequently the two sacral vertebrae are fused, and have lateral plates for pelvic girdle support. The distinct tail may have as few as 14 vertebrae or less in the skink *Egernia stokesii* and most snakes, or as many as 139 in the goanna *Varanus varius* (Greer 1989). The anterior intermediate vertebrae lack a haemal arch, but it is present on the more posterior caudal vertebrae. Sacral and some caudal vertebrae have antero-lateral processes, especially in species that show tail loss. Where tail autotomy occurs, the vertebrae may have a connective tissue or cartilage fracture line or be uniformly fragile (Etheridge 1967). The replacement tail has an internal cartilaginous rod, which sometimes is calcified, but vertebrae are not reformed.

Numbers of presacral vertebrae are usually used for comparisons between groups. Agamids typically have 22 to 24 presacral vertebrae (20 to 22 in *Moloch horridus*), and geckos have 25 to 27; skinks, goannas and legless lizards have 26 to 75, 28 to 32 and 44 to 95, respectively (Greer 1989). The highly attenuated and apparently limbless pygopodid genus *Aprasia* has up to 137 presacral vertebrae (Parker 1956; Greer 1989). Snakes, which lack a sacrum, have between 120 and 320 precloacal vertebrae (Hoffstetter & Gasc 1969).

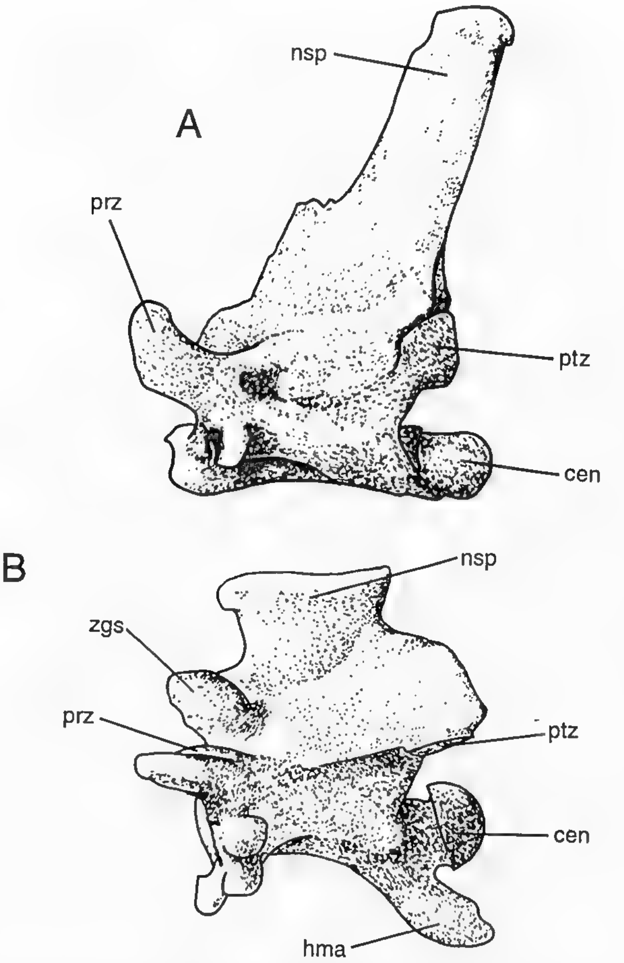

Figure 24.6 Lateral view of typical procoelous vertebrae. **A**, lizard; **B**, snake. **cen**, centrum; **hma**, haemal arch; **nsp**, neural spine; **prz**, prezygapophysis; **ptz**, postzygapophysis; **zgs**, zygosphene. (Modified after Parker & Grandison 1977) [J. O'Shea]

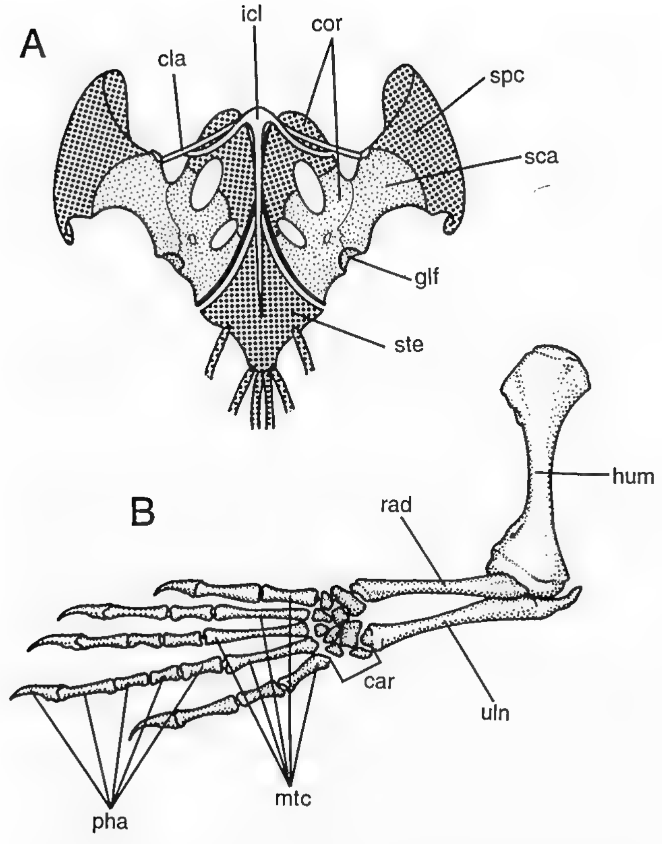

Figure 24.7 Pectoral girdle and forelimb of a varanid lizard. A, pectoral girdle, in ventral view; B, forelimb, in lateral view. In A, light and dark stippling represent bone and cartilage, respectively. **car**, carpals; **cla**, clavicle; **cor**, coracoid; **glf**, glenoid fossa; **hum**, humerus; **icl**, interclavicle; **mtc**, metacarpals; **pha**, phalanges; **rad**, radius; **sca**, scapula; **sps**, suprascapula; **ste**, sternum; **uln**, ulna. [M. Thompson]

Limbs and Girdles

The pectoral girdle of a typical tetrapod lizard consists of two halves joined ventrally by a cartilaginous sternum (Fig. 24.7A), each comprising precoracoid, coracoid, interclavicle, clavicle, scapula and suprascapula components. All lizards, including those with limb reduction or loss, have a pectoral girdle; snakes do not.

The forelimb typically consists of a humerus that articulates proximally with the glenoid fossa of the pectoral girdle and distally with the ulna and radius (Fig. 24.7B). The carpals, which articulate with the radius and ulna, consist of a radiale and ulnare, a small transitional bone between them, and four to six other small bones. The pentadactyl front foot is formed by five metacarpals, each of which articulates with one of five phalanges. The terminal digital phalanx usually has a claw. The phalangeal formula, or the number of phalanges in each digit from the thumb outward, is commonly 2, 3, 4, 5, 3 in dragons, goannas, geckos and some skinks.

There is considerable diversity in forelimb morphology. Short or absent forelimbs have been related to movement in closed vegetation or soil (Pianka 1986) and arboreality (Lundelius 1957; Collette 1961), and substantial forelimbs to digging (Ananjeva 1977). Pygopodids retain only the rudiments of the humerus. Some skinks, particularly *Lerista*, show intermediate stages from the 'normal' pentadactyl proportions (for example, fore and hind limbs with five digits; 5/5) through variable finger and toe reduction (for example, 4/4, 3/3, 2/2), and loss of forelimbs and reduction of hindlimbs (for example, 0/2, 0/1), to complete loss of external forelimbs and hindlimbs (0/0) (Fig. 24.8).

The squamate pelvic girdle, unlike the pectoral girdle, is bound dorsally to the vertebral column. Like the pectoral girdle, it consists of two halves that are joined ventrally by cartilage. Each half of the girdle is formed by the fusion of three bones, the pubis, ilium and ischium (Fig. 24.9). The ribs or lateral processes of the sacral vertebrae are fused to the posterior projections from each ilium. Ventrally, the anteriorly directed pubic bones are joined by cartilage at the pubic symphysis. The junction of the pubic bone with the ilium and posteriorly projecting ischium forms a specialised articulation socket, the acetabulum, which holds the head of the proximal limb bone, the femur.

Pelvic girdles show adaptive variation within the squamates. Reduction in the size of the components of the pelvis is invariably related to limb reduction in snakes, legless lizards and some skinks. All snakes except the pythons and a few of the more primitive groups lack a pelvis. Even when present in these snakes, the pelvis is vestigial. Pygopodids retain all of the components of the pelvis, most of the bones of the forelimbs and often have at least one phalange, even though they lack locomotory limbs (Greer 1989). The pelvis is usually well developed in groups capable of bipedal locomotion such as goannas and dragons. Modification of the pubic bones of the pelvis to produce anterior projections has been reported in dragons that climb and run quickly (Mitchell 1965; Greer 1989).

The hindlimbs of squamates consist of a femur that articulates with the pelvis proximally and with the fibula and tibia at the knee (Fig. 24.9). The distal parts of the fibula and tibia articulate with the foot at the ankle. Proximally, the ankle is formed by a combination of the fibulare, astragalus and tibiale with several other tarsal bones forming articulations with the metatarsals. In the primitive condition, there are five metatarsal bones. Each of these bones is associated with a digit in the pentadactyl condition. Dragons and goannas, commonly show a full phalangeal formula of 2, 3, 4, 5, 4 in the hind foot. The occurrence and development of a claw on the terminal phalanx of each digit is variable and related to life strategy. As with

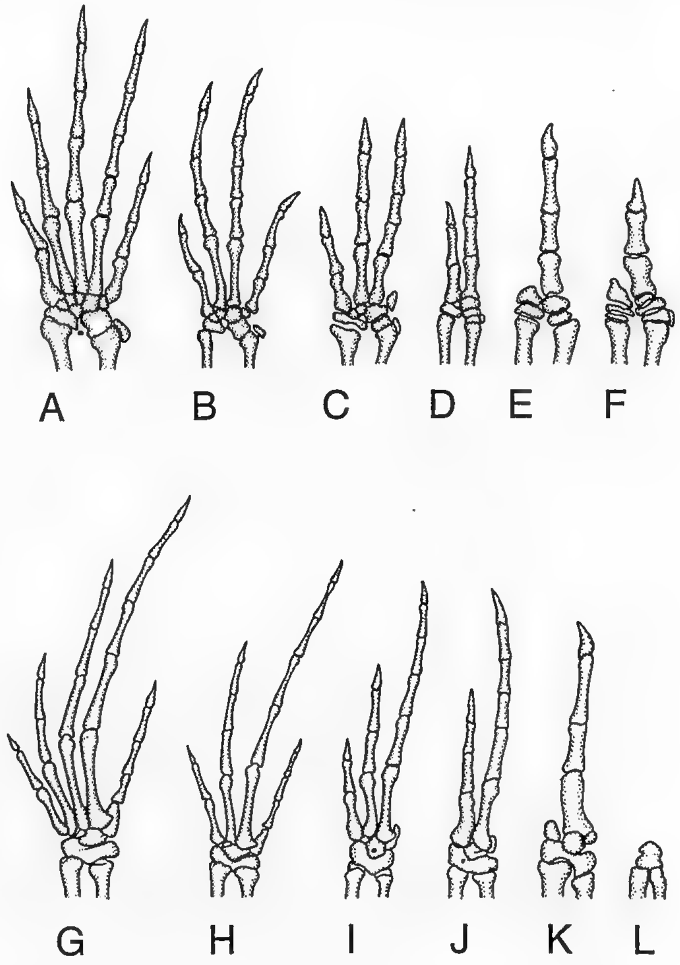

Figure 24.8 Limb reduction in species of *Lerista*. A–F; forelimb, showing reduction from the full phalangeal formula of 2, 3, 4, 5, 3 to 0, 0, 0, 2, 0; G–L, hindlimb, showing reduction from the full phalangeal formula of 2, 3, 4, 5, 4 to 0, 0, 0, 0, 0. **A**, **G**, *L. arenicola*; **B**, *L. distinguenda*; **C**, *L. fragilis*; **D**, *L. planiventralis*; **E**, *L. macropisthopus*; **F**, *L. punctatovittata*; **H**, *L. christinae*; **I**, *L. borealis*; **J**, *L. ips*; **K**, *L. cinerea*; **L**, *L. humphriesi*. (From Greer 1989) [M. Thompson]

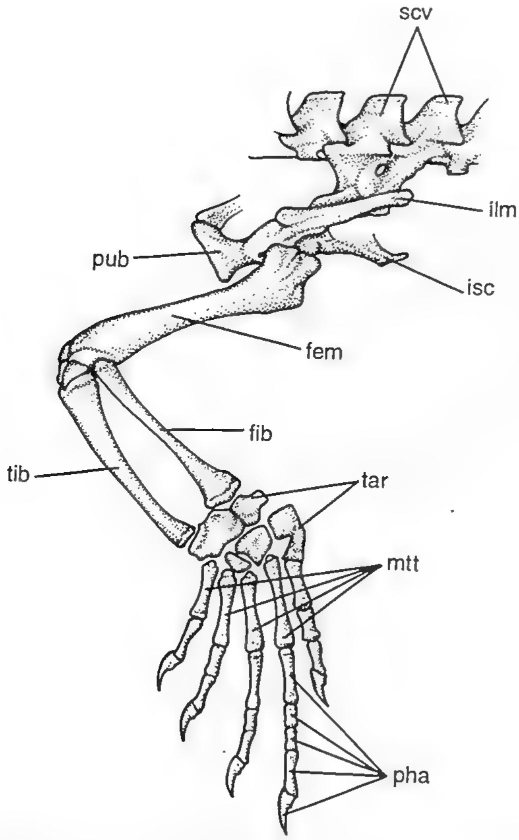

Figure 24.9 Pelvic girdle and hindlimb of a varanid lizard, in lateral view. The acetabulum, or socket for the head of the femur, is formed at the junction of the ilium, pubis and ischium. **fem**, femur; **fib**, fibula; **ilm**, ilium; **isc**, ischium; **mtt**, metatarsals; **pha**, phalanges; **pub**, pubis; **scv**, sacral vertebra; **tar**, tarsals; **tib**, tibia. [M. Thompson]

the digits of the front foot, digit reduction in the hind foot is complete in the legless lizards and very common among some lizards, particularly skinks such as *Lerista* (Fig. 24.8G–L).

MUSCULAR SYSTEM

The axial musculature is derived from segmentally arranged myotomes (Romer & Parsons 1977) that are divided by septa of connective tissue during development into the dorsal epaxial muscles and the ventral hypaxial muscles. The epaxial muscles are lateral to the vertebrae and form the dorso-lateral trunk muscles extending from the skull to the tail. The hypaxial muscles form the ventro-lateral body musculature (Gasc 1981).

Squamates have well-developed appendicular muscles, reflecting their predominantly quadrupedal locomotion and semi-erect posture. There is a tendency for reduction in relative mass and importance of the epaxial and hypaxial musculature, with simultaneous development of the limb and girdle muscles. However, body elongation, attenuation and secondary reduction or loss of limbs has increased the development and level of differentiation of the trunk muscles in snakes, legless lizards and some skinks.

Dermal musculature is poorly developed in most squamates, but is well-developed in snakes to erect the ventral scales and reduce backward slipping. In wide-bodied snakes that use rectilinear locomotion, three pairs of dermal muscles are present between the ribs and the large ventral scales (Lissmann 1950).

The main masticatory muscles of the jaw are the *muscularis adductores mandibulae* that close the jaw, and a small *m. depressor mandibulae* that opens it (Hass 1973). In snakes, which can move the upper and lower jaws independently of the brain case and each other (streptostyly), the adductor muscles are divided into numerous subunits, and other muscle groups connect the lower jaws anteriorly.

The epaxial muscles of the trunk comprise longitudinal bundles attached dorso-laterally to the vertebrae from the skull to the tail. The hypaxial muscles, together with the ribs, support the viscera and provide respiratory ventilation. The major part of the tail is a continuation of the dorsal epaxial muscles and the ventral hypaxial muscles, but the ventral portion is typically less substantial because the muscle bundles are interrupted by the pelvic girdle. The epaxial muscles of the trunk continue forward to support and move the skull and neck. The neck may also be invested with a superficial sphincter colli muscle that is closely bound to the skin. Squamates lack facial muscles and cannot easily drink by sucking.

The muscular tongue is supported by the geniohyoideus complex of the hyoid arch. In snakes, the tongue is usually anteriorly divided into tapering, highly protrusible portions that have a sensory rather than a mechanical function (Condon 1989). The tongue of goannas is also anteriorly modified for olfaction, but retains posterior musculature for swallowing. Similarly, the tongue of *Lialis* is bifid anteriorly, but is still involved in prey manipulation and swallowing (Patchell & Shine 1986a).

The forelimbs and pectoral girdle of lizards are suspended from the anterior trunk by the muscles *m. trapezius*, *m. serratus* and *m. levator scapulae*. The humerus is attached to the scapula and to the body by muscles and tendons. On the dorsal side of the body, the *m. latissimus dorsi* and *m. subcoracoscapularis* adduct and rotate the humerus, and the *m. scapulohumeralis* and *m. deltoideus* abduct the humerus. Ventrally, the *m. pectoralis*,

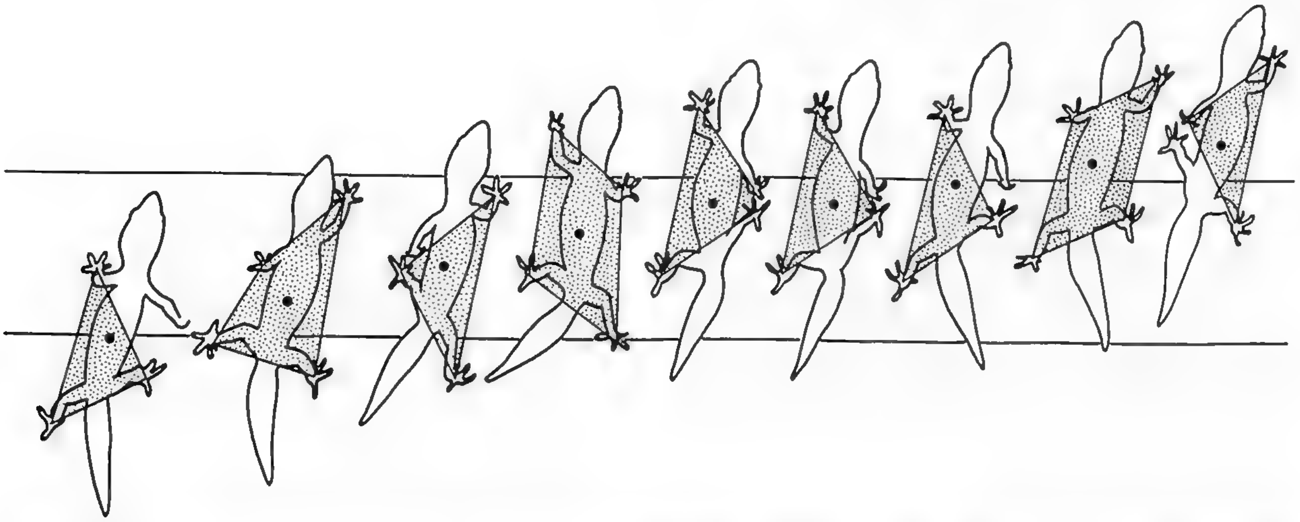

Figure 24.10 The locomotory strides of a gecko, *Diplodactylus assimilis*, involve repeated lateral undulations of the body and tail, and alternate movements of the feet. Stability is maintained by keeping the centre of gravity (●) within a triangle or quadrilateral formed by three or four feet that are on the ground. Horizontal lines are 5 cm apart, and consecutive positions of the gecko are at 40 msec intervals. [P. Withers & A. Roberts]

m. supracoracoideus and *m. coracobranchialis* muscles also adduct and rotate the humerus, and maintain semi-erect posture. The forelimb is extended by the *m. triceps* and flexed by the *m. branchialis* and the *m. biceps*. A group of ventral flexors and dorsal extensors move the front foot and its digits.

The musculature of the pelvic girdle and hindlimbs is less specialised than that of the pectoral girdle and fore limbs, because the pelvic girdle is fused to the vertebral column. Contraction of the *m. puboischiofemoralis internus* lifts the femur and the *m. iliotibialis*, *m. femorotibialis*, *m. ambiens* and *m. iliofibularis* extend the lower limb. A number of smaller more distal muscles extend the digits of the hind foot. Contraction of the *m. caudofemorales* returns the femur to a posterior position, pushes the body forward and provides much of the power for locomotion. The *m. puboischiofemoralis externus*, *m. ischiotrochantericus* and *m. adductor femoris* lower the femur. The *m. puboischiotibialis*, *m. flexor tibialis internus*, *m. flexor tibialis externus* and *m. pubotibialis* flex the hind limb. A few large muscles, including the *m. gastrocnemius* and *m. flexor digitorum longis*, extend the phalanges.

LOCOMOTION

Australian squamates move by burrowing, crawling, walking, climbing or swimming. In the typical slow, tetrapedal walk of a lizard, such as *Diplodactylus assimilis*, oscillatory movements of the limbs and undulatory movements of the body propel the lizard forward (Fig. 24.10). The centre of gravity is always within a triangle of three feet that are on the ground. Rapid running uses a similar pattern of limb and body movement, but the centre of gravity is not always supported by three feet. Bipedal running, which is a natural progression from rapid running, and bipedal standing and walking are observed in some dragons and goannas (Snyder 1962; Greer 1989). Many large goannas have a bipedal ritual combat 'dance'.

Terrestrial snakes typically move by lateral body undulations. Some snakes raise most of their body off the ground as they move forward at an angle to the body orientation ('side-winding'). In concertina locomotion, extension then contraction of body segments pulls the snake forward, as posteriorly-oriented scales prevent retrograde movement. Arboreal snakes tend to be very slender with elongate prehensile tails for climbing (Shine 1991a).

Undulatory locomotion over the ground, burrowing underground, and undulatory swimming are often associated with body elongation. The limbs are either tucked against the body during undulatory propulsion, reduced or lost. Burrowing is usually accompanied by limb and tail reduction (for example, *Lerista*). The skull of burrowers is often strengthened and the head scales reduced in number and increased in size to function as protective shields. Burrowing snakes tend to be short and stocky, in contrast to terrestrial and arboreal snakes, and have strong skulls with strengthening head scales (for example, *Ramphotyphlops*, *Vermicella*).

Undulatory swimming occurs in some limbed and limbless squamates. The laterally compressed tail of the semi-aquatic *Physignathus lesueurii* and water monitors, *Varanus indicus*, *V. mertensi*, *V. mitchelli*, acts as a rowing oar. The dorsally located nostrils of the latter two species allow breathing while the rest of the head is submerged. Seasnakes have flattened, paddle-like tails. The seasnake, *Pelamis platurus* has a ventral body keel, and subsurface swimming is achieved by torsional and rolling motions of the body rather than lateral undulation (Graham, Lowell, Rubinoff & Motta 1987). The flaccid skin folds of filesnakes act as a paddle.

In lizards, the metabolic rate during locomotion increases in linear proportion to velocity up to a maximum before reaching a plateau (Fig. 24.11A). Anaerobic metabolism contributes progressively more to energy production at higher velocities. The relationship between the rate of oxygen consumption and velocity extrapolates at zero velocity to slightly more than the resting and standard metabolic rates, and reflects an energetic cost of posture. The net metabolic cost of transport (COT_{net}) is the slope of the relationship between oxygen consumption rate and velocity. There is an inverse relationship for squamates between COT_{net} and body mass (Fig. 24.11B) that is surprisingly similar to that for mammals, birds, and arthropods (Taylor, Heglund & Maloiy 1982; Full 1989; Baudinette 1991).

Limbless squamates expend energy to push against objects by lateral undulation, but not for postural maintenance or limb acceleration/deceleration. The metabolic cost of lateral undulatory crawling by a snake increases approximately in linear proportion to velocity (Walton, Jayne & Bennett 1990) and COT_{net} is similar to that for a walking lizard of the same mass (Fig. 24.11B). The metabolic rate for a side-winding snake also increases approximately in proportion to velocity, but the COT_{net} is lower

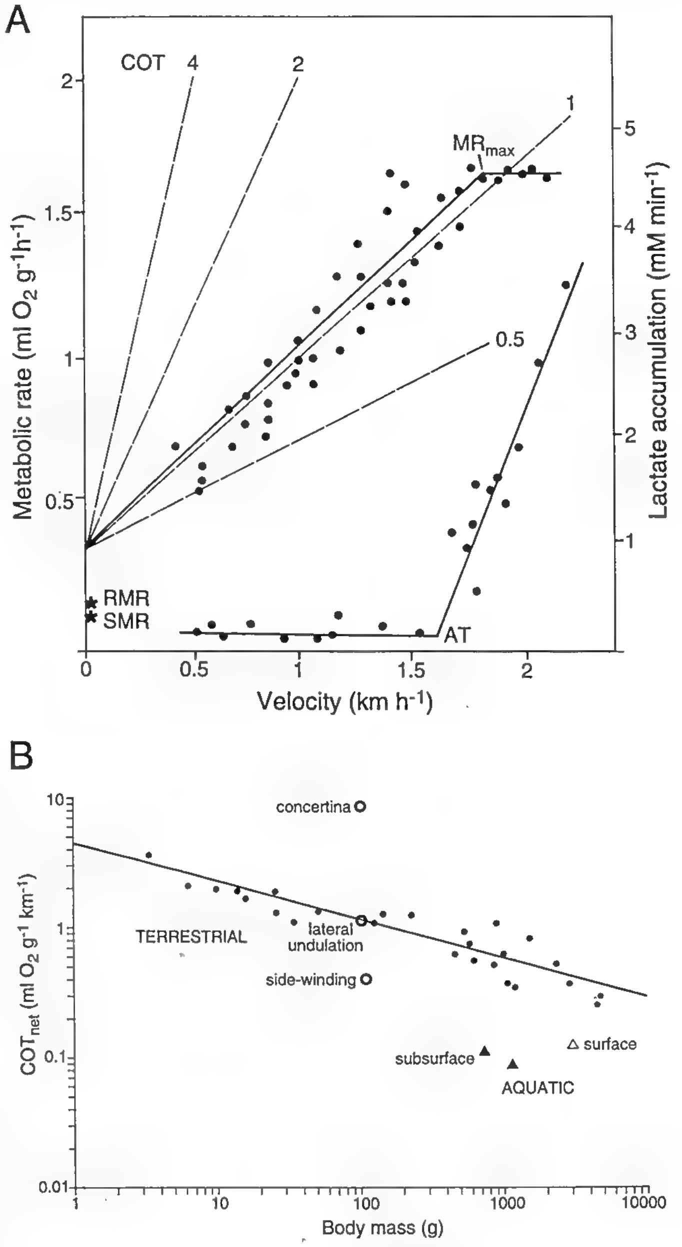

Figure 24.11 Metabolic costs of locomotion in squamates. A, metabolic rate and rate of accumulation of blood lactate of a goanna (*Varanus exanthematicus*) walking and running at a range of velocities. The standard metabolic rate (SMR), resting metabolic rate (RMR ≈ 1.3 x SMR), maximal metabolic rate (MR_{max}) and anaerobic threshold (AT) are indicated. The net cost of transport (COT) is the slope of the metabolic rate-velocity line; values for 0.5, 1, 2 and 4 ml O_2 g^{-1} km^{-1} are shown.; **B**, net cost of transport for terrestrial locomotion by lizards and snakes (concertina, lateral undulation and side-winding) and swimming (surface, Galapagos iguana; subsurface, green sea turtle). (A, data from Seeherman, Dmi'el & Gleeson 1983, predicted SMR and RMR calculated from Thompson & Withers 1992; B, data from John-Alder, Garland & Bennett 1986; Videlor & Nolet 1990; Walton *et al.* 1990; Secor *et al.* 1992) [W. Mumford]

(Secor, Jayne & Bennett 1992). The metabolic cost of concertina crawling also increases approximately linearly with velocity, but COT_{net} is much higher than for lateral undulatory crawling (Walton *et al.* 1990). There are no estimates of the metabolic cost of burrowing.

The energy requirements are substantially different for swimming compared to land surface and burrowing movement. The major energy expenditure overcomes body drag but some is dissipated as surface waves and to overcome buoyancy. The long lung of seasnakes provides positive buoyancy, but this is reduced at depth by hydrostatic compression. Metabolic rate increases linearly with swimming velocity for marine iguanas and turtles (Prange 1976; Vleck, Gleeson & Bartholomew 1981), but both have a considerably higher metabolic rate than swimming fish. The net cost of transport for squamates is essentially independent of velocity for walking/running/crawling, and (despite theoretical considerations) for swimming. The COT_{net} is substantially higher for walking/running/crawling compared to swimming (Fig. 24.11B).

FEEDING AND DIGESTION

Feeding involves co-ordinated processes such as localisation, identification, capture, immobilisation, mechanical reduction and swallowing (de Vree & Gans 1989). Internally, the digestive system of squamates varies very little, apart from changes related to body shape, particularly body elongation. Few modifications or specialisations for chemical digestion or nutrient absorption have been reported.

Squamates are predominantly carnivorous or insectivorous. Snakes and goannas prey mainly on vertebrates and, with a few notable exceptions, geckos, dragons, legless lizards and skinks prey on invertebrates (Carroll 1977b; Greer 1989). Diet may be diverse in opportunistic omnivores (for example, *Egernia*; Barwick 1965; Shine 1971; Brown 1983) or very restricted and specialised, such as that of the myrmecophagous *Moloch* (Davey 1923; Paton 1965; Pianka & Pianka 1970). Some lizards, particularly skinks, change their feeding strategy from insectivorous as juveniles to omnivorous or herbivorous as adults (Ostrum 1963; Barwick 1965; Shine 1971; Brown 1983). This change has been related to both the difficulty for large lizards to catch enough small insects, and to an energetic constraint on large herbivores (Pough 1973; Wilson & Lee 1974).

Food Acquisition

Prey is detected, then localised and captured, using vision, olfaction and audition. Olfaction is used by active predators, such as snakes, goannas and geckos (Koch 1970; Cogger 1973; Schwenk 1993) in combination with vision. Typhlopids also use olfaction to locate ant larvae and eggs. Nocturnal opportunistic foragers, especially arboreal geckos and snakes, have comparatively large eyes (Werner 1969; Pianka & Pianka 1976; Shine 1991a). Most pythons have heat-sensitive pits in some labial scales (Bullock & Barrett 1968). Attraction of prey by tail luring is found in the elapid *Acanthophis* (Carpenter, Murphy & Carpenter 1978), the legless lizard *Lialis* (Bradshaw, Gans & Saint Girons 1980; Murray, Bradshaw & Edward 1991) and some skinks (Greer 1989).

Lizards tend to feed opportunistically. Tooth differentiation and specialisation of jaw musculature is primarily related to retention, immobilisation and swallowing, rather than dismembering or crushing. In the absence of mechanical reduction of prey by the teeth and jaws, the size of prey is, with the exception of *Lialis*, proportional to jaw length and head width. Jaw dimensions have been used as reliable indicators of prey size in geckos (Pianka & Pianka 1976) and skinks (Pianka 1986).

A grasping function for the jaws is not vital if the prey is relatively small. For example, *Moloch* captures small ants with its projectile tongue, without holding or crushing them with its jaws (Pianka

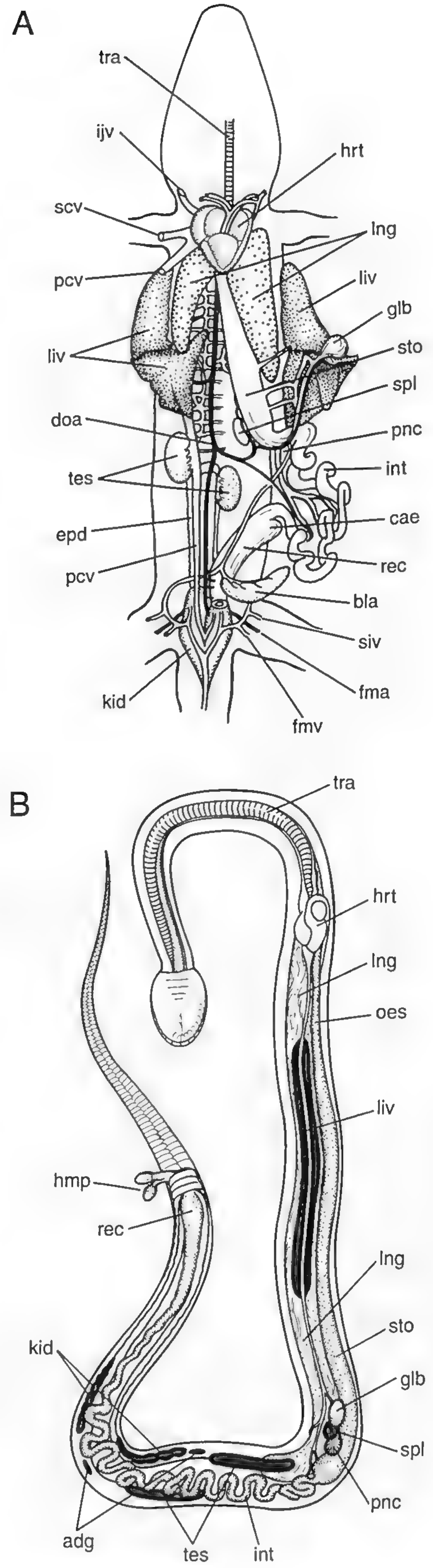

Figure 24.12 The arrangement of the viscera in squamates. **A**, a lizard; **B**, a snake. **acv**, subclavian vein; **adg**, adrenal glands; **bla**, bladder; **cae**, caecum; **doa**, dorsal aorta; **epd**, epididymis; **fma**, femoral artery; **fmv**, femoral vein; **glb**, gall bladder; **hmp**, hemipenes; **hrt**, heart; **ijv**, internal jugular vein; **int**, small intestine; **kid**, kidney; **liv**, liver; **lng**, lungs; **oes**, oesophagus; **pcv**, postcaval vein; **pnc**, pancreas; **rec**, rectum; **scv**, subclavian vein; **siv**, sciatic vein; **spl**, spleen; **sto**, stomach; **tes**, testes; **tra**, trachea. [M. Thompson]

1986). The capture of large arthropod and vertebrate prey involves the jaws, teeth, neck and body musculature. Lizards cannot move their lips and have limited use of their limbs in feeding. Snakes, some goannas and *Lialis* feed on comparatively large vertebrates by lunging with the neck and/or body. Their teeth are often recurved to securely hold prey, and cranial kinesis facilitates grasping (Frazzetta 1962; Savitzky 1980, 1983; Patchell & Shine 1986a; Condon 1989). In snakes, the simultaneous and synchronised contraction of the jaw musculature in striking, holding and subduing prey is functionally very different from the alternating action of the jaws in swallowing (Van Ripper 1953; Albright & Nelson 1959a, 1959b; Frazzetta 1966; Kardong 1974; Cundall & Gans 1979). Small prey can be killed prior to swallowing, by crushing or piercing. Larger prey may be asphyxiated by the jaws and/or body coils prior to swallowing, or killed by digestive juices after swallowing.

Venom immobilises prey and begins chemical digestion (Zeller 1948; Skoczylas 1978). The venom is saliva secreted by the superior labial (Duvernoy's) gland in colubrids and a gland overlying the superior labial gland in elapids and seasnakes. The enlarged rear fangs of colubrids and front fangs of elapids are grooved for venom delivery. Raised edges of the groove meet to form a discrete canal in some elapids (Fig. 35.8). This, together with the proximity of the venom gland to the large masseter muscles, effectively delivers venom into the prey.

The tongue of most squamates has an important role in manipulation and swallowing (Bels & Baltus 1989). Varanids, legless lizards and snakes typically swallow prey head first, using the musculature of the jaws and neck. Swallowing is assisted by large quantities of lubricating saliva and kinking of the throat and neck (Patchell & Shine 1986a). Varanids jerk prey backwards as the mouth is thrown forward, causing the prey to pass by its own inertia into the throat/oesophagus (Longley 1947; Gans 1961, 1969; Smith 1982). Snakes can work prey into the mouth by the alternate movement of the upper and lower jaws on each side (Frazzetta 1959, 1966; Gans 1961; Kardong 1977; Cundall 1983). In static inertial feeding, such jaw 'walking' allows a snake to pull itself over heavy prey (Bramble & Wake 1985).

Digestion

Chemical digestion in squamates is very similar to that described for other vertebrates (Stevens 1988). The digestive tract in both lizards and snakes consists of a muscular tube which commences as the oesophagus, passes into the stomach, small intestine and large intestine, and culminates in the cloaca (Fig. 24.12). The tube has muscular walls and an absorptive epithelium. It is lined throughout with mucous cells and, regionally, with specialised secretory cells that may be aggregated into glands.

The oral cavity is lined with ciliated or squamous epithelium containing mucin-secreting goblet cells. The oral glands include the palatine, lingual and sublingual, labial glands, mandibular and venom glands (Kochva 1978).

The palatine glands of the roof of the mouth, which are variously developed in lizards but absent in snakes, secrete mucin, as do other digestive glands. Sublingual glands are located on the floor of the oral cavity; those of some seasnakes are salt glands (Dunson 1976). Lingual glands are well-developed in geckos and dragons, but are lacking in goannas and snakes. Squamates have supra- and infralabial glands around the edges of both the upper and lower jaws. It has been suggested that the well-developed mandibular gland of goannas may secrete a venom (Gabe & Saint Girons 1969; Kochva 1978).

The longitudinally folded oesophagus is long and capable of substantial expansion in squamates that ingest large prey, and can be used for short term storage and chemical digestion. The ciliated lining of the oesophagus has many goblet cells (Parsons & Cameron 1977).

Food is stored and digested physically and chemically in the stomach. It is usually separated into fundic and pyloric regions, and a pyloric valve may be present. The lining is folded into prominent longitudinal rugae, in snakes, but these are less obvious in the thinner-walled stomachs of lizards (Parsons & Cameron 1977). The muscular walls mechanically mix and dismember prey. A variety of straight, tubular glands occur in the stomach of squamates (Luppa 1977).

The stomach capacity may be as high as 40% of the body weight in goannas and snakes that consume large prey (Weavers 1983; Greer 1989; Shine 1991a), while species consuming small prey may also have a substantial gastric capacity. For example, that of *Moloch* may hold up to 2,500 ants (Greer 1989).

Gastric juice has a low pH (about 2 to 3) and contains mainly proteolytic (pepsin) and also other enzymes (chitinase, amylase) (Skoczylas 1978). The low pH prevents putrefaction of prey, decalcifies the bone of vertebrate prey, and may help kill prey in colubrids. Chemical digestion employs hydrochloric acid (HCl) and pepsin, which is formed from pepsinogen at low pH. The dark cells of the main gastric glands in the fundus secrete pepsinogen and HCl. The pyloric glands are usually shorter and less branched than the main gastric glands, and secrete mucus and perhaps other materials.

The time required for food digestion in snakes, and presumably also lizards, is a function of both the size and type of prey being digested. It is directly correlated with the penetration rate of digestive juices and the neutralising capacity of prey tissue (Skoczylas 1970b). Fish are digested more quickly than frogs (Brown 1958; Abduschukuova 1965; Skoczylas 1970a 1978), which are digested more quickly than mice (Root 1961). Gastric enzyme activity is reduced at low body temperatures (Henderson 1970; Avery 1973). Low temperature reduces both the activity of pepsin and the production and release of pepsinogen and HCl (Skoczylas 1970b).

The pancreas secretes a mixture of bicarbonate ions and digestive enzymes into the small intestine. The bicarbonate buffers the acidic fluid from the stomach to a near neutral pH. The enzymes digest carbohydrates (amylolytic), proteins (proteolytic) and lipids (lipolytic). Many insectivorous squamates produce chitinase (Jeuniaux 1961).

Bile, produced by the liver and stored in the gall bladder, emulsifies fat to assist the hydrolysis of triglycerides by lipases and facilitates absorption of the products of hydrolysis (Haslewood 1967, 1968; Tammar 1974).

The intestine is usually coiled and longer in herbivores and omnivores than carnivores. It completes chemical digestion and absorbs the products of digestion, water and some minerals. The surface area of the intestine, which determines the rate of absorption, is increased by the presence of longitudinal folds, epithelial villi and cellular microvilli (Ferri, Junqueira, Medeiros & Medeiros 1976; Luppa 1977; Parsons & Cameron 1977).

The colon, which is usually separated from the small intestine by an ileocolic valve, typically has thin walls with little muscle. Its epithelium has goblet cells but no other secretory cells. It can be a site for fermentation of plant material. The hindgut is the primary site of the adaptive increase in gut length of herbivorous squamates (Skoczylas 1978; Stevens 1988).

The caecum, a thin walled extension of the colon at its junction with the small intestine, allows an increase in the volume of digested food and a variable passage rate for different foods. It is a common feature of herbivores and omnivores and may be a major site for symbiotic digestion of plant material (Mackenzie & Owen 1923; Greer 1989). However, dragons, which are primarily insectivorous (Pianka 1971c), possess a caecum, whereas it is poorly developed in some *Egernia* and *Tiliqua* that consume large quantities of plant material (Shine 1971; Brown 1983; Greer 1989).

The cloaca is the terminal part of the intestine where digestive and urinary waste is held prior to release. It is incompletely separated into the coprodeum, urodeum and proctodeum. The coprodeum is essentially the posterior portion of the large intestine. The urinary and reproductive tracts open into the central urodeum. The procotodeum is a short tube closed by the anal sphincter.

CIRCULATION

The circulatory system consists of a heart, a vascular circuit containing blood, and a lymphatic drainage system. It transports gases, nutrients, hormones and neurohormones. Hydrostatic pressure is generated for blood flow, glomerular filtration, and erection of hemipenes and other cavernous tissues such as the external narial sphincter. Cleaning of the eye by expansion of the orbital venous sinus, swelling of the head to initiate skin shedding, and predator defense by orbital blood squirting are also made possible by this pressure. The circulatory system also has a role in immune defense and thermoregulation. The cardiovascular adaptations of reptiles have been reviewed recently (see Lillywhite & Burggren 1987).

Heart

The heart of a typical lizard is located ventrally in the thoracic cavity between the left and right lungs, but is located more posteriorly in elongate lizards and snakes (Fig. 24.12B). It consists of a thin-walled sinus venosus, two atria, and a three-chambered ventricle.

Blood returns from the body via the anterior and posterior venae cavae to the thin-walled sinus venosus then to the right atrium, and from the lungs via the pulmonary veins to the left atrium (Fig. 24.13). The relatively thin-walled atria have a significant role in ventricular filling (Johansen 1959). The ventricle has three thick, muscular-walled chambers, the cavum venosum, cavum arteriosum, and cavum pulmonale. The right atrium communicates with the cavum venosum. The left atrium communicates with the cavum arteriosum, which would be blind-ending except that it connects to the cavum venosum via an interventricular canal. Atrioventricular valves control blood flow between the right atrium, cavum arteriosum and cavum venosum. The cavum venosum is partially separated by a thick muscular ridge from the third chamber, the cavum pulmonale.

There is considerable functional separation of oxygenated and deoxygenated blood in the squamate ventricle despite the anatomical continuity of its three chambers (Fig. 24.13; Webb, Heatwole & De Bavay 1971; White 1976). Deoxygenated blood enters the cavum venosum from the right atrium, and also passes across the muscular ridge into the cavum pulmonale. Oxygenated blood enters the cavum arteriosum from the left atrium, but remains there because the atrioventricular valves close the interventricular canal. During ventricular contraction, the atrioventricular valves close the atrio-ventricular openings and open the interventricular canal. Deoxygenated blood is first ejected into the pulmonary arteries from the cavum venosum and cavum pulmonale because of the low vascular resistance of the pulmonary circuit. As the ventricle further contracts, the muscular ridge separates the cavum venosum and cavum pulmonale. This allows oxygenated blood to flow from the cavum arteriosum into the cavum venosum then the left and right systemic arches, and prevents backflow of deoxygenated blood from the cavum pulmonale into the cavum venosum. The functional, but not anatomical, separation of oxygenated and deoxygenated blood can allow the systemic return to the heart to be shunted to the systemic output (right-to-left-shunt) to bypass the lungs during diving, or the pulmonary return to be shunted to the lungs (left-to-right shunt) during periods of intense lung ventilation. For example, blood flow completely bypasses the lung in the filesnake *Acrochordus granulatus* during prolonged quiescent diving but largely bypasses the systemic circulation during lung ventilation (Lillywhite & Donald 1989).

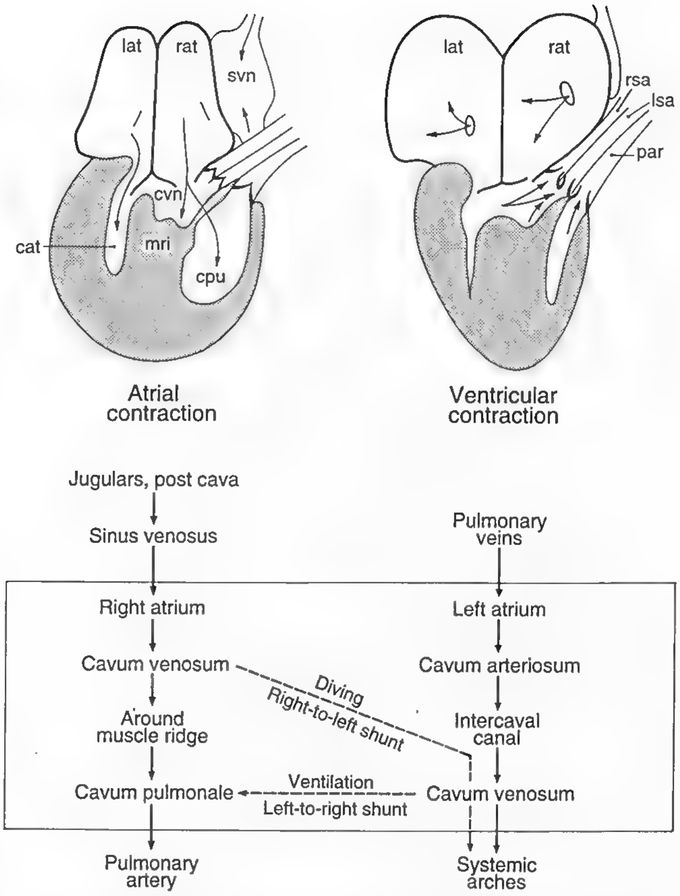

Figure 24.13 Diagrammatic representation of blood flow through the heart of a lizard, *Varanus* sp., during atrial contraction and ventricular contraction. **cat**, cavum arteriosum; **cpu**, cavum pulmonale; **cvn**, cavum venosum; **lat**, left atrium; **lsa**, left systemic arch; **mri**, muscular ridge; **par**, pulmonary artery; **rat**, right atrium; **rsa**, right systemic arch; **svn**, sinus venosus. (Modified from White 1968; Webb *et al.* 1971). [W. Mumford]

Heart rate is inversely related to body mass (Bartholomew & Tucker 1964; Licht 1965), and is generally higher during breathing than apneic periods. A diving bradycardia occurs during voluntary diving (Courtice 1981d, 1985). Temperature has a marked effect on heart rate, with a Q_{10} of about 2 to 2.5, but the maximal heart rate may decline above a critical body temperature (Bartholomew & Tucker 1963; Licht 1965; Bennett 1972; Wilson & Lee 1974). There is a considerable thermal hysteresis in heart rate (Bartholomew & Tucker 1963) during heating (higher rate) and cooling (lower rate). There is a substantial increase in heart rate during activity, but the scope for heart rate increment may decline at high body temperatures. The cardiac output of *Varanus exanthematicus* increases to match the 6.6-fold increase in O_2 demand during activity (Gleeson, Mitchell & Bennett 1980) by a 2.2-fold increase in heart rate, a 1.3-fold increase in stroke volume, and a 2.3-fold increase in the arterial-venous O_2 content difference.

Vascular System

The arterial circuit of the systemic system arises from the heart as right and left aortic arches. The carotid arteries supply the head (the right carotid is small, or absent, in many snakes). The posterior extensions of the left and right arches give rise to subclavian arteries, which supply the forelimbs, and then fuse to form the dorsal aorta. Branches from the dorsal aorta supply the gut, liver and kidneys (coeliaco-mesenteric, hepatic and renal arteries), hindlimbs (iliac arteries) and tail (caudal artery). The venous circuit enters the heart as left and right anterior and postcaval veins. Blood from the tail (caudal vein) and hindlimbs (iliac veins) can enter the renal portal system then return to the heart directly via the post cavae, or via the pelvic, ventral abdominal, and hepatic veins. Blood from the forelimbs returns via the subclavian veins then anterior caval veins to the heart. The anterior cardinal (jugular) veins drain the anterior body. An hepatic-portal system carries nutrient-rich blood from the digestive tract to the liver. The circulatory system of the limbless *Typhlops* has been described in detail by Robb (1960).

The pulmonary arch exits the cavum pulmonale then forms the right and left pulmonary arteries (the latter degenerates in snakes with a vestigial or absent left lung). Deoxygenated blood flows preferentially from the cavum venosum into the pulmonary arteries because the pulmonary vascular resistance is generally lower than the systemic resistance. However, a profound increase in pulmonary vascular resistance during diving can induce a right-to-left intracardiac shunt that bypasses the lungs (Lillywhite & Donald 1989).

During basking, a head-body temperature gradient can be maintained by countercurrent heat exchange between warm venous (internal jugular) blood and cool arterial (internal carotid) blood (Heath 1966). However, an internal jugular constrictor muscle can return cephalic blood preferentially to the body via the external jugulars, bypassing the countercurrent heat exchanger to cool the head and warm the body, and also cause the eyes to swell by expansion of the cephalic venous sinus. Such head-swelling can also loosen and break the skin for sloughing.

Terrestrial and, in particular, arboreal snakes experience gravitational hydrostatic pressure gradients, and must prevent peripheral blood pooling and maintain venous return. Their anteriorly placed heart minimises head-heart distance and their short, vascularised lungs reduce the risk of pulmonary oedema. Conversely, aquatic snakes rarely experience gravitational hydrostatic pressure gradients and may lack these circulatory specialisations (Lillywhite 1987a). For example, seasnakes have poor baroreceptor control of blood pressure (Lillywhite & Pough 1983).

There is a marked cardiovascular readjustment during voluntary diving (White 1976; Courtice 1981d, 1985; Seymour 1982). Heart rate declines dramatically, but arterial blood pressure is maintained by peripheral vasoconstriction. Cardiac output is redistributed by a right-to-left shunt that partially or completely bypasses the lungs. Cutaneous perfusion is elevated by local CO_2 in *Physignathus* and may facilitate cutaneous CO_2 excretion during diving (Courtice 1981c).

Blood

Blood has a variety of functions including transport of O_2, CO_2, nutrients, wastes, and hormones as well as pH buffering, defense, and maintenance of blood colloid osmotic pressure. Vasoconstriction and blood clotting (haemostasis) follow injury to the vascular system. Fibrinogen forms a fibrin clot, particularly in the presence of cellular factors released by tissue damage.

Blood contains many nucleated ellipsoid red blood cells (RBCs or erythrocytes) and fewer white blood cells (WBCs; Saint Girons 1970b; Courtice 1981a). RBCs vary greatly in size amongst squamate families (Wintrobe 1933/1934; Saint Girons 1970b). The RBC count of squamates is generally 5×10^5 to 2×10^6 mm^{-3} (Duguy 1970). It can vary between sexes, with age, over an annual cycle, and with pathological conditions, but generally does not increase with altitude. The WBCs include granulocytes (eosinophils, basophils, azurophils, neutrophils), lymphocytes, monocytes, plasma cells and thrombocytes (Saint Girons 1970b). The eosinophils are involved with allergic reactions and the basophils (mast cells) phagocytose foreign material. Lymphocytes have a cellular immune role. The small thrombocytes are involved with blood clotting. There is considerable variation in WBC count, from about 2 to 30×10^3 mm^{-3} (excluding thrombocytes). Lymphocytes are generally the most numerous (other than thrombocytes), and eosinophils are the second most abundant. Monocytes and basophils are the least abundant. There are generally about 50 to 300 thrombocytes per 100 other WBCs. WBC count and proportions of different WBCs vary between sexes, with age and moulting, with season, during pregnancy, and with pathological state.

The intracellular concentration of haemoglobin in squamate RBCs is about 32 g% and the oxygen carrying capacity of blood is about 8 to 10 volumes %, depending on the haemoglobin concentration. Reptilian haemoglobin tends to be more oxidised (met-haemoglobin) than mammalian haemoglobin (Wood & Lenfant 1976) and has a lower O_2 binding capacity. For example, the blood of *Physignathus* binds about 0.95 ml O_2 per gram of total haemoglobin (Courtice 1981a) compared to 1.2 to 1.3 ml O_2 g^{-1}. The sigmoidal O_2 dissociation curve reflects the cooperativity of haemoglobin subunits; cooperativity coefficients are typically 1 to 3 (Dessauer 1970; Wood & Lenfant 1976; Pough 1980a). The O_2 affinity of haemoglobin (P_{50}) is affected by body mass, temperature and pH (Bohr and Root effects). The P_{50} decreases with body mass in lizards from about 75 torr (mass < 20 g) to about 50 torr (mass > 1000 g); these P_{50} values are considerably higher than for mammals of comparable body mass (Bennett 1973; Pough 1977a, 1980a). In contrast, the P_{50} of snakes increases with mass (Pough 1977b, 1980a). Temperature affects the P_{50} of squamate blood (Pough 1969a, 1976; Courtice 1981a), but the low effect of temperature for some squamates minimises the effects of changes in body temperature on the O_2 transport capacity of blood.

Carbon dioxide transport depends on the reversible chemical combination of CO_2 with blood proteins (especially haemoglobin) and water, as well as dissolved CO_2. The CO_2 dissociation curve for blood of *Physignathus* is hyperbolic and the total CO_2 content is diminished at elevated temperature (Courtice 1981a).

Most diving reptiles do not have a higher haemoglobin content, blood O_2 capacity, blood volume and lower P_{50} than non-diving species, except for the file snakes (Johansen & Lenfant 1972; Feder 1980; Seymour, Dobson & Baldwin 1981; Seymour 1982; Pough & Lillywhite 1984; Heatwole & Dunson 1987). The blood of *Acrochordus* has a high Bohr effect to provide high utilisation of pulmonary O_2 stores during diving, and rapid reoxygenation of blood during respiratory periods (Johansen & Lenfant 1972; Seymour *et al.* 1981). The blood buffer capacity of aquatic squamates is similar to that of terrestrial species (Seymour 1982).

Lymphatic System

The lymphatic system returns interstitial fluid (lymph) from the tissues to the venous system. A major role is to return to the circulation plasma proteins that leak from the capillaries and to prevent vascular-interstitial fluid imbalance (oedema). The lymphatic system, which generally parallels the venous system, consists of superficial and deep lymphatic nets (microvascular vessels in most organs), which drain through lymphatic sinuses (or sacs, reservoirs) into lymphatic vessels and main lymphatic trunks to the venous system (Ottaviani & Tazzi 1977). However, there is considerable anatomical variation in reptiles. The reptilian lymphatic system lacks lymph nodes. In lizards, one pair of small, pulsating, vesicular lymph hearts are located near the first caudal vertebra, and their afferent and efferent lymph vessels have double valves. In snakes, the lymph hearts are postero-lateral to the cloaca, well protected against compression and trauma by the posterior ribs and vertebral zygapophyses. They communicate to the vertebral lymphatics via three valved openings, and to the renal portal veins via valved openings.

Immunology

Reptiles react to invasion by foreign material with an immunological response such as anaphylaxis and tissue rejection. Humoral (antibody-antigen) response and cellular (lymphocyte) responses occur. Specific plasma proteins, which are poorly characterised in squamates, agglutinate specific antigens to which the individual has been exposed. For example, blood of the boid *Morelia spilota* contains antibodies to antigens of infecting parasites. The immune response is temperature dependent, with a maximal response in antibody synthesis at a body temperature around 35°C. The thymus gland is presumably involved with aspects of adaptive immunity.

RESPIRATION

The primary role of the respiratory system is the supply of oxygen for cellular metabolism. Other roles include acid-base regulation (by CO_2 excretion), ionoregulation (nasal salt glands), chemoreception (olfaction and Jacobson's organ), thermoregulation (by panting or gular pumping), buoyancy (in aquatic species), vocalisation, and predator deterrence (by using lung expansion to wedge the body in crevices).

Pulmonary Gas Exchange

The respiratory system of a typical lizard consists of external nares, nasal cavity, pharynx, trachea, and two lungs. The lungs are the primary site of gas exchange. Air is usually inspired and expired via the external nares.

The external nares connect via a tubular vestibulum to a large nasal cavity, the *cavum nasi proprium* (Pratt 1948; Bellairs & Boyd 1950; Underwood 1957; Parsons 1970). A dorsal or tortuous pathway of the vestibulum prevents water or particulate material from entering the nasal chamber. Cavernous erectile tissue surrounding the vestibulum may function as an external nareal valve in most squamates. The nasal cavity is usually partly divided by a single concha (projection of the lateral wall) into a ventral choanal tube lined by non-sensory epithelium, and a dorsal nasal chamber lined by olfactory epithelium. The nasal cavity can be connected to the pharynx by a discrete nasopharyngeal duct, but in most lizards the nasal cavity essentially opens directly to the internal choanae. Jacobson's organ, an important olfactory structure, is also connected to the pharynx. The external (or lateral) nasal gland is external to the nasal capsule, but is connected by a duct to the vestibulum near the nasal cavity. This branched, tubular mucous gland excretes salt in many lizards, but not in snakes (except *Pelamis*).

All snakes have a simple, short vestibulum, except for *Laticauda* which has folds, and the nasal cavity has a moderately well-developed concha. Aquatic snakes tend to have a simple tubular nasal cavity with no concha. All snakes have short nasopharyngeal ducts and the choanae open far forward on the palate, because the snout is very short. Jacobson's organ is large, even in aquatic snakes which generally have reduced olfaction.

Lung structure is highly variable in squamates (Perry 1992). Most lizards and snakes have simple, single-chambered or transitional lungs, with a relatively small surface area for gas exchange. The lungs of *Physignathus* have small internal septae that form air pockets. The anterior half of the lungs are more vascularised than the posterior portion (Courtice 1981a). In contrast, goannas have heterogeneous, multi-chambered lungs, with considerable compartmentalisation and a high surface area. The parenchymal lining of the lung can be simple and flat, with trabeculae of smooth muscle and elastic tissues lying against the wall. The trabeculae may extend from the wall to form ediculae (with trabecular chambers wider than they are high) or faveoli (with trabecular chambers higher than they are wide). Various parenchymal types can all be found homogeneously or heterogeneously within a single lung, but generally one parenchymal type predominates. Edicular parenchyma predominates in *Acrochordus* and *Varanus*, and faveolar parenchyma in colubrid snakes and lizards.

The maximal lung volume of reptiles is generally greater than that of a mammal of equivalent mass, but has only about one hundreth of the surface area for gas exchange (Wood & Lenfant 1976); this reflects their lower metabolic requirements. More active squamates, such as goannas, have a larger lung surface area than less active species, because a greater fraction of their lung volume is compartmentalised rather than a decreased diameter of 'alveoli' (Tenney & Tenney 1970).

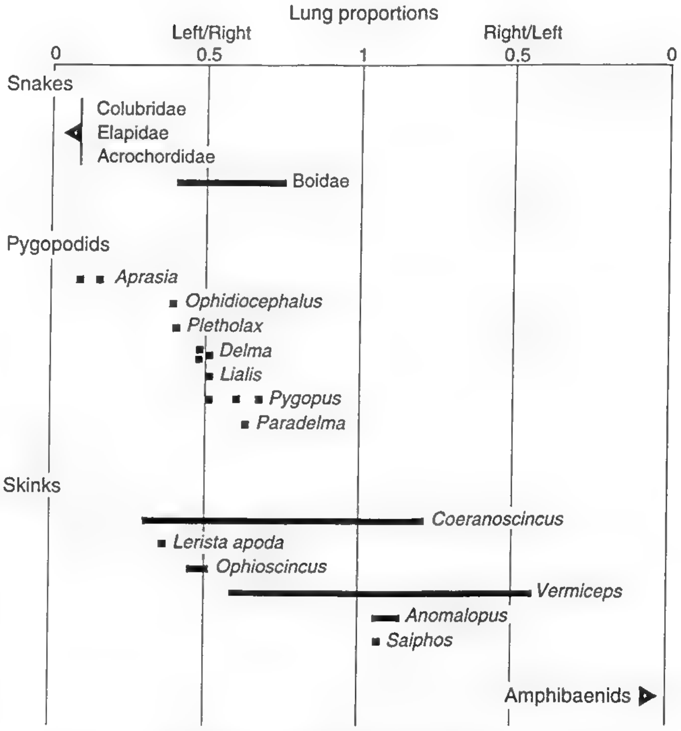

Figure 24.14 Relative proportions of the left and right lungs in various snakes and lizards. [W. Mumford]

The left lung is generally reduced in elongate squamates (Fig. 24.14). For example, the left lung is reduced to 8% and the right lung to 22% of snout-vent length in the limbless, highly-elongate *Lerista apoda* (Greer 1989). The left and right lungs of pentadactyl *Lerista* are both about 27 to 32% of the snout-vent length. The right lung is reduced in some skinks such as *Vermiseps*, but the left lung is reduced in *V. pluto*. In snakes, the left lung is typically reduced or vestigial, if not absent, but pythons have two well-developed lungs (Butler 1895). In some aquatic snakes (file snakes and hydrophiids) the large (right) lung has an avascular caudal portion that extends as far as the cloaca. In *Typhlops*, both lungs are well-developed and elongate, but the anterior (left) lung appears to exchange gases whereas the posterior (right) lung stores air (Robb 1960).

Lung ventilation is generally negative-pressure, aspiration breathing by movements of the rib-cage. Ventilation is typically a triphasic expiration-inspiration-expiration cycle, with a non-ventilatory (apneic) period of variable duration. The breathing portion of the cycle begins with active expiration by contraction of intercostal muscles and collapse of the lung, followed by passive inspiration to resting lung volume by elastic recoil of the rib cage, then active inspiration by contraction of other intercostal muscles. The glottis is then closed, and passive recoil of the rib cage creates a positive pressure in the lung during the apneic period. In some lizards, the glottis remains open and there is a passive expiration before the apneic period.

Most lizards ventilate their lungs by axillary movements. A few skinks, such as *Eremiascincus* and some *Lerista*, ventilate by vertical chest movements. This forms a ventral air pocket which enables expansion of the lungs while submerged in loose sand (Pough 1969b). Burrowing snakes may switch from lateral to vertical breathing movements when buried. Limbless, humus-living squamates, such as *L. apoda*, legless lizards and snakes, have a circumferential breathing system whereby contraction of the entire anterior body compresses the lung for expiration.

Resting respiration is typically discontinuous, with breathing periods (of multiple breaths) interspersed with often long apneic periods (for example, *Physignathus*; Courtice 1981a). Breath-to-breath rate is optimised to reduce the mechanical cost

(Frappell & Daniels 1991), but the average breathing rate over respiratory and apneic periods can be varied by modifying the relative length of the apneic periods. Much of the increase in lung ventilation during periods of elevated activity is the result of elevated tidal volume and decreased apneic period, rather than increased breath-to-breath ventilatory rate. In *Physignathus*, the breathing rate increases exponentially with temperature (Courtice 1981a).

The concept of respiratory regulation is complicated for reptiles because of their arrythmic breathing pattern, particularly at rest (Wood & Lenfant 1976). Reptiles tolerate large fluctuations of blood gas tensions during the ventilation/apneic cycle. Respiration is generally stimulated by CO_2, but tends to be less sensitive to CO_2 in diving and fossorial species. For example, respiration by the aquatic snake *Acrochordus* is more sensitive to O_2 than CO_2 (Wood & Lenfant 1976).

Cutaneous Gas Exchange

Squamate skin is highly keratinised to limit cutaneous evaporative water loss, and as a consequence there is limited cutaneous gas exchange. The cutaneous O_2 exchange is only about 2 to 3% of the total in terrestrial lizards and snakes, but is significant in aquatic lizards such as *Physignathus* (8% of total O_2 consumption rate, Courtice 1981b), filesnakes (8%, Standaert & Johansen 1974) and seasnakes (33%, Graham 1974a). Carbon dioxide is more readily exchanged across the skin than is O_2, because of its 20-fold higher diffusibility in water. Consequently, cutaneous CO_2 loss is substantial even in terrestrial reptiles (Graham 1974b; Standaert & Johansen 1974; Courtice 1981b). Over 20% of the CO_2 exchange is across the skin in the terrestrial *Boa constrictor*, 25% in the water dragon *Physignathus*, 33% in *Acrochordus* and 94% in *Pelamis*. However, no aquatic squamate has been shown to rely completely on cutaneous gas exchange. Furthermore, cutaneous gas exchange appears to be severely limited by diffusion and not amenable to physiological regulation (Seymour 1982).

Acid-base Balance

Acid-base balance is influenced by respiration, metabolism, excretion and body temperature. The pH is determined primarily by the CO_2/HCO_3^- buffer system, and hence the ratio of ventilatory CO_2 excretion to metabolic CO_2 production. Blood pH can be elevated in respiratory alkalosis by hyperventilatory excretion of CO_2, or by metabolic alkalosis due to renal excretion of H^+. Blood pH can be lowered in respiratory acidosis by hypoventilatory retention of CO_2 or metabolic acidosis as a result of renal retention of H^+. Body temperature also has a profound influence on acid-base balance because of the effects of temperature on metabolic rate, respiration and renal function, and a physico-chemical effect of temperature on the dissociation of water (Howell & Rahn 1976; Withers 1978).

Gas Exchange in Eggs

Most lizards and snakes lay eggs. Gas exchange during development occurs via pores in the eggshell. The water vapour conductance of flexible-shelled squamate eggs is up to 100 times greater than that of avian eggs (Deeming & Thompson 1991), but the rigid eggs of some geckos have a very low water vapour conductance, presumably because of the low numbers of pores. O_2 and CO_2 conductance is lower for squamate eggs than is predicted from the water vapour conductance, but it is not clear why. Gas exchange increases during incubation (Vleck & Hoyt 1991).

Metabolism

The metabolic rate of squamates varies with a number of environmental, physiological, behavioural, ecological and evolutionary variables. Metabolism is normally aerobic, but anaerobic metabolic pathways can be significant during intense activity or prolonged anoxia.

Most squamates have a considerable scope in metabolic rate, from a minimal standard metabolic rate (SMR) to a maximal metabolic rate (MMR). Some reptiles become dormant in the cold (brumation, hibernation) or heat (aestivation), and their metabolic rate is further depressed below SMR. Metabolic rate can also be depressed below SMR by anoxia.

The standard metabolic rate of squamates is very similar to that of other ectotherms (Bennett & Dawson 1976; Andrews & Pough 1985), but is about one fifth to one tenth of that of the basal metabolic rate of an equivalent sized bird or mammal, at an equivalent body temperature. The basal metabolic rate of an endothermic python (Van Mierop & Barnhardt 1978) is also about one fifth of that of a mammal at an equivalent body temperature.

The SMR is strongly influenced by body temperature, body mass and ecology (Andrews & Pough 1985). Day-active predators have a higher SMR than reclusive ones, which are higher than fossorial ones; herbivores have an SMR between that of day-active and reclusive predators. Body temperature has an exponential effect on SMR, with a Q_{10} typically between two and three (Bennett & Dawson 1976; Andrews & Pough 1985; Thompson & Withers 1992). Field metabolic rate (FMR) has been determined for many squamates (primarily lizards) to be about two to five times the SMR at 20° to 30°C.

The allometric relationship between metabolic rate and body mass is SMR = **a** $\text{Mass}^{\mathbf{b}}$, where **a** is the mass coefficient and **b** is the mass exponent. The interspecific value of **b** is about 0.8 for squamates (Andrews & Pough 1985), but there appear to be phylogenetic differences. For example, **b** is about 0.9 to 1.0 for goannas (Thompson & Withers 1992, 1993). The intraspecific allometric relationship is generally different from the interspecific relationship. The intraspecific mass exponents are generally less than 0.8, but vary dramatically from <0.6 to >1 for various species (Galvão, Tarasantchi & Guertzenstein 1965; Bennett & Dawson 1976; Andrews & Pough 1985; Dmiél 1986; Zari 1991; Thompson & Withers 1992).

Thyroid hormones (thyroxin, T_4; triiodothyronine, T_3) often affect the SMR of squamates, particularly if the body temperature is near the preferred range. Thyroxin administration generally elevates the SMR, whereas thyroidectomy decreases it.

Squamates commonly have seasonal patterns of inactivity (Gregory 1982). Hibernation is winter inactivity that occurs in temperate zones in response to cold and lack of food. Aestivation is summer inactivity that occurs in arid or tropical zones in response to heat and lack of water. The activity pattern may be bimodal, with periods of both hibernation and aestivation. The metabolic rate may decline during hibernation in some species, but with no metabolic depression other than a normal Q_{10} effect. However, the metabolic rate may be depressed even further in some species, by inverse acclimation. Some species remain active year-round and compensate for low temperatures by a partial thermal metabolic acclimation.

Squamates can rely on anaerobic metabolism of carbohydrate stores, especially glycogen, for considerable energy production during hypoxia, such as occurs during burst activity or extended submergence. Lactate is the primary metabolic endproduct of anaerobic metabolism for squamates, as for other vertebrates. The anaerobic capacity is about 1 mg lactate accumulated per gram body mass, and is essentially independent of body mass and body temperature (Bennett & Dawson 1976). The accumulation of lactate, and metabolic acidosis, make anaerobiosis a non-steadystate metabolic pathway and cause fatigue. Recovery from anaerobic metabolism is accomplished by either aerobically oxidising the accumulated lactate, or reconverting it to glucose and glycogen (Gleeson 1980). Some lizards and snakes can survive 20 to 90 minutes of anoxia (Belkin 1963).

TEMPERATURE

Almost all squamates are ectothermic because external heat sources determine their body temperature. Some thermoconform passively to their thermal environment, but others use behavioural and physiological mechanisms to regulate their body temperature (T_b). Only a few squamates are endothermic, using endogenous metabolic heat production for regulation of T_b.

Ectothermy

Thermoconformation. Some lizards and snakes, particularly nocturnal, fossorial, tropical or aquatic species, make little or no attempt to thermoregulate, and thermoconform to the ambient temperature. For example, the body temperature of many nocturnally-active geckos is essentially the same as the ambient air temperature (Fig. 24.16; Pianka & Pianka 1976). Aquatic species also thermoconform because the high specific heat and thermal conductivity of water preclude body temperature which is substantially above water temperature. For example, the T_b of the exclusively aquatic *Acrochordus arafurae* varies with water temperature from 22.6° to 35°C (Shine & Lambeck 1985). However, aquatic species such as *A. arafurae* can thermoregulate by selecting suitable microhabitats and there may be a slight body-water temperature gradient as a result of absorption of solar radiation (for example, *Pelamis platurus*; Graham 1974b).

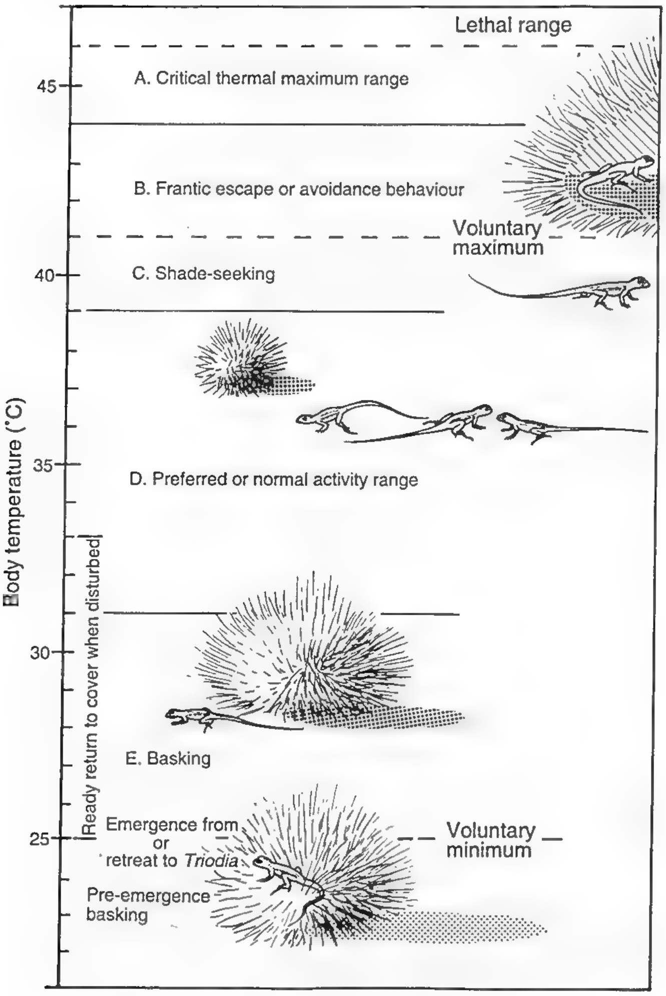

Figure 24.15 Range (A–F) of activity and thermoregulatory behaviours related to body temperature for the heliothermic dragon, *Ctenophorus fordi*. **A**, locomotor activity lost if avoidance behaviour unsuccessful; **B**, escape/avoidance behaviour of open areas intense, shade-seeking and deep entry into *Triodia*, panting, eventual heat prostration if avoidance behaviour unsuccessful; **C**, shade sought, body/tail elevated in the sun, *Triodia* avoided, alert but inactive, **D**, head/foreparts raised, alert foraging, mating and other behaviours, pigmentation light dorsally, dark ventrally; **E**, under protective fringe of *Triodia*, head/body in contact with the substrate, pigmentation dark dorsally, light ventrally. (Modified after Cogger 1974) [M. Thompson]

Thermoregulation. The thermal biology of many terrestrial squamates is dominated by the behavioural exploitation of solar radiative energy for the regulation of body temperature (Spellerberg 1972; Avery 1982; Bartholomew 1982; Huey 1982, 1991; Pough & Gans 1982; Bradshaw 1986; Heatwole & Taylor 1987; Greer 1989). Solar radiation can be used by basking in the sun (heliothermy) or by adpressing parts of the body to a substrate warmed by the sun (thigmothermy). Many snakes and lizards, including the skink, *Ctenophorus isolepis*, precisely maintain T_b substantially above ambient air temperature by behavioural and physiological means. Some reptiles, such as the thorny devil, *Moloch horridus*, have an intermediate pattern of relatively imprecise thermoregulation. For *Moloch*, this may reflect its sit-and-wait foraging mode.

Numerous behaviours are associated with heliothermic or thigmothermic thermoregulation. A range of the options available and the behaviours used or exhibited by *Ctenophorus fordi* under a variety of conditions is shown in Figure 24.15. Radiative heat gain will be maximised by choosing an appropriately exposed perch, and by flattening and orientating the body perpendicular to the sun's rays. Once the preferred body temperature is attained, shuttling between sun and shade can maintain body temperature within precise limits. Appropriate postures (for example, head directed at the sun to minimise exposed surface area and so the pale chest maximally reflects radiation) can minimise radiative heat gain, or the animal can move to shade or a cool burrow. Raising parts of the body away from the ground ('stilting') or ascending into high vegetation ('breezing') to the cooler air away from the hot ground surface minimises conductive heat gain and promotes convective heat loss. Panting or positive-pressure gular pumping can augment evaporative heat loss.

Numerous physiological adjustments also facilitate behavioural thermoregulation (Bartholomew 1982). Regulation of heart rate, cardiac output, and central and peripheral circulatory patterns can promote or retard heat gain. For example, the Bearded Dragon, *Pogona barbata* has a marked hysteresis between heating rate (which is rapid) and cooling rate (which is slower; Bartholomew & Tucker 1963). Temperature gradients can be maintained between the head and the body by passive (relative surface-to-volume ratios) or physiological means such as control of venous blood flow pattern, head orientation, or panting (Heath 1966; Webb & Heatwole 1971; Pough & McFarland 1976; Crawford, Palomeque & Barber 1977).

Many lizards can maximise radiative heat gain by adopting a dark colour, then reduce heat gain by 'blanching' to a paler colour. For example, the heliothermic dragon, *Ctenophorus nuchalis*, adjusts both dermal colour and peripheral blood flow; cool individuals have a low dermal reflectivity (about 23%) compared to warm individuals (about 32%; Rice & Bradshaw 1980). Many geckos, such as *Gehyra variegata*, exhibit profound colour change at different temperatures, generally being lightest at high temperatures (Rieppel 1971). Snakes, and some lizards, lack the capacity for colour change and may be restricted from occupying microhabitats with intense solar radiation.

Terrestrial or arboreal dragons are heliothermic with conspicuous thermoregulatory behaviours that maintain preferred body temperature between 34° and 37°C (Bradshaw & Main 1968; Cogger 1974; Bradshaw 1977, 1986). Some geckos are thigmothermic while inactive during the day, and thermoregulate by moving about under the exfoliating bark of dead trees (Bustard 1967) and some are even heliothermic (for example, the *Diplodactylus strophurus* group; Ehmann 1980). Little is known of the thermal biology of pygopodid lizards (Bradshaw *et al.* 1980). *Delma*, *Lialis*, *Aprasia* and some *Pygopus* are diurnal and bask, but some *Pygopus* are crepuscular or nocturnal (see Greer 1989). Terrestrial and fossorial skinks differ in thermal biology (see Greer 1989; Heatwole & Taylor 1987). Goannas are heliothermic and have high field body temperatures (34° to 38°C). Snakes, at least the diurnally active species, exhibit thermoregulatory behaviour and might be the most adept reptiles

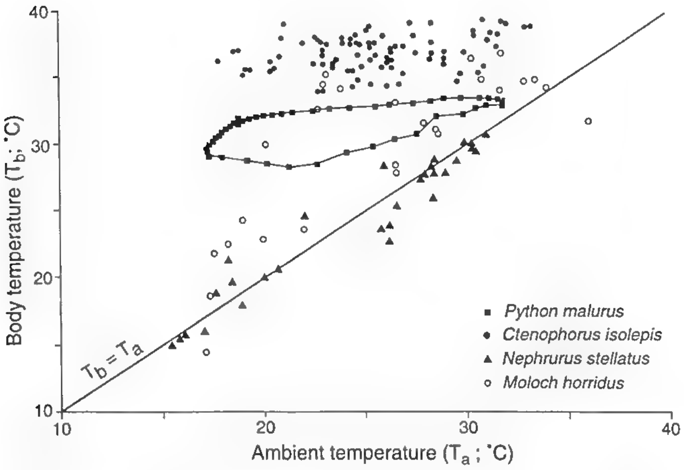

Figure 24.16 Relationship between body temperature and ambient temperature for the thermoconforming, nocturnal gecko, *Nephrurus stellatus*, the weakly-heliothermic agamid, *Moloch horridus*, the heliothermic agamid, *Ctenophorus isolepis*, and the endothermic brooding python, *Morelia spilota*, during a day-night cycle. (Data from Slip & Shine 1988; Withers unpub. data; Roberts unpub. data) [W. Mumford]

at controlling heating/cooling rates because of their elongate shape and extremely high surface-to-volume ratio. Extension of the body maximises surface area and facilitates heating, and coiling into a compact shape retards cooling. The elapid, *Pseudechis porphyriacus*, flattens its body markedly while basking, and often tilts perpendicular to the sun by using the tail as a prop (Heatwole & Taylor 1987). Its body temperature is maintained during activity between 28° and 31°C over a range of ambient temperatures and seasons (Shine 1987c).

At very high temperatures, dragons either seek cool burrows, or use arboreal perches for breezes; they will pant, but only as a last resort. When heat-stressed, geckos pant through the mouth and gular flutter. Skinks generally do not pant when heat-stressed (Greer 1989), except for members of *Tiliqua* (Heatwole *et al.* 1973). Goannas, like geckos, enhance evaporative cooling by gular pumping but do not pant like skinks.

Endothermy

Large reptiles have a low surface area to volume ratio and a high thermal inertia, and consequently warm and cool slowly. Endogenous heat production can elevate body temperature. However, the elevation of body temperature is only a degree or so, even for very large (17 kg) goannas.

A few squamates use endogenous metabolic heat production to elevate body temperature significantly above ambient temperature (Fig. 24.16). Some incubating female pythons use endogenous heat from muscle contractions to regulate egg temperature; the frequency of 'shivering' is inversely proportional to ambient temperature (Harlow & Grigg 1984; Charles, Field & Shine 1985; Slip & Shine 1988c). In contrast, non-brooding female and male pythons are ectothermic, and behaviourally thermoregulate by basking and selecting suitable thermal environments (Slip & Shine 1988b).

Preferred Body Temperature

Laboratory preferred body temperature, measured using an artificial thermal gradient, requires no cost and may not reflect a preferred field body temperature of a squamate experiencing various survival 'costs' of body temperature regulation (for example, predation, feeding, reproduction, metabolic cost of locomotion and territorial defence). In addition, laboratory and field preferred body temperature can vary between sexes, at different times of the day or year, and with physiological state (for example, when digesting, or incubating eggs). Nevertheless, laboratory and field preferred body temperatures are generally well correlated and some phylogenetic trends are evident (see Heatwole & Taylor 1987; Greer 1989). Preferred body temperature tends to be high for dragons and goannas, but low and variable for skinks and snakes. Nocturnal, fossorial and aquatic species generally have low preferred body temperatures. Geckos are somewhat enigmatic because they often have low field body temperatures when active (being nocturnal) but have relatively high laboratory preferred body temperatures.

The frequency distribution of body temperatures is generally left skewed towards lower temperatures (see Pianka 1969a, 1970c, 1971c). A left-skewed temperature distribution might reflect the dual-setpoint mode of behavioural thermoregulation by squamates (Berk & Heath 1975) or an exponential effect of temperature on physiological rate functions (DeWitt 1967).

Thermal Tolerance Range

The body temperature of lizards and snakes can vary widely. A squamate is 'ecologically' dead below a critical minimum temperature (CT_{min}) at which it is incapable of righting itself, and above a critical maximum temperature (CT_{max}) at which it is incapable of escape. There is generally a voluntary minimum temperature ($> CT_{min}$) below which the animal is inactive, and a voluntary maximum temperature ($< CT_{max}$) above which they are inactive. There are also extreme lower and upper lethal temperatures, at which the animal rapidly dies. The laboratory and field preferred T_b falls between CT_{min} and CT_{max}. For example, the CT_{min} of the skink, *Tiliqua rugosa* is 3.5°C whereas the CT_{max} is 43.0°C. The upper lethal temperature at which *T. rugosa* stops breathing is 45.5°C, the laboratory preferred T_b is about 32°C, and the field T_b is about 34.3°C.

Regulation of body temperature within some preferred range is important because most physiological functions are maximal at some optimal body temperature (Huey 1982, 1991). Thermal behaviour and physiological performance therefore tend to be coadapted (Huey 1982). For example, sprint speed and preferred body temperature are coadapted for skinks with a high preferred body temperature (Huey & Bennett 1987), and the aerobic metabolic scope is maximal for *T. rugosa* at a body temperature of 33.4°C, which is similar to field (34.3°C) and laboratory (32.6°C) preferred body temperatures (Wilson 1974).

Field and laboratory preferred body temperatures are highly correlated with critical thermal maximum (CT_{max}) but not critical thermal minimum (CT_{min}) (Fig. 24.17). Many geckos, legless lizards and dragons have a high CT_{max}, of 40° to 44°C. Field preferred body temperature is higher for terrestrial heliothermic skinks (25° to 36°C) than fossorial or nocturnal skinks (20° to 26°C). Terrestrial skinks also have a higher laboratory preferred

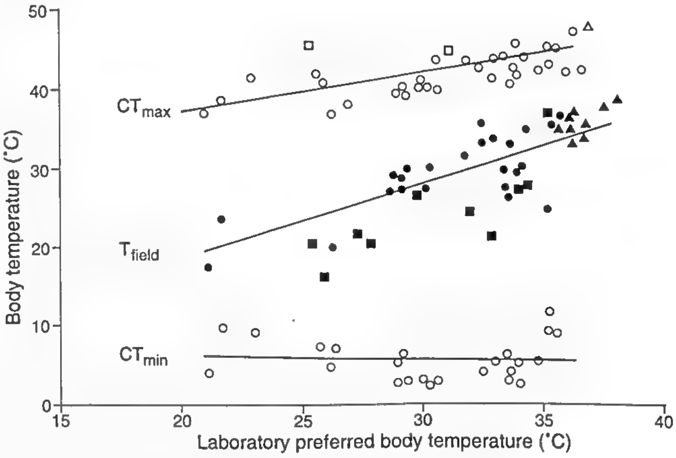

Figure 24.17 Relationship between critical thermal minimum temperature (CT_{min}), field body temperature (T_{field}) and critical thermal maximum temperature (CT_{max}) for a variety of lizards, as related to their preferred body temperature in the laboratory; open circles, skinks; squares, gekkos; triangles, agamids. (Data primarily from Heatwole & Taylor 1987; Greer 1989) [W. Mumford]

body temperature (29° to 36°C) and higher CT_{max} (40° to 46°C) than fossorial or nocturnal skinks (18° to 27°C and 34° to 44°C). Field and laboratory preferred body temperatures for diurnally active snakes are generally 25° to 34°C, and CT_{max} is about 40°C.

EXCRETION

Body Water and Solutes

The total body water content of lizards and snakes is generally about 65 to 75% of body mass (Thorson 1968; Minnich 1982), and is similar for arid and non-arid reptiles (Heatwole & Veron 1977). It is partitioned between the intracellular space (35 to 55%) and the extracellular space (25 to 35%). The extracellular space is further partitioned into plasma volume (about 5%) and interstitial fluid volume (20 to 30%). For example, the total body water content of the agamid, *Ctenophorus ornatus*, is 73.5% of body mass; the extracellular space is 25.5% (5.1% plasma) and the intracellular space is 48.0% (Bradshaw 1970). Some reptiles store water in extracellular fluid compartments, such as bladder, lymph sacs and gut.

Body fluid osmotic concentration is generally 300 to 400 mOsm. Na^+ and Cl^- are the major osmolytes (each at about 140 to 160 mM). Their concentrations can vary dramatically with hydration state for terrestrial species, especially desert reptiles, and are high and variable for marine snakes. Plasma K^+, Ca^{2+}, and Mg^{2+} are generally regulated precisely at 2 to 6 mM. Nitrogenous wastes are present at low concentrations. Intracellular solute concentrations differ substantially from plasma concentrations; the Na^+ and Cl^- concentrations are low and the K^+ concentration is high.

Many squamates tolerate dehydration of up to 30 to 40% loss of body mass. Arid species do not have a higher body water content or greater dehydration tolerance than mesic species (Heatwole & Veron 1977). Tolerance of osmotic and ionic concentration is generally more important than physiological maintenance of normal solute concentrations. For example, many dragons (*Amphibolurus*, *Ctenophorus*, *Pogona*) and skinks (*Tiliqua*) become markedly hypernatremic during drought, with plasma Na^+ levels exceeding 200 mM (Bradshaw & Shoemaker 1967; Bradshaw 1970; Braysher 1971, 1972). Dragons lack functional salt glands and accumulate Na^+ during drought, then excrete it when they rehydrate after rain.

Water Balance

The preformed water content of food varies dramatically, and the physiologically 'available' amount of water is inversely dependent on the ion and nitrogen contents. Many animal and plant food items have a high water content and may be approximately isoosmotic and isoionic to animal body fluids, but some (for example, marine algae and invertebrates, and desert plants and invertebrates) are low in water and/or are hyperionic and hyperosmotic.

Most reptiles drink fresh water when it is available. Some, such as *Tiliqua rugosa*, use their tongue to drink from puddles (Simpson 1973). *Hypsilurus spinipes* has an unusual drinking behaviour, and draws water into its mouth rather than lapping with its tongue (Longley 1943). Snakes drink by a pumping action of the lower jaw, produced by the masticatory muscles. Behaviours may facilitate drinking of rain water in arboreal and sandy environments, which are not conducive to puddle formation. Geckos lap water from moist vegetation, substrates or themselves. *Pogona vitticeps* elevates its body and laps water that drips to its mouth (Fitzgerald 1983). No reptiles have been shown to induce condensation by behavioural actions, such as entering a warm, humid environment (Lasiewski & Bartholomew 1969).

'Blotting paper' skin has been described for a number of lizards, but its role in absorbing water is best understood for the thorny devil, *Moloch horridus* (Bentley & Blumer 1962; Gans, Merlin & Blumer 1982; Sherbrooke 1993; Withers 1993). The surface architecture of the skin transports a water film by capillarity over most of the body surface to the mouth, where it is swallowed. The skin of *Physignathus lesueurii* similarly holds a surface water film, but these lizards apparently do not drink it (Heatwole & Taylor 1987). Some fossorial lizards and snakes absorb water from soil by capillary flow of water into the mouth, or by lapping at the sides of the mouth with the tongue (Krakauer, Gans & Paganelli 1968). Water flux through the skin is significant for aquatic squamates; freshwater species have more permeable skin than marine species (Dunson 1978, 1980; Lillywhite & Maderson 1982).

The biochemical synthesis of water by cellular metabolism can be an important source of water, especially for terrestrial reptiles during prolonged drought or dormancy. The metabolic production of water is greatest for carbohydrates, intermediate for lipids, and lowest for protein (Withers 1992).

A low evaporative water loss (EWL) is one of the major adaptations, or preadaptations, of squamates for terrestriality. Arid species have a lower EWL than semi-arid and mesic species (Heatwole & Veron 1977; Mautz 1982). This might be either genetically-based or acclimational. The EWL depends on body mass; the allometric relationship is of the form EWL m Mass^b, where b is about 0.6 to 0.8 (Mautz 1982). EWL increases exponentially with temperature. It also increases during moulting, although at least part of the increase might be ascribed to increased activity during shedding.

Total EWL can be partitioned into cutaneous and respiratory components. For small geckos, dragons and skinks, cutaneous EWL is 40 to 70% of the total at 20°C, and is a lower percentage at 30°C (Dawson, Shoemaker & Licht 1966). For two dragons, cutaneous EWL is 19 to 26% of the total at 35°C (Bradshaw 1970). The evaporative water loss is much lower than the rate of evaporation from a free water surface, reflecting the presence of lipids in the keratinised epidermis rather than the keratin layers *per se* (Roberts & Lillywhite 1980; Lillywhite & Maderson 1982). The keratin layers probably also act as diffusion barriers to water exchange. Scales *per se* do not limit the EWL, as mutant scale-less snakes have a typical EWL (Licht & Bennet 1972; Bennett & Licht 1975).

The eyes can have an exceedingly high EWL (up to 65% of the total EWL) because the corneal surface is essentially a free water film (Green 1969; Mautz 1980, 1982). Some lizards may restrict ocular water loss by partially closing the eyes for example, when basking. Eyelid type is often associated with body size and habitat (Greer 1983a). Some small and/or desert skinks have a transparent window in the lower eyelid, that may reduce ocular EWL without impairing vision. Large and/or non-desert species lack such a window. Snakes, geckos, legless lizards and a few skinks have a fixed and transparent scale (spectacle) covering the cornea. The spectacle restricts EWL from the eye (Mautz 1982), and is also associated with fossoriality, providing physical protection of the eye.

The respiratory water loss of reptiles is low because of their relatively low metabolic rates, and can be further minimised by a high pulmonary O_2 extraction and respiratory nasal countercurrent heat exchange. In addition, nasal salt gland secretion can be used to humidify the inspired air, thus conserving water. For example, the skink *T. rugosa* is often observed with salt encrustations around its nostrils, suggesting such a role of salt gland secretion in humidifying the inspired air.

The water content of the faeces and urine, which are voided together, is determined by the extent of cloacal water reabsorption. The water content of excreta is about 30 to 40% for terrestrial, particularly desert, species and is higher for species with more water available.

The overall flux of water through the body varies depending on the specific conditions at the time of measurement, but is generally lower for xeric than mesic and aquatic squamates. The water turnover rate is also markedly influenced by body mass. For arid and semi-arid zone lizards, water turnover rate (ml day^{-1}) is 20.5 kg$^{0.91}$, in approximate proportion to metabolic rate. In tropical and sub-tropical zone lizards, it is 45.0 kg$^{0.66}$, in approximate proportion to body surface area (Nagy 1982).

Excretory Organs

A variety of organs, including the skin, kidneys, intestine and cloaca, and nasal and lingual salt glands, function directly or indirectly in water and solute balance (Bentley 1976; Dantzler 1976; Dunson 1976; Minnich 1979, 1982).

The paired retroperitoneal kidneys are elongate and lobed organs, usually of equal size, located posteriorly on the dorsal surface of the body cavity; they may fuse posterior to the cloaca. The ureters are short, and an elongate and pear-shaped bladder, with a single ventral opening into the cloaca, is often present.

The kidneys are more elongate and lobulate in snakes and lizards with reduced limbs; the right kidney is often larger and extends more anteriorly in snakes, but there is little or no asymmetry in legless lizards (Underwood 1957; Robb 1960; Shine 1991a). In many snakes the elongate ureters dilate near the openings into the cloaca as a urinary bladder is absent. The embryological origins and development of the reptilian kidney have been reviewed by Fox (1977). The mesonephric kidney is functional in embryonic development, but the metanephric kidney is functional in adults.

The renal vasculature consists of a variable number of renal arteries, a renal portal system arising from various veins (pelvic, caudal, intercostal, cutaneous, spinal), and renal veins. The glomerulus is poorly developed. There are about 500 to 20 000 glomeruli per kidney, depending on body size (Fox 1977; O'Shea, Bradshaw & Stewart 1993). Lizards tend to have smaller glomeruli (50 to 70 µm diameter) than snakes (60 to 120 µm), which also tend to have fewer glomeruli and nephrons with aglomerular diverticula.

The generalised nephron consists of a pavement epithelium (Bowman's capsule) surrounding the glomerulus, a short and narrow partly-ciliated neck, a glandular proximal tubule segment, a fine tubular segment, a distal segment, and a terminal segment leading to the collecting duct. The terminal segment hypertrophies in male lizards and snakes to form a sexual segment. The tubular arrangement of each nephron is a linear array of numerous convolutions, a hair-pin bend, and a termination at right angles into the collecting duct. The total length of the nephron is about 2 to 4 mm.

The glomerular filtration rate (GFR) varies dramatically with hydration state, being highest for water-loaded individuals and lowest for dehydrated or salt-loaded individuals (Dantzler 1976). It also increases with temperature for example, about 10-fold from 14° to 24°C in *T. rugosa* (Shoemaker, Licht & Dawson 1966). The glomerular filtrate is highly modified during its passage through the nephron. Typically, more than 95% of the filtered water is reabsorbed and so ureteral urine is much reduced in volume. Most solutes are reabsorbed from the filtrate, but K^+, H^+, NH_4^+, urate, PO_4^{3-}, and some organic acids are actively secreted. Ureteral urine is isoosmotic or hypoosmotic to plasma; apparently no reptile can produce a hyperosmotic ureteral urine (but see below). The volume and composition of the ureteral urine is subsequently modified in the colon and cloaca.

The colon, cloaca and urinary bladder can highly modify ureteral urine before it is voided (Minnich 1979, 1982). Ureteral urine enters the distal cloaca via the ureteral openings, and it can be refluxed retrogradely into the proximal cloaca and colon, which is the major site of urine storage in most lizards and snakes. Urine can be stored in a urinary bladder, if present, and sometimes is modified before it is voided or returned to the colon/cloaca.

Active solute (especially Na^+; Bentley & Bradshaw 1972) reabsorption by the colon/cloaca, and osmotic water reabsorption, highly modifies the urine and promotes urate precipitation, which further removes solutes (especially Na^+, K^+ and NH_4^+) both as urate salts and as ions trapped within the precipitated urate. Squamates are unable to osmotically concentrate the voided urine to higher than the plasma osmotic concentration by the colonic/cloacal solute-linked reabsorption of water. However, the Lake Eyre Dragon, *Ctenophorus maculosus*, appears to be exceptional in that its voided urine can be more osmotically concentrated than plasma. The urine is presumably osmotically concentrated by solute-linked water reabsorption in the colon/cloaca (Braysher 1972, 1976).

Salt glands have evolved independently in several lineages of marine, estuarine and terrestrial squamates (Dunson 1976). Salt glands are derived from nasal glands in lizards and lingual glands in snakes. Salt glands are found in some dragons, skinks, goannas and geckos, but their role is most developed in goannas and skinks (Saint Girons & Bradshaw 1987). There are no obvious correlations between nasal salt gland development and geographic distribution, or diet. Salt glands excrete hyperosmotic solutions of Na^+, Cl^-, K^+ and HCO_3^-. The salt glands of an estuarine goanna (*Varanus semiremex*) secrete 460 to 750 mM Na^+, 600 to 800 mM Cl^-, and 35 to 80 mM K^+ (Dunson 1974). The salt glands of marine reptiles secrete primarily Na^+ and Cl^-. *Pelamis platurus* secretes about 650 mM NaCl, but salt glands of terrestrial species excrete high concentrations of Na^+ or K^+ as required.

Nitrogenous Wastes

The primary nitrogenous waste is urate in most squamates (Dantzler 1976; Minnich 1979, 1982). Urate is highly insoluble (Na urate, 6.8 mM; K urate, 12 mM), and solute-linked reabsorption of water from the colon/cloaca precipitates most of the urate present in ureteral urine. Urate precipitation also eliminates ions, particularly K^+ (Minnich 1979, 1982). Ammonium is a significant constituent (2 to 5%) in the precipitated cloacal urine of non-boid snakes and goannas, and significant levels of urea (2 to 5%) are excreted by a few aquatic squamates. Seasnakes excrete primarily uric acid, but *Laticauda colubrina* excretes up to 60 mM ammonia (Schmidt-Nielsen & Mackay 1972).

Water Balance and Excretion in Eggs

Some squamates lay cleidoic, parchment-shelled or calcareous-shelled eggs (Packard, Tracy & Roth 1977; Minnich 1979). Parchment-shelled eggs are typically buried in soil, and absorb water during development by hydraulic/osmotic force. Water absorption appears to be essential for normal development. Selection of a suitably humid environment is important for egg deposition, as the subsequent water balance state of the developing embryo affects hatchling size and hatching success (Muth 1980; Packard & Packard 1980; Tracy 1980; Lillywhite & Ackerman 1984; Somma 1989). The calcareous eggshell of some geckos primarily exchanges respiratory gases rather than water (Bustard 1968a).

Squamate embryos osmoregulate during development. Plasma osmotic concentration and tissue water content are independent of the extent of water absorption by the egg, but hatchling size depends on the magnitude of the water uptake (Vleck 1991). Mineral requirements for embryonic development are derived from the eggshell and especially the egg fluids. The first half of embryonic development in *Pogona barbata* is slow and calcium is mobilised from the yolk, whereas the second half of development is rapid and 40% of the required calcium is mobilised from the shell (Packard, Packard, Miller, Jones & Gutzke 1985).

Developing snake embryos form about equal amounts of ammonia and urea; relatively little uric acid is produced during oviparous or viviparous development (Clark 1953; Clarke & Siskin 1956). Developing lizard embryos produce both urea and urate (Athavale & Mulherkar 1967). Ammonia formation allows gaseous nitrogen excretion across the eggshell as ammonia. Urea accumulation allows osmotic absorption of water from the substrate (insoluble urate formation does not provide an osmotic force for water absorption).

SENSE ORGANS AND NERVOUS SYSTEM

Sense Organs

The principle senses of squamates include mechanoreception (touch, hearing and gravity), chemoreception (taste and smell), photoreception (lateral and median eyes), and thermoreception. These sensory modalities are important in most terrestrial squamates, but are reduced in marine and fossorial species. Goannas and dragons rely primarily on visual stimuli whereas skinks and geckos depend more on a combination of tactile, olfactory and vocal stimuli (Evans 1961). Vision and olfaction dominate the sensory modes for intraspecific communication in snakes (Bellairs 1969).

The epidermis has few external mechanoreceptors, but there are some intraepidermal endings, connective tissue mechanoreceptors lacking Schwann cells, connective tissue receptors with Schwann cells, and Merkel cells (von Düring & Miller 1979). Branched intraepidermal sensory nerve endings in the hinge regions may be stretch receptors. The unencapsulated and encapsulated nerve endings of the dermis may be pressure, stretch and rapidly-adapting mechanoreceptors. Merkel cells in the dermis and epidermis may be slow-adapting mechanoreceptors. Tactile sense organs (touch papillae) are also present, some of which are highly modified to form a tactile area with epidermal bristles, separated from the rest of the scale by a groove. For example, the second infralabial scale of *Delma* is covered by a number of scale organs, some of which bear hairs (Underwood 1957). The joint capsules also contain free nerve endings that convey information concerning joint position and movement.

The auditory system consists of outer, middle and inner regions. The typical external ear is a slight depression situated postero-laterally on the head (Fig. 24.18; Wever 1965; Baird 1970). Some lizards have a deep external ear meatus, which widens to a large tympanic membrane (for example, some geckos and terrestrial skinks). The middle ear cavity is connected to the pharynx by the auditory (eustachian) tube (Fig. 24.18). The extrastapes (extracolumella) and stapes (columella) span the air gap between the tympanic membrane and the inner ear and mechanically transmit sound vibrations. The short extrastapes, which is firmly attached to the tympanic membrane, articulates with the paraoccipital process of the skull, the quadrate of the lower jaw, and the stapes. The medial end of the stapes lies within the opening of the vestibular window of the inner ear. The inner ear consists of a complex membranous system filled by endolymph, and surrounded by perilymph. The saccule and utricle of the inner ear contain sensory maculae which respond to gravity. The three semicircular canals contain maculae which respond to movement of the endolymphatic fluid, thus giving a three-dimensional sensation of movement. The elongate cochlear duct provides auditory sensation and frequency discrimination. *Tiliqua rugosa* has a maximal sensitivity at about 800 Hz, and markedly reduced sensitivity above 2500 Hz (Holmes & Johnstone 1984a). Hearing sensitivity is dependent on body temperature and hydration state, and it increases in spring (Holmes & Johnstone 1984b; Holmes, Fergusson & Johnstone 1984).

The external ear is reduced or absent in a variety of lizards and most legless lizards (Greer 1989). In some burrowing forms, the tympanic membrane is thickened and reduced, the tympanic cavity is reduced, the stapedial footplate is expanded, and the extrastapes articulates firmly with the quadrate. The tympanum and middle ear is almost completely absent in some legless lizards, such as most *Aprasia* (Underwood 1957). These adaptations might reflect the cranial strengthening required by fossorial species, and the transmission of substrate sound vibration to the inner ear by the lower jaw. The inner ear, unlike the external and middle ear, is less modified. For example, the inner ear of pygopodid lizards resembles that of geckos (Shute & Bellairs 1953), to which they are closely related. In some geckos, parts of the endolymphatic sacs are enlarged for calcium storage, and may even extend through openings in the skull posteriorly along the muscles of the neck.

Snakes have no obvious external ear, and the middle ear lacks a tympanic membrane and cavity, and Eustachian tube. The stapedial footplate is expanded in many burrowing snakes to facilitate sound transmission from the quadrate of the lower jaw to the inner ear.

Chemoreception

Detection of scents from the environment, other animals, and in particular from conspecific animals, is important for many terrestrial squamates (Allison 1953; Parsons 1967; Bertmar 1969;

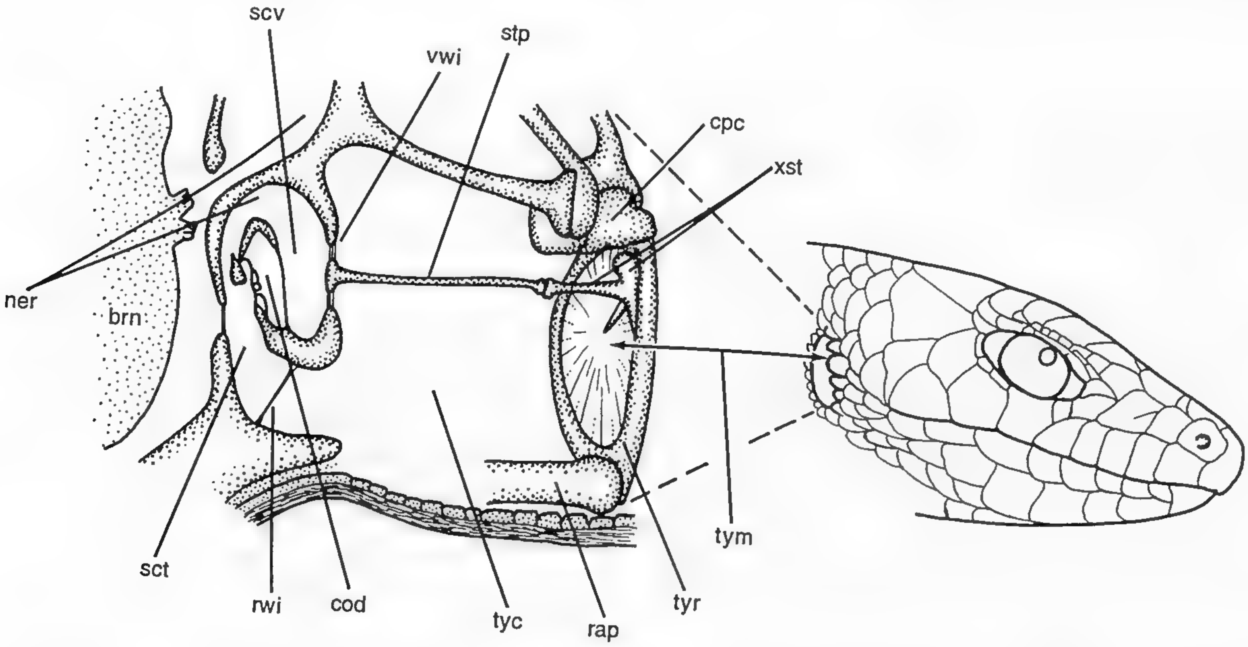

Figure 24.18 Auditory structure of the skink, *Ctenotus grandis*, showing the outer, middle and inner ear of a typical terrestrial lizard. **brn**, brain; **cod**, cochlear duct; **cpc**, cephalic condyle; **ner**, eighth nerve; **rap**, retroarticular process; **rwi**, round window; **sct**, scala tympani; **scv**, scala vestibuli; **stp**, stapes; **tyc**, tympanic cavity; **tym**, tympanum; **tyr**, tympanic ring; **vwi**, vestibular window; **xst**, extrastapes. (Modified from Storr, Smith & Johnstone 1981; Wever 1965) [M. Thompson]

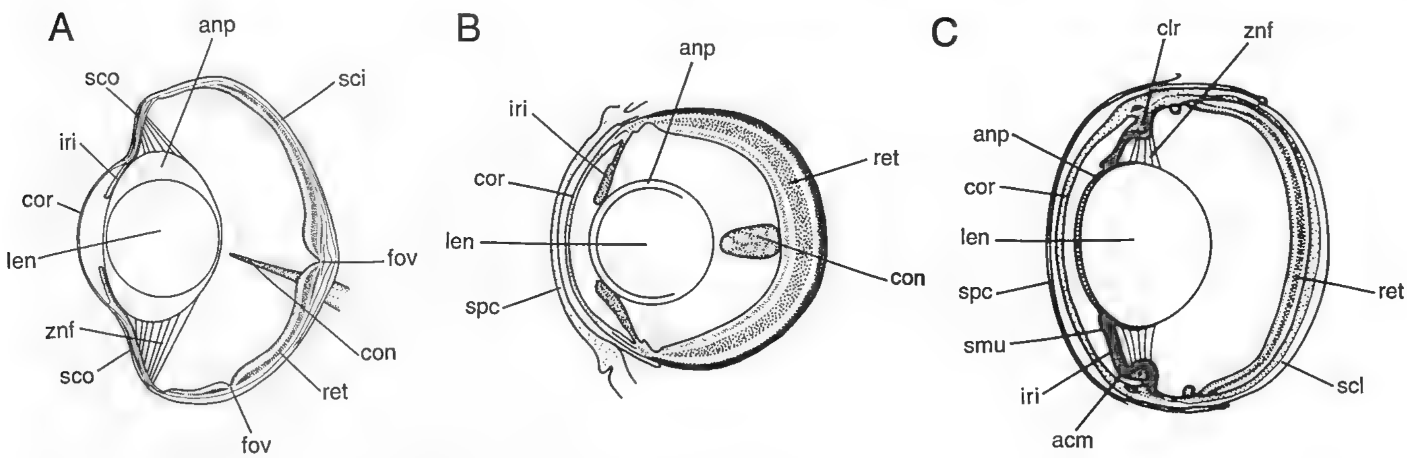

Figure 24.19 Diagrams of eye structure of squamates. **A**, a typical diurnal, terrestrial lizard, *Anolis lineatopus*; **B**, the reduced eye of a pygopodid, *Aprasia repens*; **C**, a snake, *Natrix natrix*. **acm**, accomodation muscle; **anp**, anterior pad of lens; **clr**, ciliary roll; **con**, conus; **cor**, cornea; **fov**, fovea; **iri**, iris; **len**, lens; **ret**, retina; **scl**, sclera; **sco**, scleral ossicle; **smu**, sphincter muscle; **spc**, spectacle; **znf**, zonular fibres. (After A, Underwood 1970; B, Underwood 1957; C, Walls 1942). [M. Thompson]

Burghardt 1970; Madison 1977). Odours for communication may be derived from hormones in urine, or faeces, but are commonly produced by specialised integumentary scent glands. The importance of olfaction varies greatly in different squamates. Taste is a poorly developed sense; some taste buds are found in the lining of the pharynx and a few are located on the tongue.

Jacobson's vomeronasal organ is an important chemosensory structure in many squamates, particularly in terrestrial groups, such as goannas, but is poorly developed in arboreal species. The organ in adults is nearly spherical, and the ventral side is invaginated to form a mushroom-shaped body. The hollow space of Jacobson's organ retains its connection (Stenson's duct) to the pharynx. The dorsal and lateral walls are covered by a sensory epithelium that resembles the olfactory epithelium of the nasal cavity. It is widely believed that scent is directly transferred to the ducts of Jacobson's organ by the tips of the tongue, but recent evidence suggests that scent is first transferred from the tongue to the anterior lingual processes, then to the ducts of Jacobson's organ (Oelofsen & van den Heever 1979; Young 1990).

Photoreception

Light reception is an extremely important sense for most squamates. The eyes are the primary sensory organs for light reception, although a median (parietal) eye is also present in reptiles and it generally retains a photoreceptive role. The infrared detection by crotaline and boid snakes is also a photoreceptive system, although the actual sensory modality is temperature detection.

The squamate eye generally resembles that of other vertebrates, but there are numerous differences peculiar to squamates and particular modifications in specific groups, especially snakes (Walls 1942; Underwood 1970). Some arboreal species have greater eye mobility but a more limited visual field than terrestrial species.

The large orbits of a typical, diurnal lizard contain the eye, ocular muscles, optic nerve, vascular system, and connective tissues (Underwood 1970). The cornea of the eye is delimited from the sclera by a marked change in radius of curvature (Fig. 24.19A). The sclera contains bony and cartilaginous sclerites which maintain the concavity of the corneal-scleral junction against the intraocular hydrostatic pressure. The clear, soft lens is covered by an epithelial layer which is equatorially thickened as an annular pad. The lens is held in place by zonular fibres extending from the ciliary body, an annular structure located internal to the ring of sclerites. Accomodation (near focussing) is accomplished by radial muscle fibres of the ciliary body (Brücke's and Crampton's muscles) which draw it against the annular pad and squeeze the lens to increase its curvature. Radial and circular muscle fibres of the iris, an anterior extension of the ciliary body, form and control the diameter of the usually circular pupil. The retina consists of an avascular pigmented epithelium, a layer of rod and cone photoreceptors, and layers of neural cells. It extends on the inner surface of the back of the eye from the point of entry of the optic nerve to the ora serrata at the point of inflexion of the sclera. A part of the retina may form a fovea to provide high visual acuity. The retina contains only cone photoreceptor cells in a typical diurnal lizard. The cones contain yellow oil droplets to minimise chromatic aberration by screening out short wavelengths (blue, violet). A highly vascularised conus papillaris, consisting of pigmented neuroglia, may provide nutrients to the eye.

Arboreal geckos have larger eyes than terrestrial geckos (Werner 1969; Pianka & Pianka 1976), possibly because they require a wider visual field. All Australian geckos have a spectacle and a vertical pupil that constricts to form four or five separate pinholes. The retina, which lacks a fovea, appears to contain only rods, but some of these may be derived from cones. The rods may lack oil droplets, have only small oil droplets, or have colourless oil droplets. Pygopodids, like geckos, have a vertical pupil and a spectacle, their retina lacks a fovea, and their photoreceptors lack oil droplets. In *Lialis*, the ciliary body is fairly muscular and the lens has an annular pad. *Delma* has some ciliary muscle, but the lens lacks an annular pad, and *Aprasia* has a markedly reduced ciliary body (Fig. 24.19B).

The eyes of snakes (Fig. 24.19C) and the associated visual parts of the brain are considerably different from those of lizards (Walls 1942; Underwood 1970). These uniquely ophidian structures presumably reflect a reduced eye structure in ancestral fossorial snakes (*cf. Aprasia*), and the subsequent return to terrestrial and arboreal environments required the redevelopment of eye structures. The ophidian cornea and sclera have a similar radius of curvature, and there are no sclerites. The ciliary body is reduced to a non-functional 'ciliary roll'. The nearly spherical, hard lens often has an anterior pad. The lens is yellow in many diurnal species to minimise chromatic aberration. Accomodation is achieved by contraction of circular muscles at the base of the iris, which increases the intraocular pressure in the posterior chamber and forces the lens anteriorly. In some snakes, accomodation is also accomplished by direct deformation of the lens by the pupillary sphincter muscles. The retina has a blood supply, and some species also have a vascular conus. Ophidian cones have a unique structure, having been derived from the rods of fossorial ancestors. Some diurnal snakes have lost the rods, and only have cones. All ophidian photoreceptors lack oil droplets.

The midbrain of vertebrates has two dorsal outgrowths, an anterior parietal body (parapineal organ) and a posterior pineal body (epiphysis); primitively, both have photoreceptive structures (Eakin 1973; Quay 1979). In lizards, both the parietal body and pineal body develop, to form the parietal eye and the pineal gland respectively. In snakes, the parietal body fuses at an early embryonic stage with the pineal body and only a single epiphysis develops.

The integument over the parietal eye often forms a clear cornea, but may be pigmented (Quay 1979). The parietal eye is typically a simple epithelial vesicle, in which the outer epithelium is modified to form a lens and the inner wall to form a retina; additional vesicular structures may sometimes be present. The retina of the parietal eye is similar in many respects to that of the lateral eyes, but the photoreceptors project towards, rather than away from, the light source. Functional light reception has been demonstrated by physical, electrophysiological and behavioural means. The parietal eye probably provides photic information for behavioural responses, such as thermoregulation, and endocrine functions, such as reproduction, which are related more to light intensity and to photoperiod than image formation (see Quay 1979).

The parietal eye is reduced and is not externally visible in many nocturnal or crepuscular lizards, such as geckos, legless lizards, a few skinks, and particularly species that live at low latitudes (Gundy, Ralph & Wurst 1975; Quay 1979).

Thermoreception

'Hot' and 'cold' thermoreceptors and pain receptors are present in the skin. Anterior hypothalamic and cutaneous thermoreceptors control themoregulatory behaviour (Berk & Heath 1975). The specialised infrared thermoreceptors of boid and crotalid snakes have been well-characterised (Barrett 1970; von Düring & Miller 1979). Boid snakes have pits sensitive to radiant heat that can be located on the supra-labial, infralabial, rostral and probably the mental scales (Bullock & Barrett 1968; Barrett 1970; Maderson 1970a; von Düring & Miller 1979).

Central Nervous System

The cranium consists of ethmoid, orbitotemporal, otic and occipital regions (Starck 1979). The brain usually lies parallel to the basal axis of the neurocranium (Fig. 24.20A), but the forebrain may be inclined in species with large eyes. The shape of the skull is influenced more by feeding apparatus and relative development of the sensory organs, especially the nose, eyes and ears, than brain shape. Brain size is often markedly smaller than the endocranial volume. The size of the brain varies with taxonomic affinity, terrestriality, arboreality or fossoriality, and body mass (Platel 1979).

The brain develops from the neural tube in three main sections, the forebrain (prosencephalon), midbrain (mesencephalon), and the hindbrain (rhombencephalon), which is continuous with the spinal cord (Fig. 24.20A; Senn 1979). The forebrain has an anterior telencephalon and more posterior diencephalon. The telencephalon consists primarily of the olfactory bulbs and lobes, the cerebral hemispheres, and the corpus striatum. The diencephalon consists of the pretectum, the dorsal and ventral thalamus, the hypothalamus, and the epithalamus which connects to the parietal eye and pineal organ. The roof of the midbrain contains the optic tectum and tori semicirculares, and the floor is the midbrain tegmentum. The optic tectum, which can be small and covered by the forebrain, processes optic information. It is large in species which rely primarily on sight, and projects to the surface of the brain between the telencephalon and cerebellum. In contrast, the midbrain of snakes has two nuclei and a torus and paratorus; this difference reflects the ancestral reduction of vision in snakes and the subsequent redevelopment of both eye and visual brain structures. The hindbrain consists of a dorsal cerebellum, ventral tegmentum, and medulla oblongata. The tegmentum consists of the reticular nuclei. The medulla oblongata contains the nuclei of the cranial nerves III–XII.

The organisation of sensory inputs, the brain, and motor outputs is exceedingly complex (see Belekhova 1979; ten Donkelaar & Nieuwenhuys 1979), but an overview is summarised in Figure 24.20B. Olfactory input is via the olfactory bulb and lobes to the corpus striatum. Visual input is via the optic nerve to the midbrain tectum, which also receives inputs from the thalamus and spinal cord. Ascending pathways from the tectum extent to the dorsal thalamus, pretectum and telencephalon, whereas descending tracts extend to the reticular formation of the brainstem. Auditory information enters the cochlear nuclei of the rhombencephalon, then passes via the torus semicircularis to the thalamus and telencephalon. Equilibrium information enters the vestibular nuclei and passes to the cerebellum, brainstem and spinal cord. Other sensory information from the head enters via the trigeminal nerve to the sensory trigeminal nuclei, then passes to the cerebellum, tectum and motor nucleus of the trigeminal nerve. Sensory information from the body enters the brain via the dorsal sensory nuclei of the hindbrain, and spinal cord. There are numerous ascending spinal pathways to the cerebellum, vestibular nuclei, tectum and dorsal thalamus. The cerebellum receives sensory inputs from the spinal cord, tectum and trigeminal and vestibular nuclei, and has motor output via the vestibular nucleus and red nucleus to the spinal cord. The higher brain centres, especially the telencephalon, have output to the tectum, tegmentum, and ventral thalamus.

The spinal cord extends the entire length of the vertebral canal except the end of the tail (Kusuma, ten Donkelaar & Nieuwenhuys 1979). Its structure reflects the shape and development of the trunk and tail. Limbed squamates have cervical and lumber enlargements of the spinal cord, but these are absent in limb-reduced and limbless forms. The outer white matter of the spinal cord consists of nerve fibres and the inner gray matter consists of the cell bodies of interneurons and motor neurons.

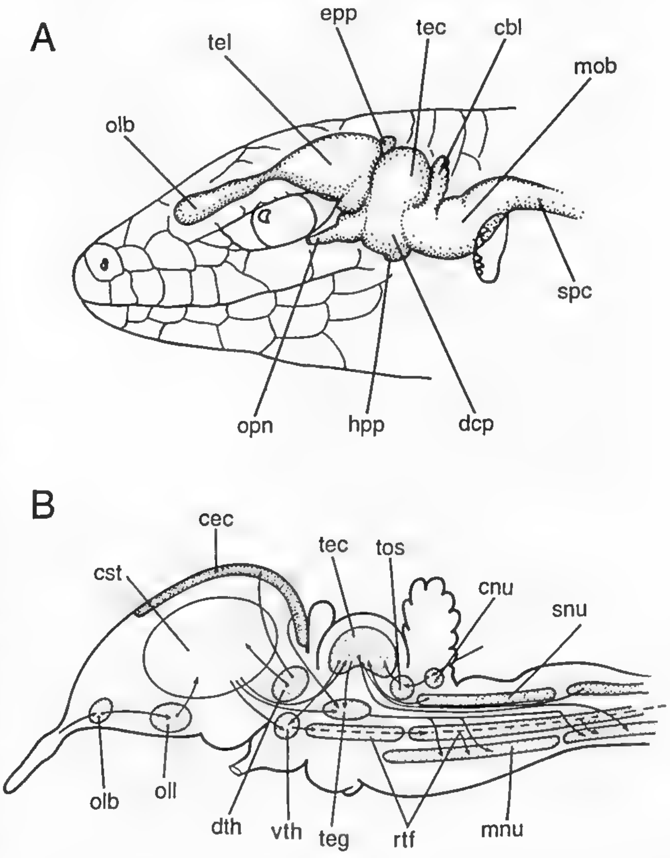

Figure 24.20 Structure of the brain in a typical lizard. **A**, general schema; **B**, schema of the major connections of various brain centres.**cbl**, cerebellum; **cec**, cerebral cortex; **cnu**, cochlear nucleus; **cst**, corpus striatum; **dcp**, diencephalon; **dth**, dorsal thalamus; **epp**, epiphysis; **hpp**, hypophysis; **mnu**, motor nuclei; **mob**, medulla oblongata; **olb**, olfactory bulb; **oll**, olfactory lobe; **opn**, optic nerve; **rtf**, reticular formation; **snu**, sensory nuclei; **spc**, spinal cord; **tec**, tectum; **teg**, tegmentum; **tel**, telencephalon; **tos**, torus semicirculares; **vth**, ventral thalamus. [M. Thompson]

Peripheral Nervous System

The peripheral nervous system consists of nerves which enter or leave the brain and spinal cord. The sensory nerves can be divided into somatic nerves carrying sensory information concerning the external environment, position of limbs, and visceral nerves carrying interoceptive sensory information. The efferent nerves can similarly be divided into somatic motor nerves, controlling the voluntary muscles of the body, and visceral motor nerves controlling involuntary muscles and glands.

The parasympathetic and sympathetic branches of the visceral motor (autonomic) nervous system have important effects on the heart, gastrointestinal tract, respiratory system, vasculature, urinogenital system, endocrine and exocrine glands, chromatophores, and the eyes (Berger & Burnstock 1979). Parasympathetic nerves are present in some cranial nerves (III, X and probably VII and IX) and sacral spinal nerves. Their preganglionic and postganglionic neurotransmitter is mainly acetylcholine. The sympathetic system has a thoraco-lumbar spinal nerve organisation with bilaterally arranged ganglia. The preganglionic neurotransmitter is acetylcholine and the postganglionic neurotransmitter is noradrenaline.

The heart is innervated by parasympathetic (vagal) and sympathetic nerves. Vagal stimulation decreases heart rate and force of contraction whereas sympathetic stimulation increases both heart rate and force of contraction. The autonomic nervous system controls motility, secretion and blood flow in the digestive tract; parasympathetic activity generally stimulates these actions. The lungs have an excitatory cholinergic and an inhibitory adrenergic innervation. The parasympathetic innervation contricts the pulmonary artery and increases vascular resistance, and sympathetic innervation vasodilates. The sympathetic innervation of the systemic vasculature regulates peripheral distribution of blood flow, for example during heating and cooling and diving, and contracts the spleen. The parasympathetic innervation of the bladder mediates contraction. There is a sympathetic innervation to the kidney, vas deferens and hemipenes. The thyroid, pancreas and adrenal glands each have a sympathetic and/or parasympathetic innervation. The sympathetic nervous system may affect colour by direct effects on chromatophores and indirect effects on blood flow. There may be autonomic control of the iris, nictitating membrane and glands of the eye.

ENDOCRINE AND EXOCRINE SYSTEMS

Hypothalamus and hypophysis

The hypothalamus and hypophysis (pituitary) are 'master endocrine glands' which enable nervous system regulation of many other endocrine organs. The structure of the hypothalamus-pituitary axis has been described for many reptiles (Saint Girons 1970a). The adenohypophysis consists of the distal and intermediate lobes of the pituitary. The neurohypophysis consists of the neural lobe and median eminence. Neurosecretory cells of the supraoptic and paraventricular nuclei of the hypothalamus, the median eminence and neural lobe collectively form the hypothalamo-neurohypophyseal tract.

The supraoptic and paraventricular nuclei, which lie near the optic tract-diencephalic junction, contain small neurosecretory cell bodies with axons descending along the floor of the third ventricle to the infundibulum and then the neural lobe. This spherical or ovoid extension of the infundibulum is usually located dorsal to the distal lobe of the pituitary. Neurosecretory products of the supraoptic/paraventricular cell bodies are apparent in the neural lobe as colloidal granules. The median eminence, a vascular swelling of the ventral wall of the infundibulum, liberates hypothalamic releasing factors, which are transported to the distal lobe of the pituitary by the hypothalamo-hypophyseal portal system.

The distal pituitary lobe, which is generally ventral to the neural lobe and postero-ventral to the median eminence, consists of cellular cords of different cell types. The gonadotropic LH (γ) cells secrete luteinising hormone (LH). The gonadotropic FSH (β) cells secrete follicle stimulating hormone (FSH). The thyrotropic (δ) cells secrete thyroid stimulating hormone (TSH). The function of the alpha (α) cells is unknown. There are also X cells and chromophobic cells. The distal lobe hormones regulate growth, reproduction, the thyroid gland and the adrenal (interrenal) gland. The neural pituitary lobe contains arginine vasotocin (AVT), oxytocin and mesotocin. AVT has important effects on renal function, producing antidiuresis, but the physiological roles of oxytocin and mesotocin are unclear (Bradshaw 1976). The structure of the intermediate pituitary lobe, which consists of external and internal layers, varies considerably. Its hormone, intermedin, disperses melanophore pigment granules.

Thyroid

The lobular thyroid gland is single, bilobed or paired in lizards (Lynn 1970) but is single and elongate in snakes. Spherical follicles of thyroid epithelium (50 to 300 mm diameter) secrete thyroxin (T_4) and tri-iodothyronine (T_3) into the follicular lumen. The thyroid gland incorporates and stores iodine, for synthesis of T_4 and T_3. The thyroid gland is under the control of the anterior pituitary gland, via TSH. It stimulates the reproductive cycle and cellular metabolism. Thyroid activity appears to promote ecdysis in lizards, but inhibits ecdysis in snakes. The thyroid gland also affects other endocrine organs such as the parathyroids and ultimobranchial glands.

In temperate-zone lizards, there is a marked seasonal cycle in thyroid activity, with a peak during summer. Lizards in warmer climates may have the reverse cycle, with greater thyroid activity during winter when feeding activity is maintained, and lower activity during summer when activity is curtailed. Thyroid activity is generally reduced during hibernation or aestivation. Similar seasonal changes in thyroid activity occur in snakes.

Parathyroids

The parathyroid glands are derived from two pairs of pharyngeal pouches (Clark 1970). In most adult lizards, the rostral pair persist, but the caudal pair degenerate. Snakes retain both rostral and caudal pairs. The parathyroids are composed of cords of secretory cells, separated by capillary or sinusoidal channels. They secrete parathormone (PTH, or parathyroid hormone), which elevates blood Ca^{2+} levels by promoting Ca^{2+} mobilisation from bone, Ca^{2+} absorption from the gut, and renal PO_4^{3-} excretion.

Ultimobranchial Glands

The two ultimobranchial glands are located near the heart (the right may be rudimentary or absent). Their hormone, calcitonin, has an antagonistic action to PTH, whereby it decreases blood Ca^{2+} and PO_4^{3-}.

Adrenals

The paired adrenal glands, which are incorporated into the mesentery of the gonads, are typically globular or cylindrical in lizards, but elongate in snakes. The adrenal (interrenal) tissue corresponds to the mammalian adrenal cortex, and the peripheral (chromaffin) tissue corresponds to the mammalian adrenal medulla (Gabe 1970).

The interrenal tissues secrete the corticosteroid hormones, aldosterone and corticosterone (and occassionally cortisol), but their roles in squamates are unclear (Bradshaw 1986). Renal retention of Na^+ and excretion of K^+ by aldosterone, a mineralocorticoid hormone, has been reported in goannas and a water snake. Corticosterone has a similar role in *Varanus gouldii* (Rice, Bradshaw & Prendergast 1982). Aldosterone and corticosterone also affect electrolyte secretion by salt glands.

The chromaffin tissue consists of small cells organised into a dorsal noradrenaline-secreting layer and ventral clusters of adrenaline-secreting cells. Secretion is under sympathetic control (Berger & Burnstock 1979); squamates may be able to independently secrete noradrenaline and adrenaline. Adrenaline and noradrenaline have a variety of actions on the heart, gastrointestinal tract, respiratory system, circulatory vasculature, urinogenital system, endocrine glands, chromatophores, eye and central nervous system.

Pineal Organ

The photosensitive pineal organ arises from the right-side vesicle of the posterior pair of structures of the parietal-pineal complex (Quay 1979). The pinealocytes resemble parietal eye photoreceptors, but their outer (photoreceptive) segments often degenerate. The pineal organ has both sensory (pinealofugal) and autonomic (adrenergic) nerve fibres. The pineal has high concentrations of serotonin, the precursor to the indoleamine melatonin, which affects the reproductive cycle, particularly ovarian activity.

Pancreas

In lizards, the pancreas lies between the stomach and duodenal curve, and has three limbs, one extending towards the gall bladder, one towards the small intestine, and one towards the spleen (Miller & Lagios 1970). The compact pancreas of snakes is often elongate. The pancreatic endocrine tissue consists of numerous islets among the exocrine tissue, mainly in the splenic portion. In lizards, the islets are large, irregularly branched cords of two cell types, but in snakes the cords form more compact structures. The more numerous α cells secrete glucagon, a hormone which increases the blood glucose level, and the fewer β cells secrete insulin, which decreases the blood glucose level.

Exocrine systems

The ducted exocrine glands of the skin, nasal and oral cavities, digestive tract and pancreas have diverse functions in squamates.

The external nasal gland, which lies outside the cartilaginous nasal capsule, is a branched tubular mucous gland that excretes salt in some lizards. Its duct typically enters the nasal vestibulum. Squamates lack a medial nasal gland. In some squamates, the goblet cells of the respiratory epithelium may become concentrated into gland-like structures.

The oral glands are complex in structure and function (Kochva 1978). The gland of Duvernoy of colubrid snakes is located behind the eye and opens via a single duct to a fold of oral mucosa near the teeth. Its secretion is toxic in a number of species. The venom glands of elapid, laticaudid and hydrophiid snakes occupy the lateral side of the head. The main venom gland may be divided into several lobules, each containing numerous tubules. Venom enters a groove near the base of the fang and travels along a groove to exit near the tip. Envenomation rapidly immobilises prey and commences chemical digestion. Venoms may contain neurotoxic, coagulant, haemolytic, haemotoxic, cytotoxic and myotoxic agents (Gow 1989). Neurotoxins prevent peripheral nervous transmission and paralyse skeletal muscle; respiratory failure is a typical cause of death. The toxicity of venom varies markedly (Elliot 1978; Mebs 1978; Latifi 1978). The LD_{50} varies from 0.01 mg kg^{-1} for the seasnake *Enhydrina schistosa* to over 10 mg kg^{-1} for other species. The toxicity of a snake bite depends on both the LD_{50} of the venom and the volume of venom injected. For example, the inland taipan, *Oxyuranus microlepidotus*, has one of the most dangerous bites because of both the high toxicity and the large quantity of venom injected (Shine 1991a).

The exocrine portion of the pancreas consists of zymogen cells that secrete into the lumen of branching tubules (Miller & Lagios 1970). The secretion contains bicarbonate and enzymes, including amylase, proteases (chymotrypsin, trypsin, carboxypeptidase), ribonucleases, lipases, and chitinase (Skoczylas 1978).

REPRODUCTION

Reproductive Systems

The male reproductive system consists of paired testes, vasa deferentia, the sexual segment of the kidney, and paired hemipenes. In females, there are paired ovaries, and oviducts with uteri. The reproductive tracts open into the central urodeum of the cloaca, often at papillae extending into the lumen. In many male squamates, the ipsilateral vas deferens and ureter fuse near the cloaca and open together at a papilla, but there may be separate vasa deferentia and ureteral openings in some species. Oviducal and ureteral openings are separate in female squamates.

The paired gonads develop into testes or ovaries (Fox 1977). In males, Müllerian ducts transiently develop but they usually degenerate, and Wolffian ducts (the collecting duct of the mesonephric kidney) form the vasa deferentia to convey sperm from the testes to the cloaca. In females, the Müllerian ducts persist as the oviducts and uteri, and the Wolffian ducts degenerate. Rarely, the bisexual potentiality of both gonads and ducts persist to produce a hermaphroditic adult.

The paired ovoid testes are located posteriorly in the body cavity, the right usually extending more anteriorly than the left (Fox 1977). They are particularly elongate in snakes and limb-reduced and limbless lizards. The white connective tissue tunic divides the testes into lobules, containing blind-ending seminiferous tubules, interstitial cells, and vascular and connective tissues. Sustentacular (Sertoli) cells of the seminiferous tubules presumably have a nutritive or phagocytic role. Interstitial (Leydig) endocrine cells are present between the tubules. These numerous, large cells secrete testosterone. The testes have various accessory ducts; the ductuli efferentia lead into the ductuli epididymides and ductus epididymidis, and then into the vas deferens which joins the ureter near the cloaca.

There is often a seasonal sexual cycle during which the gonads enlarge (Duvall, Guillette & Jones 1982; Saint Girons 1985). Interstitial cells become more numerous and active. Spermatogenesis occurs, at least at temperatures above 20°C (Saint Girons 1985). In immature males, the seminiferous tubules are only one cell thick and there are usually no signs of spermatogenesis, but during breeding the tubule diameter increases and spermatids and sperm are abundant in the lumen. The epididymis becomes distended by a milky fluid. The testes regress during breeding inactivity. The seminiferous tubule lumen decreases in diameter; many spermatogonia and spermatocytes are present but there are few spermatids and sperm. The epididymis is shrunken and empty. Sperm may be stored in the vas deferens during the winter in some snakes, or spermatogenesis may begin in late summer and be arrested at an early stage during winter, to continue in spring. In tropical species, spermatogenesis may be continuous, even though the female reproductive cycle may not.

The paired ovaries are suspended in the body cavity, usually with the right anterior to the left (Fox 1977); they are elongate, sac-like structures in limb-reduced and limbless lizards, and snakes. The ovaries consist of connective tissue stroma, blood vessels, nerves, and ova. They contain two genital beds of oogonia and oocytes in various stages of development. Each oviduct has a thin-walled fallopian tube that terminates in a wide intra-abdominal ostium, and a thicker-walled uterus that is separated from the fallopian tube by a muscle sphincter. The left oviduct is degenerate in some limb-reduced and limbless lizards, and some blind snakes, *Typhlops*, presumably because of 'crowding' by the stomach. However, the right oviduct is lost in *Vermiseps pluto*, which also uncharacteristically has an enlongate right lung (Greer 1989). The oviducts open into the cloaca, separately from the ureters.

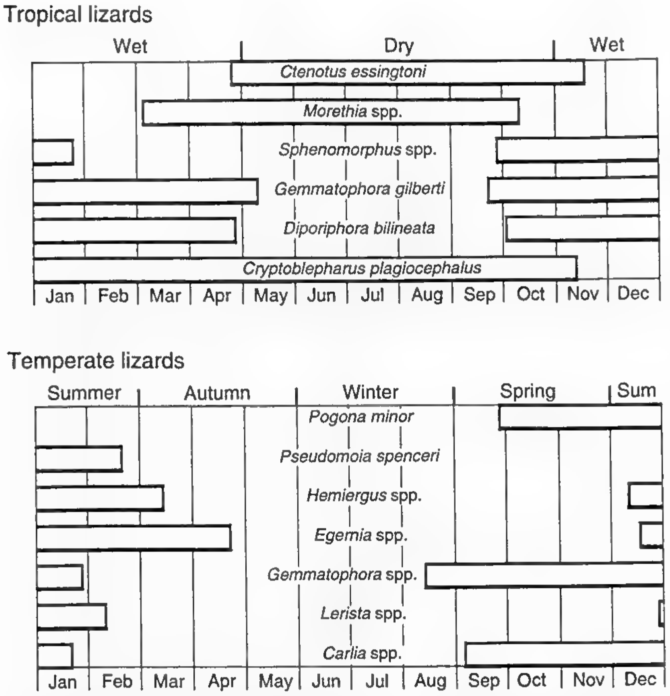

Figure 24.21 Schematic summary of pattern of reproductive cycles in some tropical lizards (above 26th parallel) and temperate lizards (below 26th parallel). (Data from James & Shine 1985) [W. Mumford]

Often a seasonal ovarian cycle occurs, influenced by external environmental cues (light, temperature) and internal endocrinological feedback (oestrogen and progesterone). During the inactive phase, immature ova (often two to 20) and some atretic ova are present. Yolk is deposited in the oocytes shortly before ovulation. During oestrus, theca cells of the stroma release oestrogens (Joss 1985). Ovulation may be synchronous from both ovaries, may alternate between ovaries, or only one ovary may be active at a time. After ovulation, corpora lutea are formed, which resemble those of mammals, and similarly secrete progesterone to maintain gestation. The oviducal glands are large during egg-laying but the oviducts regress during inactive periods.

Vitellogenesis is probably less temperature dependent than spermatogenesis, but the high energetic cost of egg formation means that it must be fuelled either by body fat stores or feeding (Saint Girons 1985). Temperate squamates generally have a pronounced seasonal reproductive cycle, but females may reproduce only every second or third year. Even tropical squamates often have a highly seasonal reproductive cycle coinciding with the most favourable time of the year.

In lizards, sperm quickly reach the caudal oviduct after mating (within 1 to 2 days), and remain there for a few days to weeks, until they move to the rostral part of the oviduct before ovulation (Saint Girons 1985). In snakes, mating may preceed ovulation by two to three months, and sperm remain in epithelial crypts of the oviducal funnel until ovulation occurs. Sperm are generally not present in the oviduct after egg-laying (or mid-gestation in viviparous species).

Breeding Cycles

Climatic factors, particularly temperature, influence the seasonal reproductive cycle of squamates (Fig. 24.21). The cycle of female lizards appears to be constrained by temperature, at least in temperate regions. Typically, ovulation occurs in late spring, eggs are laid in early summer, and young are born, or hatch, in late summer (Bustard 1970b; James & Shine 1985; Greer 1989; Saint Girons, Bradshaw & Bradshaw 1992). However, the great diversity in clutch size, offspring size, mating systems, parental care, and timing of mating results in a number of variations in this basic cycle (see Shine 1985b; Greer 1989). The male and female reproductive cycles usually coincide in spring, although the male cycle may be different if females store sperm. For example, female *Hemiergis peronii* are inseminated in autumn and store sperm over winter until they ovulate in spring (Smyth & Smith 1968).

In tropical lizards, the reproductive cycle may remain seasonal although it varies for different species (James & Shine 1985; Greer 1989). Agamids and terrestrial goannas typically breed in the wet season (November to April), whereas geckos and the dragon *Chelosauria* breed in the dry season (May to October). Aquatic goannas breed in the early dry season. Amongst skinks, most *Ctenotus* breed in the dry season and *Carlia* and *Sphenomorphus* breed in the wet. In contrast, *Cryptoblepharus plagiocephalus* breeds throughout the year in the tropics.

The reproductive patterns of arid-zone lizards are variable. Reproduction may occur in early or late spring, summer, autumn or be continuous during suitable periods (James & Shine 1985; Saint Girons *et al.* 1992).

Snakes also have seasonal reproductive cycles (Duvall *et al.* 1982; Shine 1991a). Females generally ovulate in spring and lay their eggs about a month later, or give birth about three months later, in temperate climates. Males may not be so seasonally constrained, particularly as sperm storage occurs in many species; mating can occur months (or even years) before ovulation. In the tropics, the reproductive cycle may remain seasonal despite continually favorable temperatures, depending more on water availability. However, the precise timing of ovulation by females may vary markedly in different species. Reproductive cycles may be aseasonal or seasonal in seasnakes. For example, female *Aipysurus laevis* ovulate in spring, are gravid during summer, and give birth in autumn (Burns 1985).

Oviparity

Many squamates are oviparous. Most agamids lay more than one clutch; clutch size varies from two to about 30. Geckos and pygopodids lay one, two or more small (one to two eggs) clutches per year. Goannas lay one clutch of about three to 30 eggs per year. Temperate skinks generally lay one clutch of one to eight eggs per year.

Squamate eggs vary from < 0.1 g to over 300 g (Iverson & Ewert 1991). There is a correlation between egg and adult size. Species with large clutches tend to have spherical eggs to maximise oviducal packing, whereas attenuated species tend to have elongate eggs. Incubation time increases with egg size (Vleck & Hoyt 1991). Incubation temperature has many effects on development (Deeming & Ferguson 1991). Elevated temperature decreases the incubation time, but only to a critical temperature above which incubation time increases. Temperature can influence the sex, pigmentation pattern, post-hatchling growth rate, and thermoregulatory and sexual behaviours of the hatchling.

Most eggs have a multi-layered shell membrane that is either a flexible, parchment shell (most squamates) or a rigid, calcareous shell (some geckos; Packard & DeMarco 1991). Flexible-shelled eggs have a thin crust or isolated calcareous deposits, whereas rigid-shelled eggs have calcareous columns attached to the underlying shell membrane. Most oviparous squamates retain their eggs for a period from a few weeks to just before hatching. For example, the skink, *Saiphos*, and the elapid, *Pseudechis*, retain the eggs until a week or so before hatching. Although technically these are egg-laying squamates, they are functionally better classified as live-bearers.

Viviparity

Viviparity (live-bearing) has evolved numerous times in Australian skinks (see Shine 1985a; Greer 1989). For example, all *Carinascincus*, *Claireascincus*, *Egernia*, *Eulamprus*, *Gnypteoscincus*, *Harrisoniascincus*, *Hemiergis*, and *Tiliqua* are viviparous. Viviparity has evolved independently in some *Anomalopus*, *Lerista*, and *Glaphyromorphus*. *Saiphos equalis* and *Lerista bougainvillii* are oviparous or viviparous in different geographic regions. Numerous terrestrial snakes are viviparous.

Some seasnakes (hydrophiids, file snakes and the homalopsine colubrids *Ceberus*, *Fordonia* and *Myron*) are viviparous, but laticaudids are not. Embryonic development is completed within the oviduct and the thin eggshell allows gas and water exchange. A placenta may form to facilitate gas exchange, and even nutrient exchange in some species (Yaron 1985).

Viviparity has evolved in cold-climate squamates (Packard *et al.* 1977; Shine & Bull 1979; Blackburn 1982; Shine 1985a) by physiological modifications for egg retention (Guillette 1985). There is a clear correlation between mean annual temperature and viviparity in skinks and elapid snakes (Shine 1985a). Cold soil temperatures presumably inhibit development or are lethal to eggs, but eggs retained by females are maintained at higher temperatures, at least during the day.

Parthenenogenesis

Parthenogenetic (all-female) reproduction has been reported for about 13 genera of reptiles (Cole 1975; Darevsky, Kupriyanova & Uzzell 1985). The Australian gecko *Heteronotia binoei* is a complex species with two sexual diploid and probably three parthenogenetic triploid forms (Moritz 1983; Moritz & King 1985; Moritz 1991). The origin of pathenogenesis in *Heteronotia* is a hybridisation event between distinct populations, but the meiotic mechanism which maintains the somatic ploidy level is unclear.

Chromosomes

The chromosomes are generally large (macrochromosomes) or small (microchromosomes; Gorman 1973) with a central/near-central centromere (metacentric) or a terminal/near-terminal centromere (acrocentric).

In lizards, the diploid chromosome number varies from 20 to 56, with $2n = 36$ a likely primitive condition. Skinks have $2n = 24$ to 32 while goannas have $2n = 40$. The diploid number for geckos is 32 to 46 (King 1977c; Moritz & King 1987; Moritz 1991). Pygopodids have $2n = 38$, but in *Lialis burtonis* $2n = 33$ (females) and $2n = 34$ (males) (Gorman & Gress 1970). All Australian dragons are diploid with $2n = 22$ or 24.

For snakes, $2n = 32$ is a common and perhaps the primitive condition, but varies from $2n = 24$ to 50: for pythons, $2n = 34$, 36, 40 or 44; for colubrids and viperids, usually $2n = 36$; in elapids, $2n = 36$, 38, 42 or 44 (or 43 in male *Bungarus caeruleus*). The laticaudid, *Laticauda semifasciata*, has $2n = 38$.

Sex differentiation

Sex determination can be either genotypic (genetic) or epigamic (environmental; Bull 1980). Two common forms of genotypic sex determination (GSD) are male and female heterogamety, wherein one chromosome, or chromosomal segment, segregates according to sex. The sex-determining chromosomes may be cytologically indistinguishable (homomorphy) or are cytologically distinguished as sex chromosomes (heteromorphy). In male heterogamety, the possession of two different sex chromosomes determines males, as XY(male)/XX(female); female heterogamety is the opposite, as ZZ(male)/ZW(female). Sometimes, more than one chromosome may segregate according to sex, as X_1X_2 X_1X_2 (female)/X_1X_2 Y (male).

The pattern of homomorphy or heteromorphy is complex in lizards, indicating sporadic and multiple origins of heterogamety (Gorman 1973; King 1977c; Bull 1980). Except for legless lizards, heteromorphism is uncommon, and most species do not have sex chromosomes. No dragons have been reported to have sex chromosomes. The heterogametic sex varies in different families, and within families. The heterogametic sex is male in skinks and legless lizards, and female in geckos and goannas.

In snakes, there appears to be a relatively straightforward evolutionary development of sex chromosomes, and the extent of Z-W differentiation increases from primitive homomorphy to a major heteromorphy in W and Z chromosomes. Pythons generally have homomorphic sex chromosomes whereas colubrids have female heterogamety with unequal W and Z chromosomes. The elapid *Bungarus caeruleus* has a multiple Z_1Z_2W sex chromosome system, with $2n = 44$ (male) and $2n = 43$ (female).

Temperature is the most common factor in epigamic sex determination. Thermal-dependent sex determination (TSD) has been reported infrequently for lizards but not at all for snakes. In species with TSD, the sex ratio is dramatically dependent on the egg incubation temperature. Often a high temperature results in female offspring and a low temperature in males. In both *Eublepharus macularius* and *Agama agama*, the sex ratio increases from predominantly female to male at temperatures above about 28°C (Charnier 1966; Wagner 1980).

Embryology and Development

Squamate eggs have a large yolk mass surrounded by a comparatively small layer of albumen with a surrounding vitelline membrane. The yolk provides the nutritional requirements for the developing embryo, and sometimes for the neonate.

The sequence of development is only well-described for the lizard *Lacerta vivipara* (Dufaure & Hubert 1961) and the snake *Thamnophis sirtalis* (Zehr 1962). Fertilisation begins embryonic development. The first cell divisions of the fertilised ovum are incomplete on one side of the yolk (meroblastic), and produce a germinal disc of comparatively small cells (Hubert 1963). Further cell divisions form a double layered blastoderm, which invaginates during gastrulation to form endoderm and ectoderm. Cells migrate into the space between these two layers to form mesoderm (Hubert 1970). Gastrulation differs slightly in snakes. Lateral folds, formed by the ectodermal cells, migrate and unite ventrally to form a neural tube that is closed anteriorly to form the brain (neurulation). The cells at the margins of the neural tube differentiate and migrate to form the dorsal nerve cord. The mesoderm differentiates symmetrically into a notochord and lateral somites. The notochord is replaced later in development by the axial skeleton. The somites segment antero-posteriorly and split dorso-ventrally to form the segmented body musculature, and form the coelom. The endoderm and part of the mesoderm form the gut. Much later in development, the accessory glands of the digestive tract (pancreas and liver) and the lungs develop from the intestine. The mesoderm also gives rise to nephrotomes, which form the embryonic kidney, and a specialised germinal ridge that forms the gonads.

The endoderm encloses the yolk sac and forms three extraembryonic membranes. The amnion and chorion form first, and extend dorsally to envelop the embryo, which continues its development in the fluid filled amniotic cavity that protects the embryo from shock and desiccation. The chorionic membranes form an extra-embryonic coelom. The final extra-embryonic membrane develops from both endodermal and mesodermal layers behind the stalk of the yolk-sac, and forms the allantois which functions as an embryonic bladder. The well-vascularised periphery of the allantoic and chorionic membranes is the major site of gas exchange. The chorio-allantoic membranes and/or yolk sac may also function as a 'placenta' for nutrient exchange in some live-bearing squamates.

The anterior regions develop and differentiate before the more posterior regions. Rapid growth of the anterior portion of the embryo bends and partially rotates it. Further elongation produces an obvious flexion that is extreme in attenuated forms. The number of somites increases, the pharynx becomes perforated by gill slits (but never develops gills) and the vasculature of the undifferentiated gill arches forms the anatomical basis for the adult vasculature. The eyes, inner ears and olfactory organs begin to differentiate and the heart forms and commences to beat. Two pairs of limb buds form paddle-like anterior limbs, which differentiate discernible digits; these appendicular skeletal components are initially cartilaginous. In snakes and some other limbless squamates, the limb buds initially form then regress (Raynaud 1985). In the final stages of development, the skin differentiates recognisable scales.

25. NATURAL HISTORY OF THE SQUAMATA

Harold Heatwole & Eric R. Pianka

The domain of Natural History includes the study of animals in their natural environment, largely by observational means. It encompasses various aspects of behaviour and ecology at the levels of the whole organism, population and community, and leads to conclusions about evolution and adaptation. Those aspects selected for treatment in this chapter partly reflect our own conception of Natural History and partly the requirement not to overlap unduly with contributions of other authors. In particular, we leave discussion of physiological ecology to the authors of Chapter 24, and only discuss experimental approaches, laboratory data, or investigations at the organ, tissue or cellular level where they have particular relevance to field studies — and then only briefly. The emphasis has been placed on the Australian fauna, and reference to the worldwide literature is made for comparative purposes or to illustrate principles not exemplified by Australian studies. The detail with which we treat particular topics is tempered by recent reviews which deal with many aspects of the ecology of lizards and snakes (Huey, Pianka & Schoener 1983; Pianka 1986; Heatwole & Taylor 1987; Siegel, Collins & Novak 1987; Gans & Huey 1988; Greer 1989).

ENVIRONMENTAL RELATIONS

An ectotherm obtains its heat from its external environment, whereas an endotherm produces most of its own heat internally by means of oxidative metabolism. The vast majority of animals are ectothermic. Continuously endothermic animals are found among birds and mammals, though even many of these become ectothermic at times. Reptiles generally are ectotherms, but some squamates, especially the larger ones, are at times at least partially endothermic (see Heatwole & Taylor 1987).

A related pair of useful terms are sometimes confused with the above designations. Animals that maintain relatively constant internal body temperatures are homeotherms, whereas those whose temperatures vary widely and closely track those of the environment, are called poikilotherms. Many ectothermic snakes and lizards have preferred temperatures and regulate their body temperatures rather precisely by appropriate behavioural means during their activity periods. When inactive, their body temperatures fluctuate and follow that of the environment. Thus they are neither strictly poikilothermic nor homeothermic. Some diurnal species bask and use the sun as a heat source and are called heliotherms. Others select substrates of particular temperatures, although they track the temperature of their immediate environment, and do not experience the full range of available conditions. These are called thigmotherms. An active desert lizard may have a body temperature just as high as that of a bird or mammal; the layman's terms 'warm-blooded' and 'cold-blooded' are thus quite misleading and should be abandoned.

Many different pathways of heat gains and heat losses exist (Heatwole & Taylor 1987) and balancing a heat budget requires very different adaptations under varying environmental conditions. At different times of day, ambient thermal conditions may change from being too cold to being too warm for a particular animal's optimal performance. Animals living in hot deserts must be able to minimise heat loads and to dissipate heat efficiently to avoid overheating. In contrast, those that live in colder places, such as at high altitudes, must be adept at acquiring and retaining heat.

Because thermoregulation clearly has costs and risks as well as benefits, an emerging conceptual framework envisions an optimal level of regulation that depends on the precise form of the constraints and interactions among costs and benefits arising from a particular ecological situation (Huey & Slatkin 1976).

Thermoregulation often involves both physiological (Lillywhite 1987; Chapter 24) and behavioural adjustments. As an example of the latter, consider a typical terrestrial diurnal desert lizard (Bradshaw & Main 1968; Heatwole 1970). During the early morning, when ambient temperatures are low, such a lizard locates itself in the warmer microclimates of the environmental thermal mosaic, and basks in the sun with its flattened body as perpendicular as possible to the sun's rays, thereby maximising heat gain. As ambient temperatures quickly rise, the lizard climbs up off the ground into cooler air and orients itself facing into the sun's rays, thereby reducing its heat load. Often these behavioural adjustments are too effective and carry the animal beyond the limits of its preferred temperatures, and it must make further, compensatory changes in posture or location. Diurnal lizards and snakes often repeatedly 'shuttle' back and forth between sun and shade as their temperatures alternately rise too high and fall too low. At high temperatures, they may seek shade or retreat into burrows. Many lizards change their colour and their heat reflectance properties, becoming dark and heat-absorbent at colder times of day but light and heat-reflectant at hotter ones (Rice & Bradshaw 1980). When these expedients fail, some lizards resort to panting (Heatwole 1970; Heatwole, Firth & Webb 1973).

Snakes have similar behavioural repertoires including basking, flattening, posturing towards the sun and shuttling (Heatwole & Johnson 1979) and in addition have one not common in lizards — coiling as a means of retaining body heat during cool periods (Cogger & Holmes 1960; Shine & Slip 1988b).

Thermoregulatory patterns are related to activity cycles. Two major strategies of thermoregulatory precision seem to be pursued by diurnal lizards (Heatwole, Lin, Villalón, Muñiz & Matta 1969). Some species are active only when they can thermoregulate precisely and consequently alter their activity period seasonally, from a short activity peak centring on midday at cooler times of year to a bimodal cycle which avoids midday heat at warmer periods. Others sacrifice thermoregulatory precision to maximise the length of the activity period and are active most of the daylight hours, during which time they are thermally passive. There may be seasonal and/or geographic shifts in mean body temperature of active animals (Heatwole 1970).

Some species may not fit conveniently into either of these categories. Shine (1987c) found that the diurnal, surficial *Pseudechis porphyriacus* adjusts its time and kind of activity in such a way that, while active, its body temperature stays between 28° and 31°C over a variety of seasons, localities and ambient temperatures. However, a later study (Shine & Lambeck 1990) revealed seasonal shifts in body temperature.

Thermoregulatory patterns are also related to habitat. Some squamates are climbers, others subterranean, while still others are strictly surface dwellers. Among the latter, some tend to be found in open areas whereas others frequent the edges of vegetation. By contrast, many burrowing species are relatively passive to environmental temperature. Arboreal lizards may display narrower variances in body temperature than do terrestrial ones (Pianka 1966).

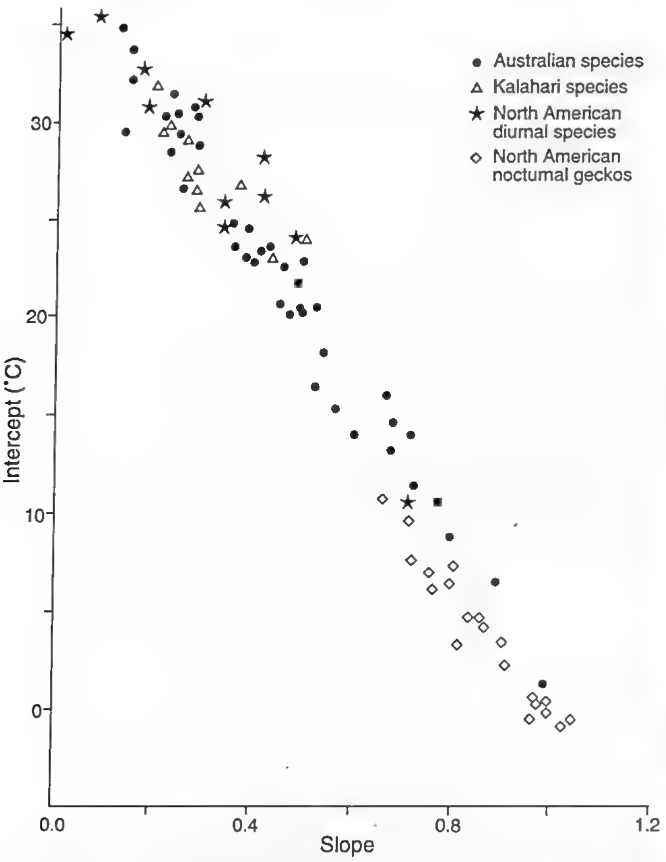

Figure 25.1 Relationship of the intercepts and slopes of lines relating body temperature to air temperature in a number of species of lizards. Each symbol represents one species (From Pianka 1986) [W. Mumford]

Differences in temporal patterns of activity, the use of space, and body temperature relationships are hardly independent. Rather, they constrain one another in complex and sometimes obscure ways. For example, thermal conditions associated with particular microhabitats change in characteristic ways in time. A choice basking site at one time of day becomes an inhospitable hot spot at another time. Perches of arboreal lizards receive full sun early and late in the day when ambient air temperatures tend to be low and basking is therefore desirable, but these same tree trunks are shady and cool during the heat of midday when heat avoidance behaviour becomes necessary (Huey & Pianka 1977). In contrast, the fraction of the ground's surface in the sun is low early and late when shadows are long, but reaches a maximum at midday. Terrestrial heliothermic lizards may thus experience a shortage of suitable basking sites early and late in the day. Moreover, during the heat of the day, their movements through relatively extensive patches of open sun can be severely curtailed. Hence ground-dwelling lizards encounter fundamentally different and more difficult thermal challenges than do climbing species.

Perching sites may vary widely between the cool morning and evening periods (Heatwole 1970). In the morning some desert lizards prefer bushes rather than sand, as the former results in less conductive heat loss to cold substrates. In the evening, warmth can be obtained from sun-heated sand and basking occurs on mounds of sand rather than on bushes.

Radiation and conduction are the most important means of heat exchange for the majority of diurnal lizards, although the thermal background in which these processes occur is strongly influenced by prevailing air temperatures. Ambient air temperatures are critical to nocturnal lizards as well as to certain very cryptic diurnal species.

In an analysis of the costs and benefits of lizard thermoregulation, Huey & Slatkin (1976) identified the slope of the regression of body temperature against ambient environmental temperature as a useful, inverse indicator of the degree of passiveness in regulation of body temperature. On such a plot of active body temperature versus ambient temperature, a slope of one indicates true poikilothermy or totally passive thermoconformity (a perfect correlation between air temperature and body temperature results), whereas a slope of zero reflects the other extreme of perfect thermoregulation. Lizards span this entire spectrum. Among active, diurnal, heliothermic species, regressions of body temperature on air temperature are nearly flat, and for several species, including some quite small ones, slopes do not differ significantly from zero. Slopes of similar plots for nocturnal species are typically closer to unity. Various other species — nocturnal, diurnal and crepuscular — particularly Australian ones, are intermediate, filling in this continuum of thermoregulatory tactics (Pianka 1986).

A straight line can be represented as a single point in the coordinates of slope versus intercept. These two parameters are plotted for linear regressions of body temperatures on air temperatures for 82 species of lizards in Figure 25.1. Each data point represents the least-squares linear regression of body temperature against air temperature for a given species of desert lizard. Interestingly, these data points fall on another, transcendent, straight line. The position of any particular species along this spectrum reflects a great deal about its complex activities in space and time, and the line plotted in Figure 25.1 thus offers a potent linear dimension on which various species can be placed in attempts to formulate general schemes of lizard ecology (Pianka 1986). Various other ecological parameters, including reproductive tactics, can be mapped onto this emergent spatial-temporal axis (Pianka 1986).

The intriguing 'intercept' of the intercepts (38.8°C) approximates the point of intersection of all 82 regression lines and presumably represents an innate design constraint imposed by lizard physiology and metabolism. It is presumably not an accident that this value also corresponds more or less to the body temperature of homeotherms, particularly mammals!

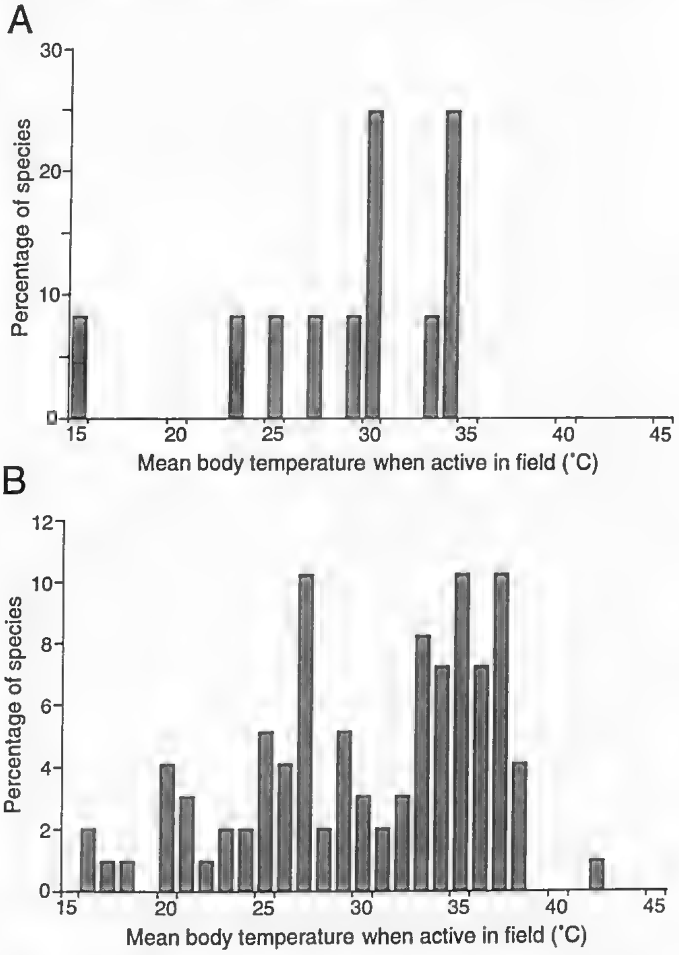

Figure 25.2 Frequency distribution of mean body temperatures of squamate species active in the field. A, snakes; B, lizards. (Data from Heatwole & Taylor 1987; Greer 1989) [W. Mumford]

Different taxa of squamates have somewhat different body temperatures when active (Fig. 25.2). Among the Australian representatives for which data are available, the frequency of lizards with high preferred temperatures is greater than for snakes. Among the snakes, more pythons tend to have higher temperatures than do elapids, and among the lizards more dragons (agamids) and goannas (varanids) operate at higher temperatures than do skinks, which in turn are higher than geckos and pygopodids (Fig. 25.3). These differences reflect, at least in part, the activity cycles and habitats of these groups. Skinks have a wide range of habits and preferred temperatures. Those species toward the lower values in Figure 25.2 are burrowing forms, whereas those at the higher end of the spectrum are diurnal, surficial ones. Similarly, the geckos with low preferred temperatures are nocturnal and the few with high preferences are diurnal. Clearly, the thermal relations of active squamates vary widely among taxa and are profoundly influenced by their spatial and temporal patterns of activity.

Reptiles in the field are not always able to achieve the body temperatures they prefer in a laboratory gradient, but rather operate over a wider activity range. Geckos depart more widely from equality of field and laboratory temperatures than do other lizard taxa, and often operate below preferred levels in the field (Fig. 25.4).

Cool forests have few lizard species and individuals; they may simply be too shady and too cold to provide adequate basking sites. Birds and mammals on the other hand do quite well in such areas, partly because of their endothermy. By contrast, lizards constitute an extremely conspicuous element of the vertebrate faunas of most deserts, especially warmer ones. Indeed, the mammalogist Finlayson (1943) referred to the vast interior deserts of Australia as 'a land of lizards'. Like other ectotherms, lizards obtain their bodily heat primarily from the external environment, as opposed to endotherms such as birds and mammals which can produce their own heat internally by means of oxidative metabolism. Moreover, along with other ectotherms (Pough 1980b), lizards are low-energy animals. Bennett & Nagy (1977) underscored the great 'economy of the saurian mode of life' by pointing out that one day's food supply for a small bird will last a lizard of the same body size for over a month. Ectothermy presumably has distinct advantages over endothermy under the harsh and unpredictable conditions that prevail in deserts (Schall & Pianka 1978). By means of this thermal tactic, snakes and lizards can conserve water and energy by becoming inactive whenever difficult physical conditions occur, such as during drought, the heat of midday, or shortages of resources. Birds and mammals must sustain these inhospitable periods at a substantially higher metabolic cost. Ectothermy thus confers lizards with the ability to capitalise on scant, unpredictable resources.

Water also has an important role in the ecology of squamates. Australia is largely desert and there are some unique adaptations to aridity among its desert lizards. Noteworthy is the imbibing of water from moist sand by the thorny devil, *Moloch horridus* (Pl. 5.6). The interscalar spaces are arranged in such a way that they carry water by capillarity from the moist sand to the corner of the lizard's mouth (Bentley & Blumer 1962).

Weather may influence different segments of the population differently. Differential survival of one sex over the other would alter sex ratios in the population. The egg stage may be particularly vulnerable. For example, Bustard (1968d) noted impairment of hatching success of eggs of the gecko *Gehyra variegata* when rainfall was slight during the incubation period, and Cogger (1978) found that *Ctenophorus fordi* suffered high egg mortality during a hot, dry summer.

Squamates are influenced by the geometry of their habitat, and population densities may reflect availability of particular structures. *Ctenophorus nuchalis* requires a small bush for a sun perch in close proximity to a taller shade perch (Heatwole 1970). Areas where perches are too widely spaced are unsuitable for these lizards and they do not occur. Thus, the population density

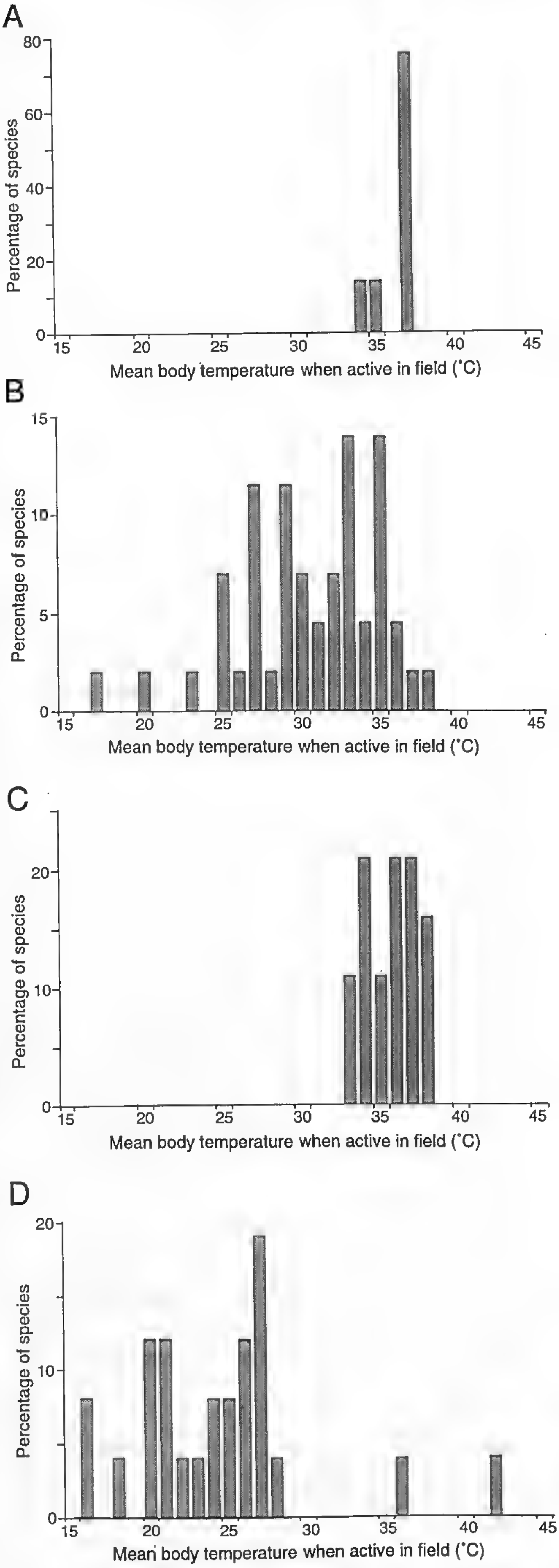

Figure 25.3 Frequency distribution, by family, of mean body temperature for lizards active in the field. **A**, Varanidae; **B**, Scincidae; **C**, Agamidae; **D**, Gekkonidae. (Data from Heatwole & Taylor 1987; Greer 1989) [W. Mumford]

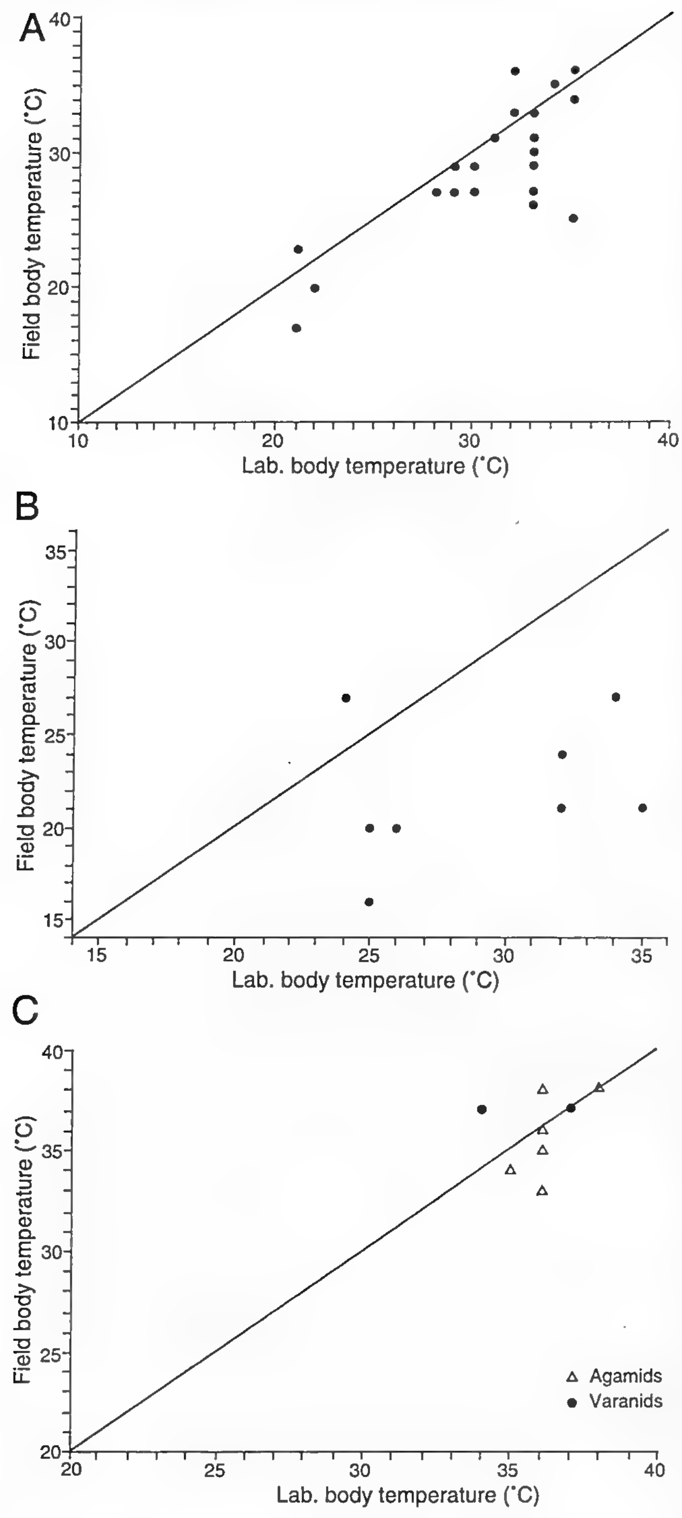

Figure 25.4 Relationship between mean body temperature of lizards active in the field and mean temperature preferred in a laboratory gradient. The diagonal line indicates equality of field and laboratory temperatures. **A**, Scincidae; **B**, Gekkonidae; **C**, Agamidae, Varanidae. The data are a subset of the data used in Fig. 25.3. (Data from Heatwole & Taylor 1987)
[W. Mumford]

of this species is partly controlled by spacing of vegetation. Similarly, the densities of the gecko *Oedura ocellata* is related to the availability of loose bark under which it shelters; almost all suitable sites are occupied (Bustard 1971). Densities of the water skink, *Eulamprus quoyii*, correlate well with the abundance of rocks in open areas. These structures are important as basking platforms (Law & Bradley 1990) and as shelter from predators (Daniels & Heatwole 1990).

Squamates that construct their own burrows are not so restricted by naturally occurring shelter and can extend their capacity to exploit their environment. The example of *Ctenophorus nuchalis* cited above is relevant. This species tires at midday after a dash of only a few metres and it digs burrows at intervals between its sun and shade perch, thereby always having available a retreat within its sprint distance (Heatwole 1970).

The complex burrow system of *Egernia striata* is a very important feature of the Australian sandy deserts (Pianka & Giles 1982). These skinks dig elaborate tunnels which are used as diurnal retreats by many species of nocturnal geckos, including *Heteronotia binoei*, *Nephrurus levis*, and *Rhynchoedura ornata*. They are also exploited as refuges by various diurnal lizards, such as *Ctenophorus isolepis* and *Varanus eremius* and the large elapid snakes, *Pseudechis australis* and *Pseudonaja nuchalis*. The burrows are elaborate, with several interconnected openings often as far as a metre apart, and vaguely reminiscent of a tiny rabbit warren. Most of the removed sand is piled up in a large mound outside one 'main' entrance (Pianka & Giles 1982).

A sympatric, but smaller species, *Egernia inornata*, digs a much simpler burrow, consisting of a U-shaped tube with but one arm of the 'U' open. The other arm of the 'U' typically stops just below the surface of the ground and can be broken through for use as an emergency escape hatch. The entrances to tunnels of *E. inornata* face north or north-west. Whereas *E. striata* is mainly active in summer, *E. inornata* is active during cooler periods by virtue of being crepuscular and less seasonal. Sitting in a northward-facing burrow entrance during the day would expose it to the relatively warm northern sky. Thus, the interspecific difference in orientation of burrows between these two species may reflect their differences in seasonality and activity period.

Foraging and Diet

Many predators attack their prey from ambush, but others usually hunt while on the move. These two modes of foraging have been called the 'sit-and-wait' versus the 'widely-foraging' tactic, respectively (Pianka 1966). Of course, these designations are somewhat artificial, although numerous animal groups seem to fall rather naturally into either one category or the other. For example, agamids and geckos primarily sit and wait for their prey, whereas many skinks forage widely. Some species are more versatile, such as the scincid *Ctenotus taeniolatus*, which uses both foraging tactics; juveniles spend proportionately more time in active foraging than do adults (Taylor 1986). The water skink, *Eulamprus quoyii*, is an active forager on land but adopts a sit-and-wait tactic at the water's edge when feeding on aquatic prey (Daniels 1987).

Desert sites in North America and Australia support similar numbers of species of sit-and-wait foragers, whereas this mode of foraging is distinctly impoverished in the Kalahari (Pianka 1986). Markedly fewer species forage widely in western North America and in the Kalahari than in the Australian deserts. Intercontinental comparisons of proportions of total species in various foraging modes are also instructive. A full 60% of North American lizard species are sit-and-wait foragers, compared to only 16% in the Kalahari and 18% in Australia.

Overall energy budgets of widely-foraging species are approximately half as great again as those of sit-and-wait species (Huey & Pianka 1981). As would be expected, sedentary foragers tend to encounter and eat rather mobile prey whereas more active, widely-foraging predators consume less active prey.

Because they are moving more or less continually, widely-foraging species tend to be more visible, and therefore suffer higher predation rates. Widely-foraging species fall prey to lizard predators that hunt by ambush whereas sit-and-wait lizard species tend to be eaten by predators that forage widely, generating "crossovers" in foraging mode between trophic levels. Widely-foraging lizard species are also more streamlined and have longer tails than sit-and-wait species (Huey & Pianka 1981).

Table 25.1 Diets of some Australian varanid lizards, expressed as the percentage of items by number in the stomach. Populations of *Varanus gouldii*, *V. mertensi*, *V. mitchelli* and *V. panoptes* sampled from northern and western Australia are denoted by (a) and (b) respectively.

Species		Mammals	Birds	Lizards	Snakes	Reptile eggs	Frogs	Fish	Aquatic insects	Non-aquatic insects	Other aquatic arthropods	Other non-aquatic arthropods	Other	Source
Varanus brevicauda		–	–	–	–	15	–	–	–	85	–	–	–	Pianka 1970a
Varanus caudolineatus		–	–	20	–	–	–	–	–	63	–	16	2	Pianka 1969a
Varanus eremius		–	–	35	–	–	–	–	–	50	–	3	12	Pianka 1968
Varanus gilleni		–	–	63	–	–	–	–	–	38	–	–	–	Pianka 1969a
Varanus gouldii flavirufus		<1	<1	10	–	37	–	–	–	39	–	11	–	Pianka 1970b
Varanus gouldii	(a)	<1	–	3	<1	7	2	<1	–	79	<1	6	–	Shine 1986d
	(b)	–	14	7	–	–	–	–	–	57	–	21	–	Shine 1986d
Varanus mertensi	(a)	<1	<1	–	<1	4	4	3	20	6	56	4	–	Shine 1986d
	(b)	1	1	–	–	2	5	5	15	36	32	2	–	Shine 1986d
Varanus mitchelli	(a)	1	1	1	–	2	1	37	4	33	5	13	1	Shine 1986d
	(b)	–	–	–	–	3	5	14	3	22	–	54	–	Shine 1986d
Varanus panoptes	(a)	1	<1	3	<1	2	7	1	<1	80	1.5	4	–	Shine 1986d
	(b)	–	5	5	–	–	16	–	–	68	–	5	–	Shine 1986d
Varanus tristis		–	2	8	0	12	–	–	–	76	–	–	2	Pianka 1971b

Another spin-off of foraging mode involves reproductive tactics. Clutch sizes of widely-foraging species tend to be smaller than those of sit-and-wait species, probably because the former simply cannot afford to weight themselves down with eggs to as great an extent as can the latter (Vitt & Congdon 1978). Foraging style constrains reproductive prospects.

Most Australian lizards are opportunistic, generalised insectivores. However, some are dietary specialists, eating only a very narrow range of prey items. For example, among pygopodids, *Lialis burtonis* (Pl. 4.10) eats principally small skinks (Patchell & Shine 1968a, 1968c) and *Pygopus nigriceps* (Pl. 4.12) eats more scorpions than most other lizards. The diet of the agamid *Moloch horridus* is restricted to ants (Pianka & Pianka 1970). Other species are termite specialists, including the nocturnal geckos *Diplodactylus conspicillatus* and *Rhynchoedura*, as well as some diurnal skinks (*Ctenotus* species) (Pianka 1969c). Food specialisation on termites and ants is economically feasible because these social insects normally occur in a clumped spatial distribution and hence constitute a concentrated food supply. Still other lizard species, while not quite so specialised, also have narrow diets.

Most lizards have much more catholic diets. Thus, Australian goannas include arthropods, frogs, reptiles, birds, mammals and carrion in their diet and some extend their prey to fish as well (Table 25.1). Diet varies interspecifically, especially between semi-aquatic and terrestrial species, and within a species differs seasonally and geographically (Shine 1986d). Pianka (1968, 1970a, 1970b, 1971b, 1982) tracked four species (*Varanus giganteus*, *V. gouldii*, *V. tristis* and *V. eremius*) as a means of studying their foraging. All ranged widely, and daily forays typically covered a distance of a kilometre. *Varanus gouldii* (Pl. 9.10) appeared to encounter most of its food by digging, whereas the tracks of *V. tristis* usually led almost directly from tree to tree, which presumably they climbed in search of food. *Varanus eremius* is attracted to fresh holes and diggings, and almost invariably will visit any man-made digging within a day or two. In a typical foraging run, an individual *V. eremius* often visits and goes down into several burrows belonging to other lizard species, especially the complex burrow systems of *Egernia striata*. In contrast to *V. gouldii*, it seldom does its own digging, but rather catches its prey above ground. Its tracks have been observed intercepting those of another smaller lizard with evidence of an ensuing tussle, and they have been seen to attack another lizard from ambush.

A surprising number of Australian lizards are omnivorous and include plant food as either a supplementary or principal component of their diet. For example, up to 82% of the gut contents of *Egernia cunninghami* may be plant material (Barwick 1965), and skinks of the genus *Tiliqua* (Pl. 6.1, 6.3) are fond of fruit as well as of snails, arthropods and carrion. Among the agamids, *Pogona barbata* supplements its insect diet with flowers and soft herbage, and the water dragon, *Physignathus lesueurii*, feeds on fruits, insects and frogs (Cogger 1992).

Within a species there may be temporal and spatial variation in composition of the diet. The type of food may change opportunistically in response to fluctuating prey abundances and availabilities (Pianka 1986; Shine 1986c; Taylor 1986).

In an environment with a scant food supply, a consumer cannot afford to bypass many inferior prey items because mean search time per item encountered is long and expectation of prey encounter is low (MacArthur & Pianka 1966). In such an environment, a broad diet maximises the return per unit effort, and favours generalisation. In a food-rich environment, however, search time per item is low since a foraging animal encounters numerous potential prey items. Under such circumstances, substandard prey items can be bypassed economically because expectation of finding a superior item in the near future is high. Hence, rich food supplies favour selective foraging and lead to narrow food niche breadths. Some lizards eat a greater diversity of foods in dry years (presumably times of low food availability) than in average ones, but contract their diet during periods of prey abundance (Pianka 1970c). The winged alates of termites, which appear in huge numbers after heavy summer rains, can form the sole food of desert lizards, even for species that do not normally consume termites. During such fleeting moments of great prey abundance, there is little, if any, competition for food and dietary overlap among members of the assemblage may be nearly complete.

Table 25.2 Diets of Australian snakes, summarised by genus. The number of taxa indicates the number of species, with the number of populations in parentheses. Diet data, expressed as the percentage of number of items in the stomach, are shown as the maximum and minimum percentages for species within each genus. The median percentage is shown in parentheses for those genera in which data for 6 or more species and/or populations were summarised.

Taxon	No. of taxa	Mammals	Birds	Lizards	Snakes	Reptile eggs	Frogs	Fish	Inverts	Source
TYPHLOPIDAE										
Ramphotyphlops	4	–	–	–	–	–	–	–	100	Shine & Webb 1990
BOIDAE										
Aspidites	2	6–44	3	47–81	3–10	2–3	–	–	–	Shine & Slip 1990
Chondropython	1	44	56	–	–	–	–	–	–	Shine & Slip 1990
Liasis	7	33–100	3–25	11–67	5	–	5–33	–	–	Shine & Slip 1990
Morelia	3(4)	69–100	8–10	17–23	–	–	–	–	–	Shine & Slip 1990; Slip & Shine 1988a
ACROCHORDIDAE										
Acrochordus	1	–	–	–	–	–	–	100	–	Shine 1986b
COLUBRIDAE										
Boiga	1(3)	7–47	19–54	28–56	–	–	6–12	–	–	Shine 1991c
Dendrelaphis	1(3)	8	–	29–39	–	–	54–95	–	5	Shine 1991c
Tropidonophis	1(2)	2	–	4	–	–	94–98	2	–	Shine 1991c
ELAPIDAE										
Acanthophis	1	32	9	53	–	–	6	–	–	Shine 1980a
Austrelaps	1(6)	2–3	–	37–90	1–5	2	10–61	–	3–4	Shine 1977b, 1987d
Cacophis	3	–	–	93–100	2	–	6	–	–	Shine 1980a
Demansia	4	–	–	73–100	–	–	9–27	–	–	Shine 1980d
Denisonia	2	–	–	–	–	–	95–96	–	4–5	Shine 1983c
Drysdalia	1	2	–	44–100	–	–	5–53	–	3	Shine 1981b
Echiopsis	1	13	2	52	–	–	32	–	2	Shine 1982
Furina	1	–	–	100	–	–	–	–	–	Shine 1981a
Hemiaspis	1	–	–	65	–	–	35	–	–	Shine 1977a
Notechis	1	3	2	2	–	–	92	–	–	Shine 1977a
Pseudechis	5(13)	2–75(11)	3-18	14–75(39)	1–29(8)	5	15–86(60)	+	7–12	Shine 1977a, 1987b
Pseudonaja	7(11)	5–100(48)	1–3	24–100(46)	1–6	1–25	2–41(6)	–	–	Shine 1977a, 1989
Rhinoplocephalus	4	–	–	89–100	5–11	–	1–6	–	–	Shine 1984a, 1988a
Simoselaps	10	–	–	25–100(100)	–	25–100	–	–	–	Shine 1984b
Suta	9(10)	–	–	59–100(98)	1–17	1–14	3–5	–	–	Shine 1977a, 1983c, 1988a
Tropidechis	1	48	7	4	–	–	41	–	–	Shine & Charles 1982
Vermicella	1	–	–	–	100	–	–	–	–	Shine 1980e

Biologically significant variation occurs between species in utilisation of certain relatively minor food categories. Thus, Hemiptera-Homoptera, mantids-phasmids and various flying insects, such as wasps, Diptera, and Lepidoptera tend to be better represented in the diets of climbing lizard species than they are among terrestrial species. Likewise, geckos tend to consume more nocturnal arthropods (scorpions, crickets, roaches, and moths) than do most diurnal species, although certain diurnal lizards capture nocturnal prey in their diurnal retreats (Huey & Pianka 1983). Such prey items are thus indicators of spatial and temporal patterns of activity.

Relatively few foods dominate diets of desert lizards (Pianka 1986). Prey resource spectra are broadly similar between three continents, although notable quantitative differences occur. In North America, 84% of the diet comprises seven food groups. They are, in decreasing order by volumetric importance, beetles, termites, insect larvae, grasshoppers plus crickets, ants, plant materials, and vertebrates. In the Kalahari, termites, beetles and ants far outweigh all others, and form 71% of the total. In Australia, the five most important categories comprise 77% of the total. In decreasing order of importance, they are vertebrates, termites, ants, grasshoppers plus crickets, and beetles. The same three categories, termites, beetles and ants, constitute major prey items in all three continental desert-lizard systems. Termites assume a disproportionate role in the Kalahari, as do vertebrate foods in Australia, which are largely a reflection of varanid diets.

Whereas most lizards eat arthropods, primarily insects, Australian snakes generally prey upon vertebrates (Table 25.2). There are exceptions (Mushinsky 1987). Australian pythons feed largely on birds and mammals with other vertebrates being of lesser importance, and then primarily in the diet of juveniles (Slip & Shine 1988a). Many of the Australian elapids have broad diets including frogs, reptiles and mammals. Shine (1977a, 1987d) found that differences in proportions of these categories in the diet is the result of opportunistic feeding and depends largely on habitat. Snake species living in wetter habitats eat more frogs whereas those from drier habitats eat more lizards. Mammals and birds are less common because of relative unavailability in preferred habitats. There are also age differences, with juveniles tending to take lizards and frogs rather than mammals or birds (Shine 1989).

There are, however, specialist feeders. Many of the smaller elapid species eat lizards, especially skinks (Table 25.2). The taipan, *Oxyuranus scutellatus*, feeds mainly on small mammals, the bandy-bandy, *Vermicella annulata*, (Pl. 8.4) feeds solely on typhlopid snakes (Shine 1980d) and some species of *Simoselaps* feed exclusively on eggs of squamates (Scanlon & Shine 1988). In addition, some species depart from the norm and eat invertebrate prey instead of, or in addition to, vertebrates. Some of the small Australian elapids eat arthropods (Table 25.2) and typhlopid snakes are specialist feeders on ants and termites (Cogger 1992).

Australia has an unusually high number of aquatic snake species, including the families Acrochordidae, Colubridae (*Amphiesma* and various genera of the subfamily Homalopsinae), Laticaudidae and Hydrophiidae, in all about 40 species. Most of these eat fish and/or crustaceans (McCosker 1975; Cogger 1992). Some of the freshwater ones include frogs in their diet. The Australian sea snakes *Emydocephalus annulatus* and *Aipysurus eydouxii* feed solely on fish eggs (Voris 1966; Heatwole 1987).

Most of the Australian elapids and pythons are active foragers. For example, the genus *Demansia* (Pl. 8.6; Shine 1980d) is convergent with diurnal, surficial colubrids in ways of facilitating chase and capture of fast-moving prey. By contrast, the highly camouflaged death adder, *Acanthophis antarcticus*, is an ambush strategist and in this regard is convergent with viperids (Shine 1980c) as is the boid *Morelia spilota* (Slip & Shine 1988a).

Acanthophis antarcticus is also the only Australian elapid known to use 'caudal-luring' (Fig. 35.1; Chizar, Boyer, Lee, Murphy & Radcliffe 1990). The tail of juveniles, in contrast to the otherwise cryptic colouration, is banded and resembles a caterpillar. On the approach of potential prey, the snake wriggles the tip of the tail in a worm-like fashion to lure its victim within striking range. The only lizard known to practise caudal luring is the snake-like, legless pygopodid *Lialis burtonis* (Murray, Bradshaw & Edward in press). Its tail is not distinctively marked.

LIFE HISTORY

Most lizards and snakes lay eggs, but some species retain their eggs internally and give birth to living young. Oviparous species may retain the eggs for varying times and lay them at different developmental stages; viviparity is merely one end of a continuum in which the eggs are retained to the hatching stage (Shine 1983b). Viviparity, or live-bearing, has arisen independently almost 100 times among squamates, even several times within a single genus (Shine & Bull 1979; Shine 1985). Viviparity and egg retention probably has evolved because of the advantage it confers in enabling successful reproduction in cooler regions at high elevations and high latitudes (Tinkle & Gibbons 1977; Shine & Bull 1979) and it may be a current determinant of geographic distributions (Shine 1987b). In the south-eastern highlands of Australia, viviparous skinks can maintain temperatures 7°C higher than the nest temperatures of oviparous skinks and accordingly produce young a month earlier than the egg-laying forms (Shine 1983d).

Some species reproduce only once every second or third year, others but once each year, while still others lay two or more clutches per year. A multivariate statistical analysis of life history patterns identified the same three clusters among both snakes and lizards (Dunham, Miles & Reznick 1988) — single brooded oviparous species, multiple brooded oviparous species, and single brooded viviparous species. In addition, a fourth cluster emerged for a few biennial viviparous lizards and snakes.

Among Australian species (Heatwole & Taylor 1987), agamids are oviparous and generally have two, or even three, clutches per year. Geckos are oviparous and have only one clutch. Skinks have single clutches each year; tropical species are oviparous but both oviparity and viviparity are represented among temperate ones. Most Australian elapids are viviparous with only one annual brood, but some such as *Vermicella* (Shine 1980d) and *Pseudonaja* (Shine 1977b) are oviparous, and the latter may have more than one clutch per year. Females of *Tropidechis* (Shine & Charles 1982) and of the hydrophiid sea snake *Aipysurus laevis* (Burns 1985) only reproduce every second year.

Average clutch size varies from one egg to 50 or more among different species of lizards and snakes (Fitch 1970). Clutch size is fixed at one or two eggs in certain families (geckos, pygopodids) and genera. Across species, modal clutch size among lizards is two, whereas it is six to eight among snakes (Fitch 1970). Greer (1989) reviewed clutch sizes in Australian lizards, and reported ranges of one to three in pygopodids, one or two in geckos, two to 35 in varanids and one to 35 in agamids. Skinks had clutch sizes of one to 11, except in *Hemisphaeriodon gerrardii* which has been reported to have clutches up to 53 eggs. Values for elapid snakes tended to be higher than for lizards, and ranged from five to 38, except for the low clutch size of two to seven eggs in *Suta gouldii* (Heatwole & Taylor 1987). Larger species

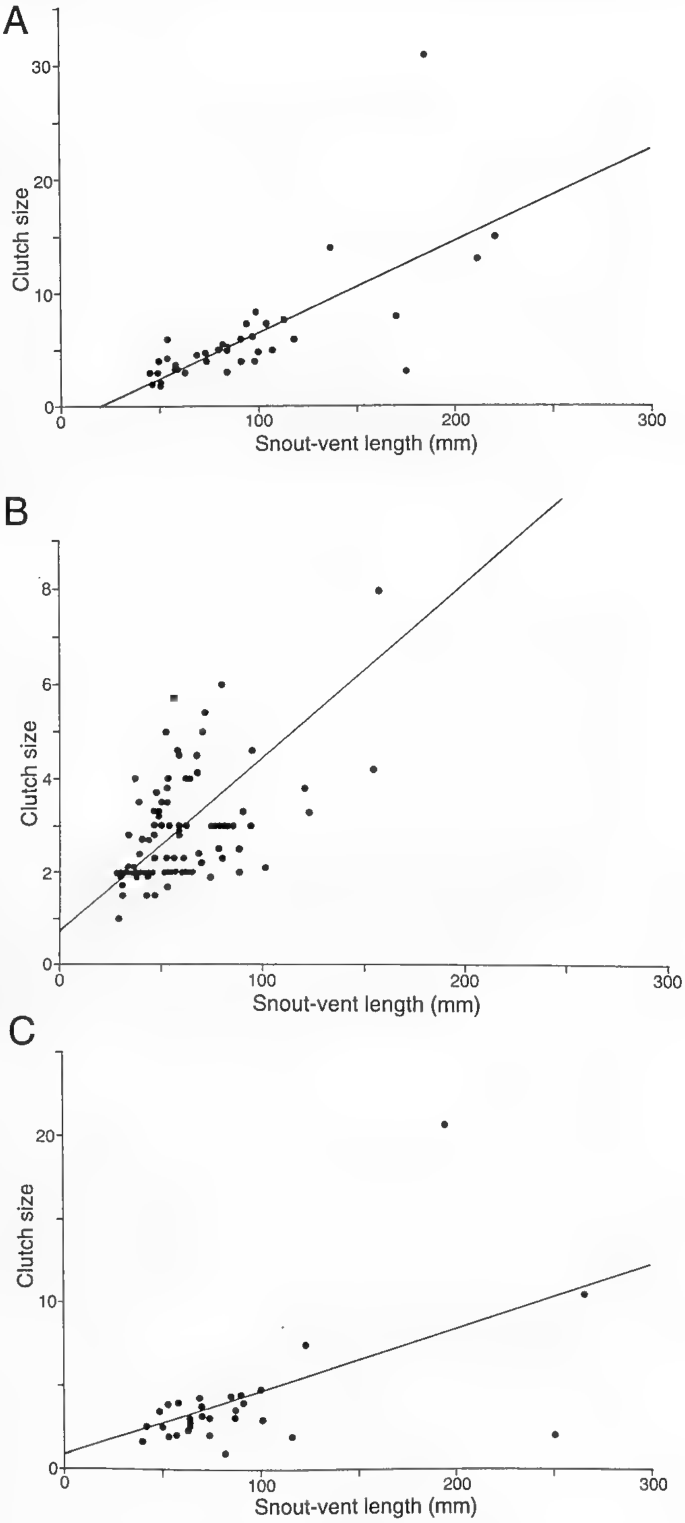

Figure 25.5 Relationship of mean clutch or brood size to mean body length of adult females of Australian skinks. A, Agamidae, all oviparous; B, Scincidae, oviparous; C Scincidae, viviparous. (Data from Greer 1989)
[W. Mumford]

tend to have larger clutch sizes than smaller species (James & Shine 1988) (Fig. 25.5).

Substantial spatial and temporal variation in clutch size exists within species. For example, in the double-clutched agamid, *Ctenophorus isolepis*, the average size of 67 first clutches (3.01 eggs, August to December) was distinctly smaller than that for 41 second clutches (3.88 eggs, January to February) (Pianka 1971a). Females increase in size during the season, and, as in most lizards and snakes (Heatwole & Taylor 1987; Seigel & Ford 1987), larger individuals tend to lay larger clutches. Interestingly, these same females appear to invest relatively more in their second clutches than they do in their first clutch. Average volume for 25 first clutches was only 11.2% of female weight, but increased to 15.1% in 15 second clutches (Pianka & Parker 1975b).

Changes in fecundity with fluctuations in food supplies and local conditions from year to year or location to location are known. Females tend to lay larger clutches in years with above-average precipitation and presumably ample food supplies (Hoddenbach & Turner 1968; Pianka 1970c; Parker & Pianka 1975; Dunham 1980).

The bulk (weight or volume) of a clutch or litter mass, expressed as a fraction of a female's total body weight is known as 'relative clutch mass', or RCM. It ranges from as little as 4 to 5% in some species up to 20 to 30% in others. Ratios of clutch or litter weight to female body weight correlate strongly with various energetic measures (Ballinger & Clark 1973; Vitt 1977) and have been used as crude indices of a female's instantaneous investment in current reproduction. In Australia, tropical lizards have about 20% lower relative clutch masses than do those from the temperate zone (James & Shine 1988).

The size (or weight) of an individual oviducal egg or newborn progeny is an inverse measure of the extent to which a juvenile lizard must grow to reach adulthood. It varies widely among lizards, from 1 to 2% up to 17% of adult weight (Pianka 1986). Small species of snakes have a greater ratio of offspring size to adult size than do larger species (Shine 1978a). Species that protect their offspring by egg-brooding or which bear living young produce larger, though fewer, progeny than related oviparous species lacking parental care (Shine 1978c).

Any two components of the triad of clutch size, female reproductive investment, and expenditure per progeny uniquely determine the third. However, the forces of natural selection moulding each of these differ substantially. Clutch or litter weight presumably reflects an adult female's best current investment tactic in a given environment at a particular moment, whereas expenditure on any given individual progeny is probably more closely attuned to the average environment to be encountered by a juvenile. Clutch or litter size is thus the direct result of the interaction between an optimal parental reproductive tactic and an optimal juvenile size, and clutch size is simply the ratio of the former divided by the latter.

Food-specialisation may be a factor in this interaction. Among Australian geckos, species with relatively restricted termite diets tend to lay comparatively larger eggs and hence have higher expenditures per progeny than do those with more catholic diets (Pianka & Pianka 1976). Habitat type also may be important. Shine (1988b) found that the aquatic species in each of four lineages of snakes had lower reproductive investments and carried the clutch further anteriorly in the body than did terrestrial ones. He suggested that the important role of the posterior part of the body in swimming is a constraint on the weight of young that can be carried.

Timing reproduction so that young begin life under conditions most favourable for their survival and growth has obvious selective advantage, and clearly such timing varies latitudinally and with patterns of seasonal change. Heatwole & Taylor (1987) recognised 11 different kinds of reproductive cycles in Australian squamates depending on the phenology of spermatogenesis, ovulation and mating in relation to seasons or to wet and dry periods. In most tropical areas, squamates tend to breed in the wet season. However, in Australia, the wide variety of reproductive cycles includes year-round breeders, wet season breeders and even dry season breeders (James & Shine 1985).

In terms of reproductive cycle, perhaps the most unusual Australian squamate is *Ctenophorus maculosus*, in which mature males mate with mature females in spring, but with first-year ones in late summer which apparently retain the sperm until they reach sexual maturity the following spring (Mitchell 1973).

Timing of reproduction may vary with yearly differences in the triggering environmental cues. In an eight-year study, Bradshaw, Saint Girons & Bradshaw (in press) found that *Ctenophorus nuchalis* and *C. caudicinctus* from the same geographic area responded in different ways to annually variable patterns of rainfall. As a result there were some years of breeding synchrony between these two species but they were out of phase in other years.

Growth rate in squamates varies interspecifically, between the sexes and with age, nutritional state and extent of stored energy (Andrews 1982). It is usually rapid in hatchlings or newly born, declines toward sexual maturity and thereafter is even slower until maximum size is attained. Growth is partly influenced by temperature, moisture, appetite and availability of food but may also be controlled by intrinsic factors (see Heatwole & Taylor 1987).

In *Ctenophorus ornatus* growth rates are variable (Bradshaw 1971; Baverstock 1975). In favourable years mortality is similar between rapidly growing and slowly growing lizards. During cold winters slow-growers have high mortality but are relatively unaffected by long, dry summers. The reverse is true of the fast-growing ones which are cold-hardy but sensitive to drought. When an unusually hot, dry summer followed an exceptionally cold winter (a rare event) mortality was high and the populations declined (Bradshaw 1981).

Weather may influence different segments of the population differently. Differential survival of one sex over the other would alter sex ratios in the population. The egg stage may be particularly vulnerable (Packard & Packard 1988). For example, Bustard (1968d) noted impairment of hatching success of eggs of the gecko *Gehyra variegata* when rainfall was slight during the incubation period, and Cogger (1978) found that *Ctenophorus fordi* suffered high egg mortality from desiccation.

Longevity and age of attainment of sexual maturity varies widely among species of squamates. Some species of lizards are essentially annuals. They reach maturity early and many adults of a given year class die by the time their offspring mature. Accordingly, there are marked shifts in population structure. Examples of short-lived Australian species are *Ctenophorus isolepis* (Pianka 1971c) and *Ctenophorus fordi* (Cogger 1978). Other species mature slowly and are long-lived, and intermediates lie along the spectrum between these extremes. *Egernia cunninghami* lives for eight years or longer (see Heatwole & Taylor 1987) and sometimes groups of at least three generations can be observed living together in crevices in limestone outcrops. The 'family groups' of *Egernia stokesii* may also include multiple age groups (Pl. 6.5). Australian snakes may be unusual, as Shine (1978a) noted that six species he studied reached sexual maturity earlier than most previously-studied snakes from other continents.

Within a given species, females may mature later than males. Shine (1978a) suggested that this arises from two selective pressures. The first of these is fecundity, which is proportional to body size in females (but not in males) and therefore larger females tend to leave more offspring. Secondly, early maturation and consequent production of small clutches may not warrant the considerable risks associated with reproduction that are peculiar to females and which are independent of body size.

In squamates the two sexes often differ in adult size, and in some sexually dimorphic species males are larger, in others the females

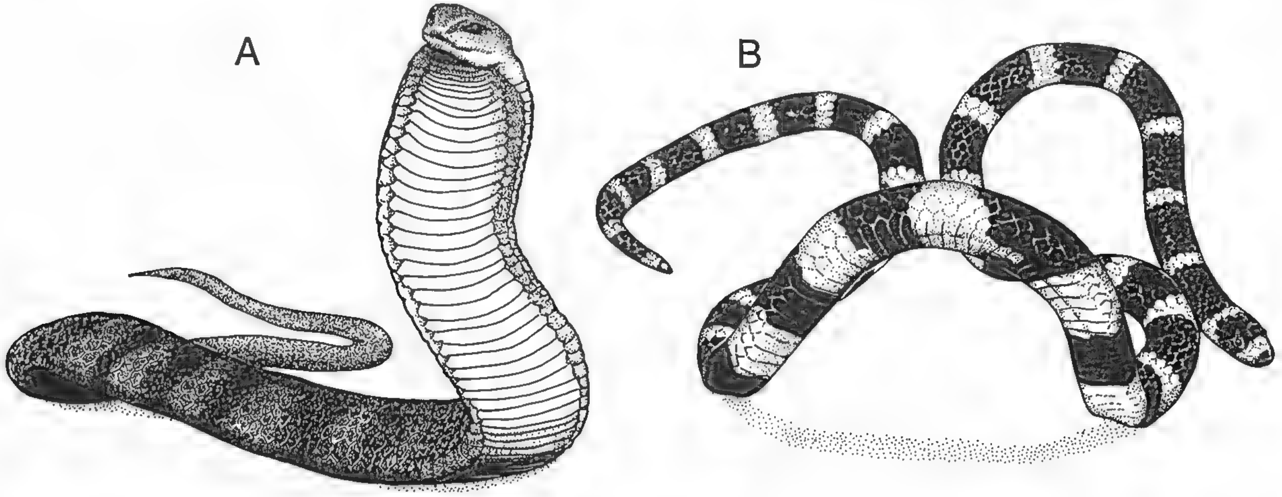

Figure 25.6 Displays of snakes. A, a tiger snake, *Notechis scutatus* rears up and flattens its neck in the typical aggressive display of elapids; B, a bandy-bandy, *Vermicella annulata*, elevates part of its body in a defensive display typical for this species. (A, from photo by David Stammer; B, from photo by Richard Shine)
[M. Cilento]

are. The difference arises either by both sexes growing at equal rates until sexual maturity is reached and then one sex continuing to grow, or the larger sex showing faster growth rates at an early age, before sexual maturity (Andrews 1982). In *Acrochordus arafurae*, even neonates display sexual dimorphism in size (Shine 1986d). The ultimate causes of sexual differences in size are probably variable and include both social and ecological factors. Shine (1978b) found a high correlation between male combat in snakes and the occurrence of sexual dimorphism in size in which males were the larger sex. Male *Pseudechis porphyriacus* engage in combat and displace rival courting males and even disrupt mating couples (Shine, Grigg, Shine & Harlow 1981), and large male size may be an advantage in such struggles. Dimorphism in which females are larger can be attributed to the greater fecundity attendant on large size in females, noted above. This generalisation does not fit all snakes, as in some species, body size seems to be related to sex-specific differences in trophic niche, where the two sexes differ in food habits, head morphology and/or foraging sites (Shine 1986c; Camilleri & Shine 1980).

Numbers of males and females are usually, though not always, equal at hatching or birth. The sex ratio may become skewed at a later age. Often it is difficult to ascertain whether this has resulted from differential mortality, or is an artifact of behavioural differences between the sexes (Parker & Plummer 1987). The greatest discrepancy in sex ratios occurs in parthenogenetic species, in which females lay fertile eggs without having been inseminated by a male. Parthenogenesis is rare in squamates although it is scattered over a number of families. In Australia, three genera of geckos (*Heteronotia*, *Nactus* and *Lepidodactylus*) are known to have species that either wholly lack males or have parthenogenetic populations as well as bisexual ones (Moritz & King 1985).

Predators and Defence

Predation is seldom seen by observers and is difficult to quantify. Indeed, it is seldom known how many species of predators a given species has, or what their relative importances are. The only attempt to provide such information for an Australian species is that of Daniels & Heatwole (1984). They listed 102 known or potential predators for the semi-aquatic skink, *Eulamprus quoyii*, of which 14% were believed to have a significant impact.

Most commonly, squamates respond to predators by remaining motionless, thereby preventing detection by visually hunting predators, by flight, or by presenting an aggressive display either as bluff or as an overt attack. These are not mutually exclusive and may occur in sequence within a given species (Greene 1988).

Cryptic colouration is common in Australian squamates, but perhaps is illustrated best by the death adder, *Acanthophis antarcticus*, a species seldom seen unless nearly trodden upon. Mouth-opening displays by various agamids and other squamates are well known. *Pogona barbata*, for example, opens the mouth to expose its yellow lining and erects the gular region as a 'beard' (Pl. 5.8; Throckmorton, de Bavay, Chaffey, Merrotsky, Noske & Noske 1985). Tongue protrusion in the scincid genus *Tiliqua* (Pl. 6.2, 6.4), erection of the neck frill in the frill-necked lizard (*Chlamydosaurus kingii*, Pl. 5.9), and rearing up and spreading the hood in large elapids (Fig. 25.6A; Pl. 8.8) are remarkable and all have become famous. In the last example real danger underlies such threats. The bandy-bandy, *Vermicella annulata*, (Fig. 26.6B; Pl. 8.4) reacts to disturbance by elevating its conspicuously banded body into vertical loops (Bustard 1969b).

If one tactic is ineffective, switching to another may be necessary, and timing of such switches may be crucial for survival. For example, once detected, a cryptic species may need to flee. If flight is left too late escape may no longer be possible, but if initiated too early, it may attract attention prematurely. The distance that an animal will permit a potential predator to approach before flight is called the 'approach distance'. In some lizards it varies inversely with degree of crypsis, well-camouflaged species having a shorter approach distance than those which are more conspicuous (Heatwole 1968). Bauwens & Thoen (1981) found that gravid females tend to rely on crypsis longer than males or non-gravid females and also stay closer to safe retreats. These behaviours compensate for slower locomotion occasioned by the load of eggs.

Approach distance also varies with temperature in a compensatory way. Lizards initiate escape earlier when they are cold and sluggish than when they are at higher temperatures and have faster responses (Rand 1964). *Ctenophorus nuchalis* allows closer approach when it is near a safe retreat, such as the entrance to its burrow, than when it is in the open (Heatwole 1970). Hertz, Huey & Nevo (1982) found that some agamids would flee when body temperatures were high enough to permit rapid running, but when colder would stand their ground and attack aggressively. This phenomenon also occurs in the Australian *Tympanocryptis cephalus* (Pianka pers. obs.).

Age and gender may influence the capacity of lizards to escape predators. Huey, Dunham, Overall & Newman (1990) studied variation in locomotor performance and showed that male lizards were faster than females, and that older adults had slightly greater stamina than young adults but were slower.

The immediate orientation and location of water skinks, *Eulamprus quoyii*, and the physical characteristics of their habitat, determine which of several escape tactics is used (Daniels & Heatwole 1990). Diversity of escape responses is higher in habitats which are structurally more diverse. Unmolested lizards usually face the water, and flee in the direction they are facing when disturbed. Running is energetically less taxing than either swimming or diving, and flight to the shelter of rocks is employed more often than aquatic escape. Where rocks are abundant they are used for escape more often than in less rocky areas. Escape to the water is less often employed where currents are swift. By choosing the least expensive option, in terms of energy, only a small part of their locomotor capacity is used in any given escape attempt, and leaves sufficient reserves for repeated attempts if necessary.

The tail is important in protection of many lizards against predation. This organ has diversified greatly and serves a wide variety of functions, including a role in locomotion and hence in escape from predators. Many climbing species, such as the Australian sandridge agamid *Gemmatophora longirostris*, have evolved extraordinarily long tails which serve as effective counterbalances. Tail removal experiments (Snyder 1952) have shown that such long tails also enable lizards to raise their forelegs up off the ground and to run on their hind legs alone, which is faster than tetrapodal locomotion. Prehensile tails are used as a fifth leg in climbing by some arboreal lizards.

Several Australian geckos of the genus *Diplodactylus* have glandular tails that secrete and store a smelly, noxious mucus. When disturbed, these lizards squirt large amounts of this sticky substance (Rosenberg & Russell 1980). Surprisingly, their tails are fragile and easily shed, though quickly regenerated. The related species *Diplodactylus conspicillatus*, which has a non-glandular and very stubby, bony tail, is a nocturnal termite specialist that hides in the vertical shafts of abandoned spider holes during the day. This gecko is thought to point head-downwards and use its tail to block off the tunnel. Similarly, a species of skink, *Egernia depressa*, wedges itself into tight crevices in mulga tree hollows and rocks, blocking off the entrance with its strong, spiny tail.

The tails of many species of lizards (especially among juveniles) are brightly coloured or otherwise conspicuous, and evidently function to lure a predator's attack away from the more vulnerable and less dispensable parts of the animal. The Australian desert skink, *Ctenotus calurus*, lashes and quivers its bright azure blue tail alongside its body continuously as it forages slowly through the open spaces between plants. Similarly, tiny *Morethia butleri* juveniles twitch their bright, red tails as they move around in the litter beneath *Eucalyptus* trees.

Some species can lose their tails voluntarily, or with minimal external force, a process known as autotomy. Many geckos, pygopodids and skinks exhibit autotomy, whereas most agamids, varanids and snakes do not. Lizards with tough tails usually cannot regenerate a very complete tail, whereas autotomous lizards quickly regenerate a new tail from the stub. Although re-grown tails are occasionally almost indistinguishable from the original externally, their internal support structure is cartilaginous rather than bony. Many autotomous lizards possess special adaptations for tail loss, including weak fracture planes within each tail vertebra, muscular attachments that facilitate autotomy and tail movement after dismemberment, as well as mechanisms for rapidly closing off blood vessels and healing.

The freshly dismembered tails of autotomous species, or pieces thereof, typically thrash around wildly. Writhing of autotomised tails distracts predators, thereby enhancing escape by the tail's erstwhile owner (Dial & Fitzpatrick 1983). When threatened, some species raise or move the tail making it a more likely target for attack than the rest of the body (Johnson & Brodie 1974).

Certain small predators, such as the pygmy varanids *Varanus gilleni* and *V. caudolineatus*, may actually 'harvest' the exceedingly fragile tails of geckos that are too large for them to subdue intact (Pianka 1969b). Some skinks, including many *Ctenotus* species, return to the site where their tail was lost and swallow the remains of their own tail! Few, if any, other vertebrates display auto-amputation and self cannibalism.

Temperature affects autotomy. Daniels (1974) found that cold *Oedura marmorata* retained the tail longer than warm individuals. By contrast, *Gehyra variegata* autotomises its tail more readily and parts with a greater portion of it, at both low and high temperature extremes than at intermediate temperatures (Bustard 1968b).

Tail size may also be important. Adults of *Oedura marmorata* have relatively larger tails than juveniles. They are better able to avoid predatory attacks by species of the dasyurid genus *Antechinus*, apparently because larger tails have a greater distractive quality than small ones when autotomised (Daniels, Flaherty & Simbotwe 1986).

Loss of the tail seems to disturb lizards surprisingly little, as individuals often resume basking and foraging within minutes, as if nothing had happened. There are longer term consequences, however. The tail is an organ of fat storage in many lizards and its loss depletes part of the energy reserve of the animal. Smyth (1974) and Taylor (1984) found that there was a significant reduction in number and/or energy content of eggs or young in skinks that had lost their tails in comparison with those with intact tails. When deprived of food, tailless *Oedura marmorata* have shorter survival times than those with complete tails (Daniels 1984). In periods of food shortage, the immediate advantage of autotomy in escaping predators would have to be balanced against the long-term disadvantage arising from loss of stored energy. Accordingly, under suboptimal conditions these geckos show a reluctance to autotomise. One might expect that lizards would conserve tail lipids by losing only that portion of the tail under attack. That expectation is not fulfilled in *O. marmorata*, which autotomises the entire tail regardless of the position of attack (Daniels 1985c).

Not all side-effects of autotomy are disadvantageous. In contrast to previous studies indicating locomotion was impaired by tail loss, Daniels (1983) found that *Oedura marmorata* increased its running speed, and presumably its ability to flee from predators, after autotomy. Different modes of escape may be differently affected by autotomy. In *Eulamprus quoyii* loss of the tail results in greatly reduced swimming speeds, but slightly increased running speeds (Daniels 1985a).

Tail-break frequency has been used to estimate intensity of predation, and in some species has been correlated with density of predators (for example, Pianka 1967). However, this method has numerous problems and limitations (Schoener 1979). Efficient predators that leave no surviving prey obviously will not produce broken tails, but nevertheless may exert substantial predation pressures. Broken and regenerated tails may therefore reflect lizard escape ability or predator inefficiency better than intensity of predation. Furthermore, conspecific fighting may lead to broken tails. In his review, Arnold (1988) noted that it is difficult to unravel the contributions of intraspecific conflict, age, predation efficiency and intensity, and ease of autotomy, and that this approach to predation rate had sampling, methodological and interpretive problems. He concluded that tail-break frequencies are often unreliable indices of predation; clearly this method should be used cautiously and only when sufficient data are available to assess independent effects on break frequencies, a condition that seldom applies.

Social Behaviour

The repertoire of social behaviour in squamates includes courtship and mating, aggression, parental care, and limited aggregation and communal activities. Australian species have received little attention in this regard in comparison with overseas species.

In lizards, courtship may involve elaborate posturing and displays. Often the same movements are involved in aggressive displays and whether mating or combat ensues depends on the sex of the individual toward which the display is directed, and/or the responses it makes. Brattstrom (1971b) has noted that head bobbing and fast waving of the forelimb in *Pogona barbata* is a challenge. If the individual towards which it is directed is a female mating may ensue, but if it is a male fighting may result unless the recipient male adopts a submissive posture and/or waves its

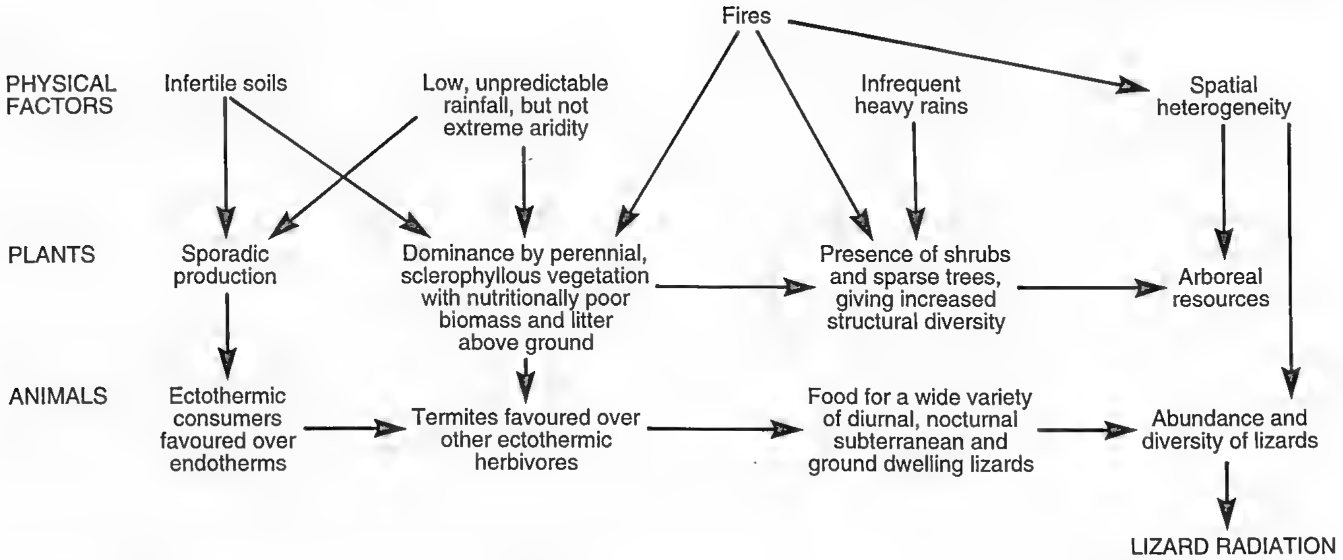

Figure 25.7 Web of ecological forces hypothesised to account for high lizard species richness in arid Australia. (After Morton & James 1988) [D. Wahl]

forelimb slowly. Similar behaviour occurs in some other species of Australian agamids (Carpenter, Badham & Kimble 1970; Shine 1990). Male varanids exhibit 'shuddering' of the head when courting (Carter 1990).

Intraspecific aggression takes various forms. In many snakes aggression between males takes the form of rearing up by antagonists, which attempt to depress the head and neck of the opponent (Gillingham 1987). In the Australian elapids *Pseudechis porphyriacus* and *Austrelaps superbus* (Shine & Allen 1980; Shine *et al.* 1981) prolonged bouts of ritual combat occur between males, and direct attack, including biting, occurs. In lizards, aggression often centres around defense of a territory, and may involve females as well as males. It is widespread among Australian agamids and skinks (for example, see Brattstrom 1971b; Done & Heatwole 1977) and has been suggested for some geckos (Bustard 1968d, 1969a). Under conditions of crowding, defense of territories may break down and be replaced by a dominance hierarchy, with the more dominant individuals having the advantage in feeding, mating and selection of basking sites (Done & Heatwole 1977).

Selection of an appropriate ovipositional site and concealment of recently deposited eggs are both widespread in lizards and snakes and can be interpreted as rudimentary parental care, as it enhances survival of the young. In addition, Shine (1988c) recognised four categories of post ovipositional parental care in squamates: the female defends the nest briefly against conspecific females; the female remains with the eggs and guards them against predators or pathogens; the female coils around the eggs and warms them by shivering thermogenesis, and protects them against predators; the female aids newly born or newly hatched young. Parental care among Australian squamates seems rare. Some Australian pythons coil around their eggs and incubate them (Slip & Shine 1988c). There is inconclusive, anecdotal evidence suggesting parental care in some varanids (Shine 1988c).

Most aggregations of squamates are seasonal or short-term (Gregory, Macartney & Larsen 1987). The spectacular denning of large numbers of snakes in winter, so characteristic of North America, is unknown in Australia, although the skink *Lampropholis guichenoti* has been reported in small winter hibernacula (Powell, Heatwole & Heatwole 1978). The whipsnake *Demansia psammophis* nests communally (Covacevich & Limpus 1972).

Home Range and Movements

Few species of terrestrial vertebrates wander randomly. Most restrict their activities to a discrete and familiar area, or to home ranges. In squamates home ranges often include one or more shelter sites, such as burrows or rock crevices, food sources and basking perches. They may overlap with the home ranges of other individuals of the same species, especially those of mates and young. A home range (or part of it) when defended against other individuals, is called a territory.

In general, snakes tend to have less well defined, and often larger, home ranges than do lizards of equivalent sizes. In both groups, but especially in snakes, an individual may remain in a small area for considerable time, before moving to a new home range some distance away (Shine & Slip 1988d). Juveniles frequently have smaller home ranges than adults, and the sexes may differ in average home range size. Gravid females may be especially sedentary (Shine 1979). Bradshaw (1971) studied a population of *Ctenophorus ornatus* in which juveniles emigrated from the area in which they hatched, probably because of harassment by adult males. They set up home ranges in marginal areas where predation upon them was high. The survivors returned to preferred habitat as sexually mature individuals one to three years later, replacing the previous generation, now in decline. Thus, there are 'adult' areas and 'juvenile' areas with individuals moving between them in ontogenetic shifts of home range.

Most home range data are from terrestrial, surficial species. The aquatic filesnake *Acrochordus arafurae*, has an exceptionally large home range (up to 4.7 ha) and individuals move on average 141 m during a single night during the wet season (Shine & Lambeck 1985). Information on burrowing snakes is practically non-existent.

Squamate Assemblages and Resource Partitioning

An assemblage is that part of a biotic community that is made up of all organisms of a particular taxon, such as the Squamata. Like the entire community, an assemblage has structure that can be characterised in terms of species richness (number of species), taxonomic composition, guild membership and equitability (apportionment of individuals among species) (Heatwole & Taylor 1987). Reviews of reptilian assemblages by Heatwole (1981, 1982), Scott (1982), Pianka (1986) and Heatwole & Taylor (1987) indicate that species richness is affected by latitude, elevation, climate (rainfall, evapotranspiration, amount of sunshine), soil fertility, habitat diversity and structural complexity of the vegetation. Most assemblages are inequitable in that they are characterised by a few abundant species and many less common ones. Various of these generalisations have received support from analysis of Australian assemblages (for example, Kitchener, Chapman, Dell & Muir 1980; Milewski 1981; Heatwole & Butler 1981).

Australian squamate assemblages from arid areas are richer than those from equivalent habitats on other continents (Pianka 1969b, 1973, 1985, 1986). Many factors have been postulated to account for this, and include: unpredictable precipitation; nutrient-poor soils; the unique hummock life-form and physical structure of *Triodia* (spinifex) grasses; abundant and diverse termite fauna; nocturnality; fossoriality; arboreality; habitat specificity; usurpation of ecological roles occupied by other taxa elsewhere; a complex fire-succession cycle that creates and maintains habitat heterogeneity via disturbance; biogeographic and historical factors (Pianka 1989).

Morton & James (1988) proposed a causal network relating a wide range of climatic, edaphic and biotic factors to the diversity of lizards in arid Australia (Fig. 25.7). In their network, unpredictable rainfall and nutrient-poor soils result in scant and erratic primary production, favouring *Triodia* grasses which are poor in nitrogen. These grasses form relatively unusable fodder for most herbivores except termites, which in turn constitute a food resource that is particularly suitable for exploitation by ectothermic lizards. Moreover, aperiodic, heavy rainfall promotes woody vegetation, thereby supporting arboreal and litter-dwelling species of lizards. Pianka (1989) added fire and fire-induced spatial heterogeneity to their scheme.

Resources are not partitioned randomly in squamate assemblages, but have been shown to be highly organised (Winemiller & Pianka 1990). Species differ in the foods they eat, in the times they are active and in the habitats and microhabitats they exploit (see above; Webb 1985); that is, they occupy different niches. Such ecological differences often have been interpreted as strategies reducing interspecific competition, and in many instances supporting evidence is strong. However, other factors, such as predation, also may influence the kinds and numbers of species that make up an assemblage, and thermoregulatory demands and social factors may alter the assemblage structure through their influence on habitat selection and use (see Heatwole & Taylor 1987).

Different assemblages sometimes contain unrelated species that have parallel niches and have independently developed similar adaptations, morphologies, physiologies and ecologies. Such convergent species-pairs, which occupy similar niches in different assemblages, are known as ecological equivalents. *Moloch horridus* from arid Australia and *Phrynosoma* spp. from American deserts are both spiny lizards subsisting on a diet of only ants (Pianka & Pianka 1970). Some snakes have jointed teeth that facilitate capture and handling of their prey of skinks with osteoderms in the scales; an Australian legless lizard, *Lialis burtonis*, is an ecological equivalent which also feeds on skinks (Fig. 28.6) and has independently evolved hinged teeth (Patchell & Shine 1986b).

Parasites and Disease

Squamates suffer from bacterial, fungal and viral infections, are hosts to endoparasitic protozoans, trematodes, cestodes, nematodes and lingulatids, are attacked by ectoparasitic mites and ticks, and are fed upon by blood-sucking flies and mosquitoes. They also have tumours and skin warts, and suffer from degenerative arterial maladies (Bellairs 1969). Manuals on the diagnosis and treatment of these diseases have been published (Frye 1973, 1990; Cooper & Jackson 1981; McCracken 1988). Incidences of infection sometimes are high in wild populations (for example, 25% for malaria in some lizards, Schall, Bennett & Putnam 1982; 35 to 40% for ticks on one species of gecko and 10% for mites on another, Bustard 1968d, 1969a). Among captive squamates, two of the most prevalent problems are ectoparasitic mites and mouth rot. One Australian parasite, the acanthocephalan *Sphaerechinorhynchus rotundicapitus*, has two semi-aquatic squamate hosts. It occurs in the rectum and large intestine of *Pseudechis porphyriacus*. Eggs released into the water are eaten by aquatic arthropods, which form prey of the skink *Eulamprus quoyii*. Infected lizards are preyed on by the snake, thus completing the cycle (Daniels 1990).

Infection in squamates leads to changes in thermoregulatory behaviour and an increase in body temperature ('behavioural fever') (Firth & Turner 1982), and metabolic rate, stamina and fat reserves may be altered. Reproduction can also be affected via reduced clutch size (Schall 1982). Daniels (1985b) noted that voluntary diving time in Australian water skinks (*Sphenomorphus quoyii*) was greater in individuals infected by acanthocephalans than in uninfected animals.

Ticks have been reported from only 32 species of Australian squamates (Roberts 1970). Information is almost certainly incomplete as many species probably have not been examined. However, analysis of Roberts' data suggests that only the larger species of lizards and snakes are host to ticks. Few small squamates are represented and then only by rare records of only one species of tick whereas most of the larger reptiles harbour several species. Varanid lizards and the larger species of skinks and snakes were especially prominent in the list of hosts. With the exception of a single record, geckos were absent.

Of the eight genera and 58 species of ticks known from Australia, only 11 species in two genera (*Amblyomma* and *Aponnomma*) have been reported reliably from squamates. Two additional genera are doubtfully recorded (one species each). Most of the tick species found on squamates are common to a number of species, including both lizards and snakes, and some occur on mammals as well. Four species account for most of the tick infestations. *Amblyomma moreliae* is the most widespread, in terms of hosts, and is recorded from 18 species in all squamate families, except the burrowing pygopodids and typhlopids. *Aponomma fimbriatum* is known from 15 host species, and *Amblyomma limbatum* and *Aponomma hydrosauri* each from 10 species.

Ectoparasitic mites infest a variety of Australian squamates and 38 species of lizards and snakes have been recorded as harbouring them (Domrow & Lester 1985; Domrow 1987); this list must be considered incomplete. Unlike ticks, mites infest small species of host as well as large ones. Many ectoparasitic mites attack warm-blooded hosts. Of the 19 genera and 107 species of chiggers (Prostigmata: Trombiculidae) recognised from Australia only seven genera (37%) and 14 species (13%) have been recorded from squamates. Similarly, of the 46 genera and 217 species of Australian ectoparasitic Mesostigmata, only three genera (7%) and seven species (3%) have been found on lizards and/or snakes. The most common hosts for mites are skinks (25 species), particularly for trombiculids. Prostigmatic mites were recorded most often on geckos (6 species).

Economic Significance of Snakes and Lizards

In addition to their scientific and aesthetic worth as wildlife, Australian squamates have an enormous, practical value. Most lizards are generalist insectivores and would be expected to play a role in controlling pest insect populations. However, there have been few attempts to evaluate their contribution quantitatively, or to make a monetary assessment of it. Crome (1981) found that lizards in an area suffering from dieback did not feed on the major defoliators of trees and therefore were not an agent of control of the malady. Similar studies in other systems, where size and habitat of harmful insects overlap to a greater extent with potential saurine predators are badly needed.

Many snakes and varanids prey on mammals and are potentially of benefit in controlling rodents. Again, information is mostly anecdotal. Many rural properties still keep carpet snakes in farm buildings as a means of rodent control, and in the recent past even urban warehouses carried out this practice.

Australian reptiles are highly prized in the pet trade and pythons and varanids exported illicitly net high prices, sometimes in excess of $1000 per animal. Reptile smuggling continues unabated and the pet trade threatens some species. It may be worth considering licensing the raising in captivity of selected species for export. Coupled with harsher penalties for infringements and more efficient surveillance of wild populations, this might serve as a conservation measure for endangered species.

Reptile leather is a prized commodity and sea snakes are harvested in Australia for this purpose. Given the reproductive properties and population characteristics of these animals it is unlikely that this industry can be sustained, except at a very low level, without depleting stocks.

Snakes and goannas, and their eggs are part of the traditional Aboriginal diet. In the Northern Territory, the larger, gravid females of the freshwater file snake, *Acrochordus arafurae*, are harvested selectively for food. Because this species reproduces infrequently, human predation has an effect out of proportion to the numbers taken (Shine 1986a).

Not all impacts of reptiles on humans are beneficial. Some reptiles serve as reservoirs for human diseases, for example, equine encephalitis. The larger venomous snakes pose a threat to the safety of humans and their domestic animals. However, with improved techniques for treating snake bite and better preparedness of the medical profession, threat to human life by snakes in Australia has become minimal. Snake venom is extremely valuable because of its uses in medicine and biochemical research. Several enterprises in Australia milk snakes and sell venom. Indeed, the venom of some sea snakes ranks among the most expensive substances for its weight in the world (Heatwole 1987).

26. BIOGEOGRAPHY AND PHYLOGENY OF THE SQUAMATA

Mark N. Hutchinson & Stephen C. Donnellan

This review summarises the current hypotheses of the origin, antiquity and history of the order Squamata, the dominant living reptile group which comprises the lizards, snakes and worm-lizards. The primary concern here is with the broad relationships and origins of the major taxa rather than with local distributional or phylogenetic patterns within Australia. In our review of the phylogenetic hypotheses, where possible we refer principally to data sets that have been analysed by cladistic methods. Analyses based on anatomical morphological data sets are integrated with the results of karyotypic and biochemical data sets.

A persistent theme of this chapter is that for most families there are few cladistically analysed morphological data, and karyotypic or biochemical data sets are limited or unavailable. Biogeographic study, especially historical biogeography, cannot proceed unless both phylogenetic data are available for the taxa and geological data are available for the physical environment. Again, the reader will find that geological data are very uncertain regarding the degree and timing of the isolation of the Australian continent from Asia and Antarctica. In most cases, therefore, conclusions should be regarded very cautiously.

The number of squamate families in Australia is low. Five of approximately fifteen lizard families and five or six of eleven snake families occur in the region; amphisbaenians are absent. Opinions vary concerning the actual number of families recognised in the Australian fauna, depending on whether the Pygopodidae are regarded as distinct from the Gekkonidae, and whether sea snakes, Hydrophiidae and Laticaudidae, are recognised as separate from the Elapidae. With the exception of the Pygopodidae, these families are represented in other parts of the world. However, several groups, such as the Scincidae, Typhlopidae and hydrophiine elapids, reach their greatest diversity, taxonomically and morphologically, in Australia (Figs 26.1, 26.2). In Table 26.1, the major groups of squamates in Australia are shown, listed by formal taxonomic name when widely accepted, but listed informally if relationships are controversial.

CHARACTER SETS EMPLOYED IN ANALYSIS OF SYSTEMATIC RELATIONSHIPS

Comparative anatomy has provided the main source of phylogenetic data for squamates and Camp's (1923) treatise on lizard relationships is usually the starting point for modern analyses of squamate phylogeny. Camp relied mainly on osteological characters of the cranium, hyoid and vertebrae, but also showed that several characters of body and throat musculature were informative. Behavioural data have been used little in reptile systematics, compared with taxa such as frogs and birds. Workers since Camp (for example, McDowell & Bogert 1954; Underwood 1957; 1967; Rieppel 1980a) generally continued to use and refine his approach. Technical advances in the last two decades have made the analysis of morphological data sets more rigourous and have permitted the analysis of increasingly large data sets. Examples involving the Australian fauna include the squamates (Estes, de Queiroz & Gauthier 1988), the gekkonoids (Kluge 1987), pygopodids (Kluge 1974, 1976a), carphodactylines (Bauer 1990), scincomorphans (Presch 1988), iguanians (Frost & Etheridge 1989) and boids (Underwood & Stimson 1990). The most comprehensive recent review is that of Estes *et al.* (1988), which attempts to revise Camp's work by

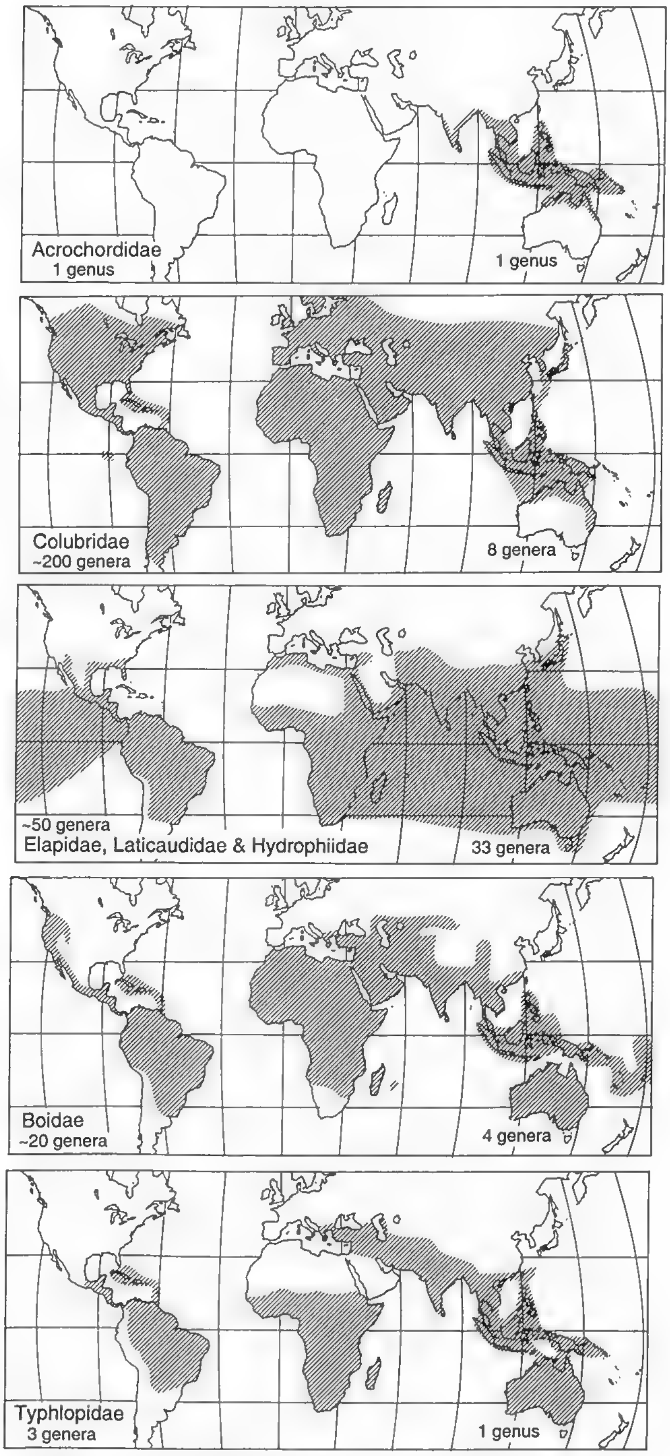

Figure 26.1 Worldwide distribution of snake families represented in Australia, and their taxonomic diversity based on numbers of genera. (After Shine 1991) [W. Mumford]

incorporating many new characters, scored across many more taxa, and analysing them in the light of recent advances in methods for reconstructing phylogeny.

In addition to the character sets provided by morphological analysis, systematists have available to them character sets derived from analysis of variation in chromosomes, proteins and nucleic acids (RNA and DNA). Chromosome studies of Australian squamates began in earnest with the work of King (1973) on skinks, and subsequent studies have included further work on skinks (Donnellan 1985; 1991a; 1991b) and considerable work on geckos (reviewed by King 1985; see also King 1987a, 1987b, 1987c, 1990; Moritz & King 1985), varanids (King & King 1975) and terrestrial elapids (Mengden 1985a, 1985b).

At the same time that computer programs have enabled more sophisticated analysis of morphological data, biochemical character sets have become more accessible and have improved in resolution. Recent reviews have dealt with methods for gathering, and analysis of, these latter types of character sets and the current controversies in each of these areas (King 1985; Baverstock & Schwaner 1985; Baverstock 1989; Hillis 1987; Hillis & Moritz 1990). Protein-based studies have included immunological comparisons of serum proteins of several groups including boid and elapid snakes, skinks and dragons (Baverstock & Donnellan 1990; Hutchinson 1980; Hutchinson, Donnellan, Baverstock, Kreig, Sims *et al* 1990; Cadle & Gorman 1981; Minton & Da Costa 1975; Mao, Chen, Yin & Guo 1978; Schwaner & Dessauer 1981; Schwaner, Baverstock, Dessauer & Mengden 1985a), as well as other allozyme-based studies aimed mainly at problems of alpha taxonomy (for example, Donnellan & Hutchinson 1990; Harris & Johnston 1977; Hutchinson & Donnellan 1992; Hutchinson & Schwaner 1991; Mather 1990; Milton, Hughes & Mather 1983; Milton 1990).

Table 26.1 The major Australian squamate taxa. Numbers for both genera and species are approximate for most taxa.

Taxon	Number of genera	Number of species
IGUANIA		
Agamidae	12	65
GEKKOTA		
Gekkoninae	7	29
Diplodactylinae	9	68
Pygopods	8	33
SCINCOMORPHA		
Scincidae	31	320
ANGUIMORPHA		
Varanidae	1	25
SCOLECOPHIDIA		
Typhlopidae	1	35
BOOIDEA		
Pythoninae	4	15
COLUBROIDEA		
Acrochordidae	1	2
Colubridae	8	10
Elapids	20	80
Sea Snakes	13	33
TOTAL	114	715

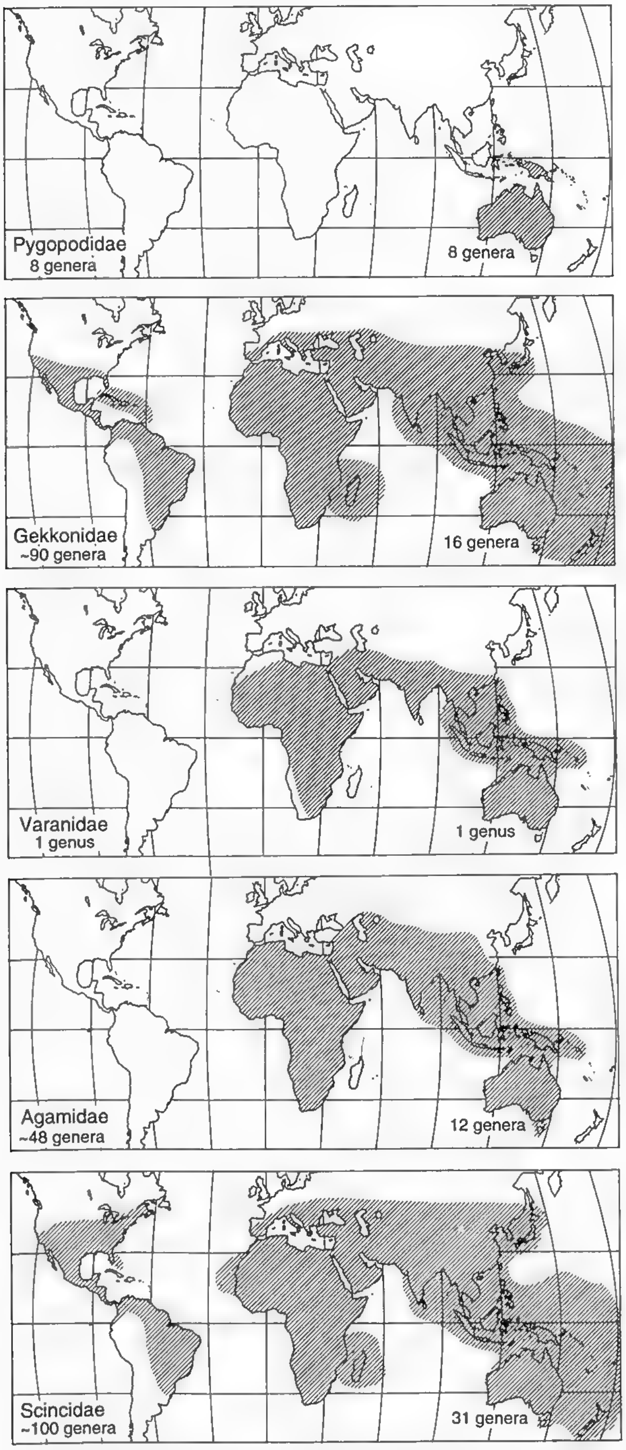

Figure 26.2 Worldwide distribution of lizard families represented in Australia and the taxonomic diversity based on numbers of genera.
[W. Mumford]

Readers should note that when we use the term 'primitive' in relation to a taxon, this does not imply 'selective inferiority' but rather refers to the taxon as having diverged earlier in the history of the group. Early divergence does not imply complete retention of the ancestral phenotype; mosaic evolution generally ensures that all lineages develop some unique specialisations (autapomorphies).

PHYLOGENETIC RELATIONSHIPS OF THE SQUAMATE FAMILIES

Relationships of the Squamata

The Squamata is by far the larger of the two surviving lineages of diapsid reptiles belonging to the Lepidosauria (Gauthier, Estes & de Queiroz 1988), and is represented by over 6300 species (Halliday & Adler 1988). The second lineage, the Sphenodontida, encompasses the two living species of tuatara (Daugherty, Cree, Hay & Thompson 1990), which are both confined to New Zealand. Squamates preserve, in many respects, the general size and habitus of the earliest reptiles (Carroll & Baird 1972), but all living squamates possess many derived character states compared with early diapsids (Benton 1985; Gauthier *et al.* 1988; Laurin

1991). Character states which diagnose squamates are loss of the lower temporal bar, including the quadratojugal bone, a streptostylic (movable) quadrate bone, a transverse hinge between the frontal(s) and parietal(s), which has been lost secondarily within some squamate groups, loss of gastralia and the unique male copulatory organs, the paired hemipenes.

The limits of the Squamata are still being established, and vary according to the data set used, the interpretations put on some characters and the stringency with which particular workers adhere to cladistic systematic methods. Carroll (1975, 1988) identified the Permo-Triassic Paliguanidae as the earliest known lizards, proposing that they had already diverged from the sphenodontid + squamate common ancestor. He also included the extinct, gliding kuehneosaurs of the Triassic (Robinson 1973) within the Squamata. Gauthier *et al.* (1988) rejected 'Paliguanidae' as a non-diagnosable assemblage and also excluded the kuehneosaurs from the Squamata. The divergence of these two rejected groups was placed prior to the divergence of sphenodontids and squamates. While there is still room for argument concerning the definition and composition of the Squamata, the scheme of relationships proposed by Gauthier *et al.* (1988), which effectively restricts the taxon to a group of lineages which still have living members, is accepted as a basis for this chapter.

Relationships within Squamata

The most exhaustive attempt to resolve interfamilial relationships among squamates was that of Estes *et al.* (1988), using a large data set which comprised 148 morphological characters. That study confirmed the existence of six monophyletic lineages within the Squamata: the Iguania (agamids, chameleons and iguanids), Gekkota (geckos and pygopods), Scincomorpha (cordylids, lacertids, scincids, teiids and xantusiids) and Anguimorpha (anguids, helodermatids, lanthanotids, and varanids), traditionally regarded as infraorders of lizards, the Serpentes, and the Amphisbaenia (Fig. 26.3). Though the existence and content of major phylogenetic lineages was confirmed and refined, branching patterns among lineages were recovered with much less confidence. The relationships of one lizard family, the Dibamidae (Greer 1985; Rieppel 1984b) also remained unresolved.

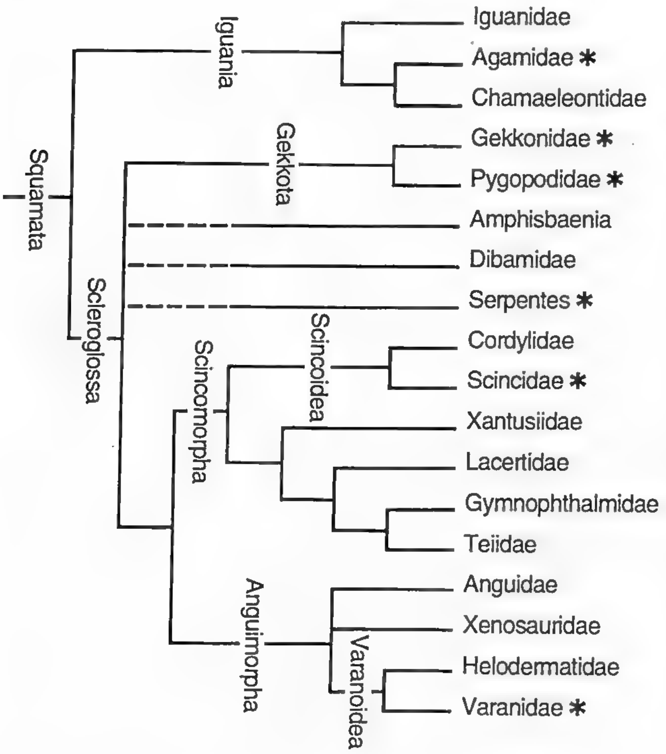

Figure 26.3 Interfamilial relationships within the Squamata. Australian taxa are indicated by *. (After Estes *et al.* 1988) [D. Wahl]

A major reason for the failures, recognised and well documented by Estes *et al.* (1988), is the very large amount of homoplasy evident in the data set. Very few of the characters available could be shown to have undergone unique changes, and reversals and convergences/parallelisms were the rule rather than the exception. Alternative branching patterns, differing little from one another in such measures as consistency or tree length, are commonly found in broad scale phylogenetic studies. The 'best' tree often is scarcely better than several others suggesting alternative branching patterns. Such a situation does not inspire great confidence that the historically true branching pattern has been discovered. One response to finding weakly supported phylogenetic hypotheses is to search for additional characters to provide corroborating synapomorphies for one of the competing trees. However, as illustrated by the data of Estes *et al.* (1988) convergence, parallelism, reversal and conservatism are so common that increasing the number of characters surveyed appears inevitably to increase the number of homoplastic similarities as well as providing additional synapomorphies, and the impasse may remain. After reviewing that study, Kluge (1989) concluded that additional and, more importantly, alternative sources of data appeared to be necessary to better resolve relationships among the major squamate lineages.

While well-corroborated hypotheses relating the major squamate lineages to one another are not available, some proposals on these relationships do exist and are moderately well-supported. The Iguania has been identified consistently as the sister taxon of all other squamates (Camp 1923; Estes *et al.* 1988). All other lizards, snakes and amphisbaenians are collectively termed the Scleroglossa (Estes *et al.* 1988 = Scincogekkonomorpha, Sukhanov 1961).

Morphological features such as a flattened and at least partly keratinised tongue, descending processes of the frontals and expanded septomaxillae which meet in a midline crest (indicating the importance of Jacobson's organ) are present primitively in other squamates (Estes *et al.* 1988), but are lacking in iguanians.

Other taxa have sometimes been considered as basal squamates, but based on one or a few character complexes. The retention in most geckos of persistently notochordal vertebrae has been a particular source of conflict — is this character a plesiomorphy or neotenic reversal? Similarities also have been noted in the cranial structures of fossil iguanians and teiids (Scincomorpha) (Estes & Price 1973), but these similarities may be symplesiomorphies. Based on shoulder anatomy only, Russell (1988) found that anguimorphans, not iguanians, were the sister group of all other squamates.

Even given the basal split of the Iguania, relationships among the three other lizard infraorders are still uncertain. Scincomorpha and Anguimorpha may be sister taxa (Estes *et al.* 1988), or Scincomorpha and Gekkota may be (Presch 1988; Schwenk 1988).

Relationships of the snake families, both to each other and to the several squamate lineages grouped as 'lizards', are a continuing source of debate. McDowell & Bogert (1954) presented a detailed case for a sister group relationship between snakes and varanoid lizards (helodermatids, lanthanotids, and varanids), that is, they saw snakes as arising within the Anguimorpha. By no means has this been universally accepted (Underwood 1967; Rieppel 1983; Rage 1984), but Estes *et al.* (1988) concluded that this general relationship probably was supported better than any other. However, the problems with the interpretation of some character state changes, and the significant support which could be found for alternative relationships, meant that the hypothesis of varanoid origin was not obviously better than other alternatives. Greer (1989) recently reviewed this problem and came to similar conclusions.

Three major grades of snakes are generally recognised, the blind snakes, 'primitive' snakes and the 'advanced' snakes. Blind snakes (Anomalepididae, Leptotyphlopidae, and Typhlopidae) are

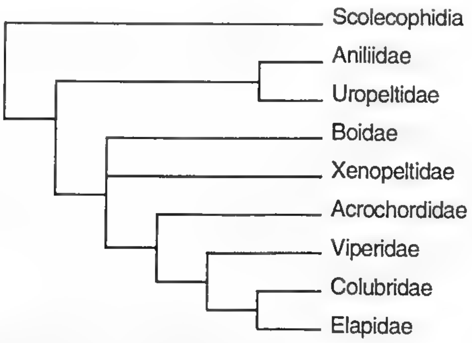

Figure 26.4 Summary of current views of the phylogeny of the major living snake taxa. (Modified after Rage 1984: fig. 37) [D. Wahl]

so extensively modified in relation to their fossorial, myrmecophagous (anteating) life that their anatomy leaves few clues regarding their relationships to other snakes. Recent authors (for example, McDowell 1987; Rage 1984; 1987) tend to place them as the sister group of all other Serpentes, as the Scolecophidia (an infraorder, or suborder if Serpentes is given ordinal status), and the remaining snakes form the Alethinophidia. Rage (1984), following in part the earlier work of Rieppel (1977; 1979), subdivided living alethinophidians into four superfamilies, the Anilioidea, Booidea, Acrochordoidea and Colubroidea, and suggested a phylogeny for these groups (Fig. 26.4). Relationships are uncertain among the anilioids and booids, either or both of which may be paraphyletic. An earlier, widely used scheme of higher taxonomy (Hoffstetter 1939) was certainly a grade classification, combining the acrochordoids and colubroids as the Caenophidia, and the anilioids and booids as Henophidia. McDowell (1987) used a more subdivided superfamilial scheme, which differed from that of Rage and Rieppel in the suggested affinities of some primitive snake taxa and elevated others (Tropidophiioidea and Bolyeroidea) to superfamilies of their own.

Uncertainties regarding the position of some extinct snakes, such as *Dinilysia* and the madtsoiines (Rage 1984; Scanlon 1992), and of some living snakes, notably the acrochordids (Dowling, Highton, Maha & Maxson 1983; McDowell 1987; Rage 1984; Underwood 1967), mean that any phylogenetic schemes must be tentative. In addition, compared to the four lizard superfamilial groups, there is much less evidence that the four snake superfamilies are natural groups. Relationships among primitive snakes, the Anilioidea and Booidea, have been considered by McDowell (1975; 1987), Rieppel (1977) and Rage (1984). The composition of the families included has been unstable, several genera were switched from one family group to another, and no general consensus on the phylogeny of these snakes was reached. At best there is a consensus that aniliids (*Anilius* and *Cylindrophis*) are the most generally primitive living snakes, with boines and pythonines being more advanced and tropidophiines closest to the origin of the advanced 'caenophidian' (colubroid) snakes.

The great majority of living snakes are colubroids, and only a broad outline of relationships is available, notwithstanding the considerable body of literature on the subject. Family boundaries have been very difficult to establish, and subfamilial schemes much more so. Relationships between taxa have not been satisfactorily established. The most recent, primarily morphological review, is that of McDowell (1987) who recognises four families, Atractaspididae (an African group; see also Underwood & Kochva 1993), Elapidae (with six subfamilies), Viperidae (with three subfamilies) and Colubridae (with nine subfamilies).

As McDowell (1987) pointed out, morphological classifications have generally proven to be poor at predicting the outcomes of biochemical phylogenetic studies. Cadle (1987, 1988) summarised the literature on immunological data relating to interfamilial relationships of colubroid snakes. Cadle's (1988) own data on serum albumin divergences suggested that the viperids, atractaspidids and elapids (including hydrophiines) were each early monophyletic offshoots of the basic advanced snake stock, leaving an unresolved, highly diverse group of colubrids as a further monophyletic lineage. This study included relatively few colubrids in reciprocal comparisons, leaving some doubt as to the monophyly of the colubrid 'family' as a whole. Dowling *et al.* (1983), using similar immunological methods, showed that considerable heterogeneity existed within the traditional Colubridae, although both their data and Cadle's (see also Cadle 1984) suggest that several monophyletic units exist, including *Atractaspis*, homalopsines, colubrines, natricines, boaedontines (= lamprophiines) and two groups of xenodontines.

As there is no comprehensive, well-corroborated phylogeny available for the Squamata as a whole, the following discussions begin at the level of the identifiable monophyletic groups that include Australian taxa. These groups and their Australian representative families are: the Iguania (Agamidae), the Gekkota (Gekkonidae and pygopodids), the Scincomorpha (Scincidae), the Anguimorpha (Varanidae) and the Serpentes (Typhlopidae, Boidae, Colubridae and Elapidae).

Iguania

The Agamidae plus Chamaeleonidae are recognised as a monophyletic sublineage, the Acrodonta (Estes *et al.* 1988; Frost & Etheridge 1989), based on the distinctive dentition in which tooth replacement is lost (except for the anteriormost few tooth loci), and adjacent tooth bases become confluent. Frost & Etheridge (1989) concluded that their data best supported the chameleons as nested within the traditional 'Agamidae', and the older name, Chamaeleonidae, would therefore have to be applied to this taxon (agamids + chameleons) in order to produce a monophyletic taxonomy. Such a confusing nomenclatural change has not found immediate favour, partly because the evidence for relationships among acrodont iguanians is conflicting and because a nomenclatural alternative (recognition of an additional family, Leiolepididae) could preserve the traditional taxon Agamidae without sacrificing the goal of a monophyletic taxonomy. The closest iguanian sister taxon of the Acrodonta was not established clearly by the analysis of Frost & Etheridge (1989).

Relationships among Australian agamids have been studied using morphology by Cogger (1960) and Witten (1982), by Moody (1980) as part of a study on all agamids, and by Frost & Etheridge (1989) as part of a study of iguanian relationships. The recent consensus concerning Australian agamid relationships is that the fauna is highly endemic, consisting of three lineages, the amphiboluroids, *Hypsilurus* and *Physignathus*. The amphiboluroids comprise *Amphibolurus*, *Caimanops*, *Chelosania*, *Chlamydosaurus*, *Cryptagama*, *Ctenophorus*, *Diporiphora*, *Moloch*, *Pogona* and *Tympanocryptis* (Witten 1982). Character states supporting the monophyly of this group include great reduction or loss of the lachrymal bone and an apomorphic karyotype ($2n = 32$, 10 pairs of microchromosomes, versus the plesiomorphic karyotype of $2n = 36$, 12 pairs of microchromosomes; Witten 1983).

The two remaining Australian genera, *Hypsilurus* (shared with New Guinea) and *Physignathus*, were thought to be more recent arrivals in Australia (Witten 1982), because of their phenetic similarity to some Asian taxa. However, Covacevich, Couper, Molnar, Witten & Young (1990b) have shown that *Physignathus*, at least, has been present in Australia for at least 20 million years, implying that the similarity between the living *P. lesueurii* of Australia and *P. cocincinus* of South-East Asia is the result of a lack of divergence rather than recency of origin. This view is supported by the immunological data (microcomplement fixation, or MC'F, of albumin) of Baverstock & Donnellan (1990), which suggests a closer relationship of *Physignathus* and *Hypsilurus* to the Australian radiation than to Asian *Gonocephalus* or other Asian genera (for example, *Calotes*). The data of Baverstock & Donnellan (1990) actually suggested a closer relationship of the Australian taxa to African *Agama* than to the Asian genera tested,

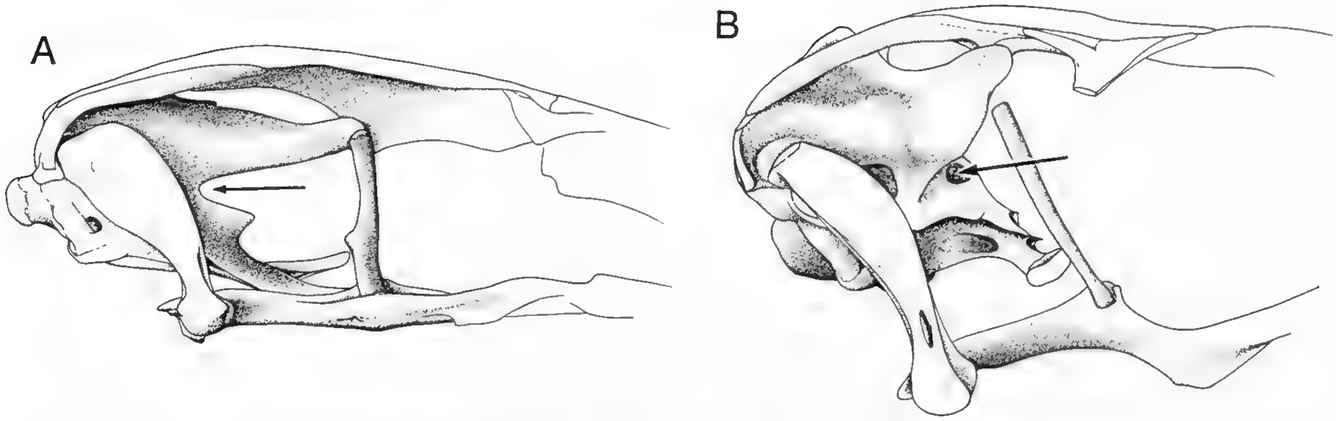

Figure 26.5 Lateral view of the trigeminal notch (marked with an arrow) on the anterior braincase of gekkotan lizards. A, a pygopodid, in which the notch remains open; B, a gekkonid, in which the notch closes to form a foramen. [J. Thurmer]

although this conclusion needs corroboration from further generic comparisons.

Relationships within the amphiboluroid radiation are very poorly known, even though there have been recent major generic rearrangements (Storr 1982a). Greer (1989) summarised the evidence put forward by Houston (1978) and Witten (1982) for two sublineages within the Australian radiation, which could be termed informally the *Amphibolurus* and *Ctenophorus* groups. The two are defined on preanal pore characteristics and presacral vertebral counts, but relationships within these assemblages have not been analysed explicitly. The genus *Moloch* has caused difficulty, partly because of its highly autapomorphic morphology, but also because of the anomalous behaviour of its serum albumin in MC'F experiments (Baverstock & Donnellan 1990). Greer (1989) suggested that fundamentally this monotypic genus is a highly modified relative of *Tympanocryptis*, a member of the *Ctenophorus* group.

Gekkota

Ideas on gekkotan relationships have fluctuated considerably, based on conflicting interpretations of some characters, notably vertebrae. Some authors argue for either very primitive divergence of the group or great specialisation, although both views may be correct. In such apparently primitive features as notochordal vertebrae and paired, median skull bones, geckos may exhibit neotenic reversals to more embryonic stages of development rather than retained primitive features. In the great reduction of skull arch elements, living gekkotans are highly specialised.

The limbless Australian pygopod lizards feature strongly in the problems currently besetting a better understanding of relationships within the gekkotans. Three recent studies differ on pygopod relationships. Estes *et al.* (1988) indicated a sister group relationship between pygopods and all other gekkotans, recognising the traditional family Pygopodidae (Fig. 26.3). Kluge (1987) concluded that the pygopods were the sister group only of the Diplodactylinae, and advocated the transfer of the latter subfamily from the Gekkonidae to the Pygopodidae. King's (1990; King & Mengden 1990) karyotypic studies led him to conclude that pygopods share a common ancestor with some diplodactylines.

The conflict between the two morphological data sets appears to be reducible to interpretation of two characters. Kluge (1987) united pygopods and diplodactylines on the basis of their shared possession of an O-shaped muscle which closes the auditory meatus. Estes *et al.* (1988) did not identify the characters they used to reject Kluge's hypothesis, but inspection of their data reveals at least two characters (possibly not independent; Hutchinson pers. obs.) of the prootic which unite the geckos, but exclude the pygopods. They are the anterior closure of the trigeminal notch to form a foramen, and ventro-lateral prolongation of the crista alaris to form a projecting triangular flange (Fig. 26.5A, B). Biochemical data relevant to this problem are lacking.

Within the traditional family Gekkonidae, representatives of two lineages occur in Australia, the globally distributed Gekkoninae, and the Diplodactylinae, endemic to the Australian region. The most recent assessment of their relationships to each other and other gekkonoids is that of Kluge (1987) (Fig. 26.6). He concluded that the diplodactylines (plus pygopods) are the sister group of gekkonines (excluding eublepharines), but relationships of the several non-Australian gekkonine lineages (teratoscincines, sphaerodactylines, ptyodactylines, *etc.*) to one another are incompletely resolved.

Gekkonines show little generic endemism in Australia, although species endemism is almost complete (the only exceptions are some shared with New Guinea and some more widespread human commensals). The only endemic genus is *Heteronotia*, unless the Australian *Phyllodactylus* species are recognised as the endemic genus *Christinus*, but phylogenetic data supporting the latter are yet to be presented. No scheme of relationships has been proposed for the Australian gekkonines.

Most phylogenetic information available for Australian geckos concerns the diplodactylines. Kluge's (1987) evidence for diplodactyline monophyly is based on two synapomorphies, an O-shaped muscle closing the auditory meatus, and a thickening of the tectorial membrane of the auditory papilla. The latter character is poorly surveyed in geckos and is known to be present in at least one gekkonine, *Thecadactylus* (Wever 1978). Two tribes have been proposed, the Diplodactylini and the Carphodactylini (Kluge 1967a), but only the latter has been subjected to a detailed phylogenetic study (Bauer 1990). Indeed, the monophyly of the two tribes has been taken for granted since Kluge's (1967a) pre-cladistic revision. King (1987a, 1987b) and King & Mengden (1990), on the basis of their karyotypic data, have suggested that *Oedura*, currently placed in the Diplodactylini, should be transferred to the Carphodactylini. Bauer (1990) provided a detailed phylogeny for the carphodactylines (he did not include *Oedura*). He placed *Carphodactylus* and *Phyllurus* as the sister group of *Nephrurus*, the latter expanded to include *Underwoodisaurus*. These three genera were placed as the sister group of *Pseudothecadactylus* and the remaining carphodactyline genera from New Zealand and New Caledonia, and the Australian

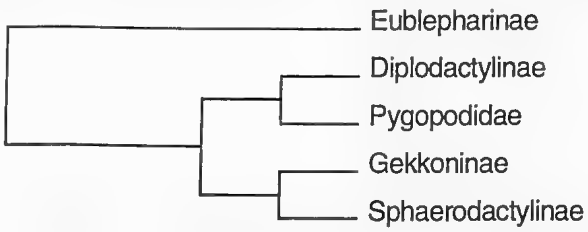

Figure 26.6 Major lineages of gekkonoid lizards. (After Kluge 1987) [D. Wahl]

endemic genus *Pseudothecadactylus* was placed as the sister taxon of some members of the New Caledonian genus *Rhacodactylus*. On karyotypic evidence, King (1987b) had already suggested a close relationship of *Pseudothecadactylus* and *Rhacodactylus*.

Within the pygopods, Kluge (1974) proposed a phylogenetic scheme (Fig. 28.8) which can be summarised as having a basal group of taxa, *Pygopus, Paradelma, Delma* and *Aclys*, between which relationships were poorly resolved, and four derived genera, *Lialis, Pletholax, Ophidiocephalus* and *Aprasia*, which form a monophyletic lineage. Problems among the basal genera, include the possible paraphyly of both *Pygopus* and *Delma* and the relationships of these forms to the more derived genera. *Pygopus* has been identified as the most generally plesiomorphic pygopodid (Kluge 1974), although *Delma* species are more primitive (= gecko-like) than *Pygopus* in the elongation of the body (Greer 1989) and the dentition (Hutchinson pers. obs.).

Scincomorpha

Skinks have been the core group of the scincomorpha since its inception (Camp 1923), but their relationships to other scincomorphans are unclear. Recent workers have consistently regarded the African cordyliforms (Cordylidae and Gerrhosauridae; Lang 1991), especially the gerrhosaurs, as close relatives of the Scincidae, either alone (Greer 1979b; Estes *et al.* 1988), or together with the xantusiids (Estes 1983; Presch 1988). It is noteworthy that the studies of Presch (1988) and Estes *et al.* (1988), based on large morphological data sets which overlapped significantly, agreed that the Cordylidae (including gerrhosaurs) and Xantusiidae are the nearest relatives of the Scincidae, but differed on whether the Cordylidae (Estes *et al.*) or Xantusiidae (Presch) are the sister group of skinks. Lang's (1991) revision of cordyliform lizards supports Estes *et al.* (1988) in placing them as the sister group of skinks and he reported also that one possible (but not preferred) phylogenetic hypothesis placed Cordylidae as the sister group of Scincidae + Gerrhosauridae. Other unresolved issues include the relationships of the Dibamidae to the Scincidae (Greer 1985; Rieppel 1984b) and the monophyly of the plesiomorphic subfamily Scincinae (Chapter 31).

Scincid relationships are summarised in Figure 26.7. The subfamilial scheme of Greer (1970a) comprises three monophyletic groups: the African limbless, fossorial, Acontinae and Feylininae; the predominantly Australian-Asian Lygosominae; and the Scincinae. Rieppel (1981) queried the validity of Greer's family concept, but his doubts revolve around the dibamids, feylinids and acontines; no one has suggested that the core scincines and lygosomines (98% of living skinks) are not monophyletic.

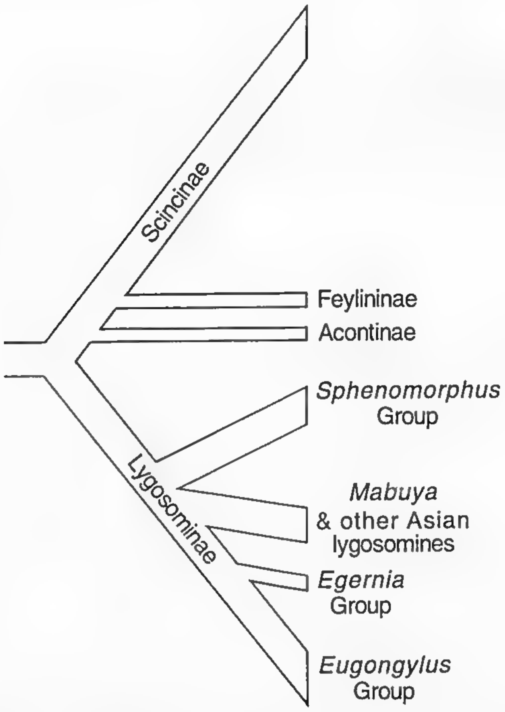

Figure 26.7 Phylogenetic relationships among the major skink lineages. (After Greer 1970, 1979a) [D. Wahl]

Table 26.2 Endemic scincid genera of the *Eugongylus* group arranged by geographic unit.

Australian	Melanesian	New Caledonian	New Zealand
Bartleia	*Emoia*	*Caledoniscincus*	*Cyclodina*
Bassiana	*Eugongylus*	*Geoscincus*	*Oligosoma*
Carlia	*Geomyersia*	*Graciliscincus*	
Cautula		*Lioscincus*	
Cryptoblepharus		*Marmorosphax*	
Lygisaurus		*N. (Nannoscincus)*	
Menetia		*Phoboscincus*	
Morethia		*Sigaloseps*	
N. (Nannoseps)		*Tropidoscincus*	
Niveoscincus			
Proablepharus			
Pseudemoia			

The lygosomines are the only recognised Australian skinks. Three monophyletic lineages have been identified (Greer 1979b): the *Egernia* group, the *Eugongylus* group and the *Sphenomorphus* group (Fig. 31.3). Greer's (1979b) analysis of ten characters suggested an hypothesis of relationships between the groups in which the *Sphenomorphus* group is the sister of the other two. This relationship was supported by immunoelectrophoretic evidence (Hutchinson 1980).

The genera of the *Egernia* group, *Egernia, Cyclodomorphus, Tiliqua* and *Corucia* (a monotypic Solomon Islands endemic) constitute a radiation of relatively primitive lygosomines confined to the Australian region. Morphological (Mitchell 1950; Greer 1979b; Shea 1990), biochemical (Hutchinson 1980; Baverstock & Donnellan 1990) and karyotypic evidence (King 1973; Donnellan 1985, 1991a) all corroborate the monophyly of this lineage. Relationships within the group are not resolved yet beyond the sister group relationship suggested (Shea 1990) between *Cyclodomorphus* and *Tiliqua*. *Egernia* is a grade genus, possibly paraphyletic with respect to the rest of the group, while *Corucia* possesses a confusing mixture of numerous autapomorphies plus some very primitive character states, such as pterygoid teeth.

The *Eugongylus* group is a diverse assemblage, and has undergone several distinctive geographic radiations, all centred in the Australian region. Thus, there is an Australian radiation, a New Guinean-Solomon Islands radiation, a New Caledonian radiation and a New Zealand radiation (Table 26.2). In each area, there are species with striking, superficial similarities to taxa in other areas, but accumulating evidence indicates that relationships are closest within, rather than between, the major geographic units (Sadlier 1987; 1990; Hutchinson *et al.* 1990).

The *Sphenomorphus* group is diverse in the Australian region, resembling the *Eugongylus* group in having independent radiations in Australia and Melanesia, but not including New Caledonia-New Zealand (Baverstock & Donnellan 1990). Relationships across the group, which is also diverse in South-East Asia, are very poorly understood. A major impediment to understanding the group is the very large grade genus *Sphenomorphus*, as it includes a wide variety of species from throughout the range of the group which lack diagnostic character states of other genera. Recent Australian usage has suggested dividing Australian *Sphenomorphus* among two genera, *Eulamprus* and *Glaphyromorphus*, but neither, as currently defined (Greer 1990c, 1992; Cogger 1992) is readily distinguishable from extralimital *Sphenomorphus*. Within Australia, several clusters of taxa have been recognised as closely related, such as *Saiphos* and *Calyptotis* (Greer 1983b, *Hemiergis* and *Glaphyromorphus gracilipes* (Choquenot & Greer 1989), and *Lerista* and the *G. crassicaudus* species group (Greer 1979c). Greer (1990c) also proposed a monophyletic assemblage, the *Glaphyromorphus isolepis* species complex, members of which occur in both Australia and the Lesser Sunda Islands.

The skinks have been a notoriously difficult group for phylogenetic study and, in spite of the progress made so far, many aspects of the relationships of the Australian skinks are still unclear. Baverstock & Donnellan (1990) and Hutchinson *et al.* (1990) made MC'F comparisons of serum albumin to elucidate the phylogeny of the major lineages and relationships among the species formerly lumped as the grade genus, *Leiolopisma*. The divergences among the three Australian lygosomine groups were shown to be profound (Baverstock & Donnellan 1990), but so great that albumin MC'F could not reliably test Greer's (1979b) suggestion that the *Sphenomorphus* group is the sister of the other two. The magnitude of the divergences does, however, suggest strongly a considerable antiquity for these lineages, possibly as old as the early Tertiary. The study of *Leiolopisma* showed that the several Australian species groups were more closely related to other Australian genera than they were either to each other or to the type species of the genus (*L. telfairii* from Mauritius). Integration of morphological data permitted diagnosis of several new genera to accommodate the Australian '*Leiolopisma*' and preliminary data, plus subsequent unpublished MC'F comparisons of New Caledonian and New Zealand '*Leiolopisma*', also suggest that these regions support endemic genera, not disjunct congeners of *L. telfairii*.

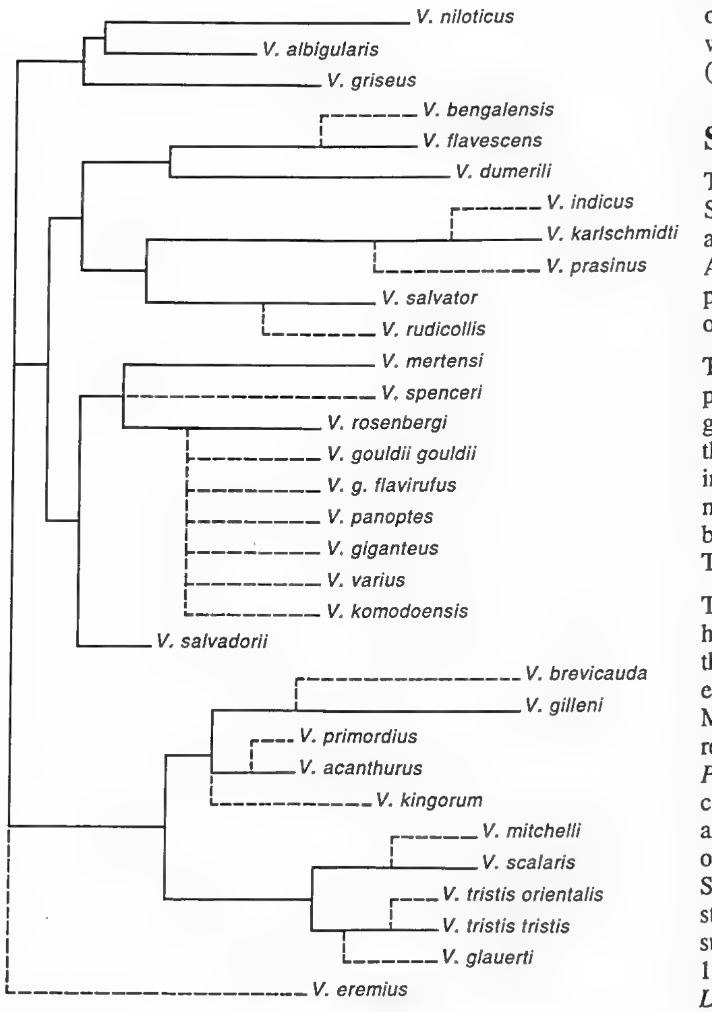

Figure 26.8 Possible relationships among the major species groups of the genus *Varanus*. (After King, King & Baverstock *et al.* 1991) [D. Wahl]

Anguimorpha

Anguimorphs are regarded as a derived group of lizards, most authors placing them as the sister group of Scincomorphans. Indeed, some anguids (for example, diploglossines) are very similar externally and internally to skinks. The living Australian monitors (Varanidae) belong to a still more derived subgroup of the Anguimorpha, the superfamily Varanoidea (= Platynota), which also includes the Helodermatidae (now restricted to Mexico–southwestern North America, but known as fossils in Europe's early Tertiary) and the extinct, totally aquatic, Mosasauridae and Necrosauridae.

The interfamilial relationships of the Varanidae perhaps have been examined more rigorously than any other Australian squamate group. McDowell & Bogert (1954), Rieppel (1980a) and Estes *et al.* (1988) collectively provided a large morphological data set showing that the Varanidae (including Lanthanotidae, Estes *et al.* 1988) is probably most closely related to the extinct Mosasauridae, and the Helodermatidae are more remote (Fig. 26.3).

Relationships among the extant members of the widespread genus *Varanus* have been investigated with morphological (Branch 1982; Böhme 1988; Becker, Böhme & Perry 1989), karyotypic (King & King 1975; King 1990) and microcomplement fixation of albumin data sets (Baverstock, King, King, Birrell & Kreig 1993) (Fig. 26.8). Australia's varanids have been placed traditionally in two subgenera, *Varanus* and *Odatria* (Mertens 1963). King *et al.* (1991) suggest that neither of Merten's subgenera is monophyletic. However, they identified two monophyletic clusters among the varanids that are largely confined to Australia. The first of these is a diverse group of small species confined to arid and northern Australia, which essentially represents Merten's *Odatria* minus the New Guinean *V. prasinus*. The second cluster of large species is the core of Merten's subgenus *Varanus*, but without several South-East Asian and New Guinean endemics (*V. indicus*, *V. karlschmidti*, *V. salvator*).

Serpentes

The Australian snakes belong to three major assemblages, the Scolecophidia (typhlopid blind snakes), the Booidea (pythons) and Colubroidea (acrochordid file snakes, elapids and colubrids). As noted earlier, relationships between the three major groups are poorly established, but divergences date back to the early Tertiary or before (Rage 1982; Cadle 1988).

The phylogeny of typhlopid snakes has attracted little attention. At present, the allocation of the members of the family to just three genera — *Ramphotyphlops* in the Australian region, *Typhlops* throughout the Old World except for Australia, and *Rhinotyphlops* in Africa (Roux-Estève 1974) — implies a distinctive, monophyletic origin for the Australian typhlopids. No work has been done on phylogenetic relationships within the Australian Typhlopidae.

The pythons and boas have attracted much more study, but this has yet to result in a clear consensus regarding the relationships of the Australian pythons with each other, or with pythons elsewhere. A long period of taxonomic inactivity ended with McDowell's (1975) revision of the pythonines of the Australian region, which allocated some species to the Afro-Asian genus *Python*. Schwaner & Dessauer (1981), based on immunological comparisons of transferrins, disagreed with McDowell's scheme, and indicated instead that the Australian species were closer to one another than to any non-Australian species. Underwood & Stimson (1990) also concluded, from a multi-character cladistic study, that Australian pythons are monophyletic. Further, they suggested that the conventional taxonomy (for example, Cogger 1992) over-split the group. They recommended synonymising *Liasis* and *Chondropython* with *Morelia*, leaving only this genus, plus *Aspidites* which differs from other pythonines in lacking heat-sensitive labial pits. Underwood & Stimson (1990) interpreted this as a reversal, but Kluge (1991) identified the

Australian pythonines as generally primitive, implying that the lack of pits could represent a primitive character state. If so, Australia supports not only the most structurally diverse, but also the most primitive pythonine radiation. Further studies by Kluge (in press) may shed more light on Australian boid relationships. Within Australia, Underwood & Stimson (1990) found that their concept of *Morelia* comprised several groups: the small *M. childreni* species complex (Smith 1985; conventionally *Liasis childreni*), the elongate, slender *M. amethistina* and *M. oenpelliensis*; the large *M. fuscus* and *M. olivaceus* (both conventionally *Liasis*) and the heavily built *M. spilota*, *M. carinata* and *M. viridis* (conventionally *Chondropython viridis*).

The state of knowledge regarding phylogenetic relationships among the advanced colubroid snakes is chaotic. The following are among many unresolved questions. Are the acrochordid file snakes primitive colubroids or advanced booids? Should the Elapidae include hydrophiine and/or laticaudine sea snakes or not? Are all proteroglyphs monophyletic? What are the limits of the enormous assemblage still conventionally referred to as the family Colubridae? This last problem is one which mostly concerns areas elsewhere, as the 'family' is poorly represented in Australia, and shows practically no endemism (Shine 1991c). Australian colubrids represent three subfamilial units, the Colubrinae (*Boiga*, *Dendrelaphis*), the Natricinae (*Stegonotus*, *Tropidonophis*) and Homalopsinae (*Cerberus*, *Fordonia*, *Myron*). Preliminary MC'F comparisons of representatives of these three subfamilies (Dowling *et al.* 1983) suggest a possible sister group relationship between the first two, but a very remote relationship between them and the homalopsines.

Within the Elapidae in its broadest sense, the sea snakes share craniomuscular and biochemical similarities with the Australian elapids (McDowell 1969a; 1969b; 1970), although these similarities have not been analysed rigourously in terms of shared-derived character states. Immunological studies by Mao *et al.* (1978), Cadle & Gorman (1981) and Schwaner *et al.* (1985a) strongly support a close relationship between the Australian terrestrial elapids and the sea snakes, especially the large hydrophiine radiation. Afro-Asian and Neotropical elapids are much more distantly related. Schwaner *et al.* (1985a) showed that biochemical divergence across the Australian elapid/sea snake group is relatively low, implying a recent origin (since mid-Tertiary). It appears, therefore, that if the Hydrophiidae or Hydrophiinae is to be recognised as a distinct taxon, it must also include the Australian terrestrial elapids.

A major attempt to resolve relationships among the Australian terrestrial elapids is represented by the articles drawn together in a volume edited by Grigg, Shine & Ehmann (1985). Articles based on biochemistry (Schwaner *et al.* 1985a), karyology (Mengden 1985a), and morphology (Wallach 1985) provided some consensus, although considerable disagreement remained. Several major themes are supported by the separate studies. The earliest diverging groups are the large, surface dwelling, oviparous forms (*Demansia*, *Pseudonaja*, *Pseudechis* and *Oxyuranus*). A monophyletic origin for the large radiation of viviparous species with entire subcaudals was supported, but it is within this apparently relatively recent radiation that the greatest uncertainty exists regarding relationships. Hutchinson (1990b) attempted a consensus generic classification based on the data in Grigg *et al.* (1985).

BIOGEOGRAPHY

As is becoming clearer for more and more groups, the Australian members of a particular squamate family appear to be monophyletic to the exclusion of non-Australian members of the same family. Biogeographic inferences therefore depend on how much is known of the relationships of the Australian clade with these extra-Australian lineages. The details of these relationships are poorly known, if at all, for most Australian families.

Most discussions regarding the origins of major taxa in Australia reduce to choosing between an Asian and a Gondwanan origin; origin within Australia has seldom been considered (see King 1990). This has depended on a relatively simple palaeogeographic interpretation of Australia. Recent advances in understanding past geology of Australia and Asia (Audley-Charles 1987; 1991; Burrett, Duhig, Berry & Varne 1991) show that the picture has probably been much more complicated, and geology is not likely to provide rigid constraints on biogeographic hypotheses. The reverse is almost closer to the truth, as knowledge of the relationships among living taxa guides geologists to the discovery of terranes (Veevers 1991).

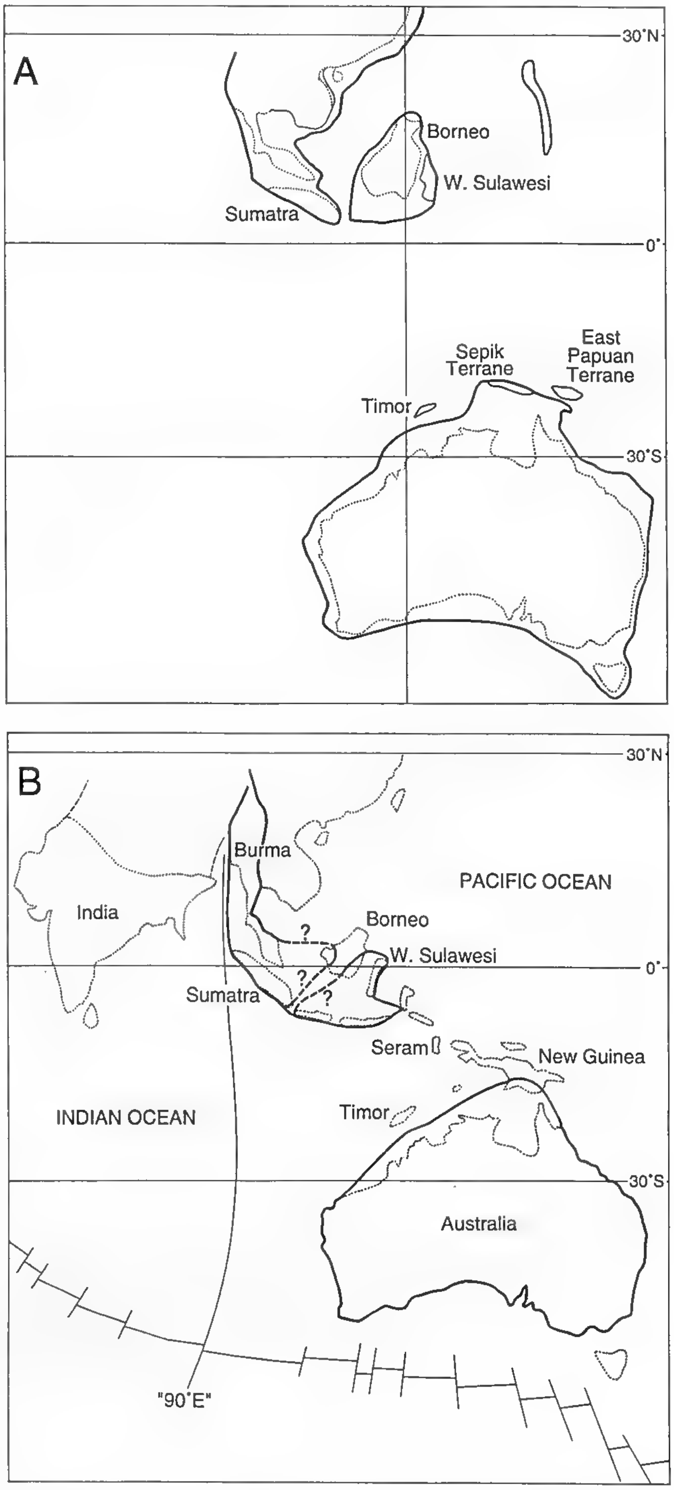

Figure 26.9 Two recent views on the presence of insular 'stepping stones' between Australia and Asia during the early Tertiary (Oligocene). Uncertainty regarding the geological history of this area is a major barrier to understanding the origins of Australia's reptile fauna. **A**, presence of a broad ocean gap; **B**, gap filled by Indonesian-Malaysian archipelago. (A, after Burrett *et al.* 1991; B, after Audley-Charles 1987) [W. Mumford]

The orthodoxy of static continents clouded attempts to explain Australian squamate biogeography until about 1970. Thus Keast

(1959), Storr (1964a) and Kluge (1967a) all explained the patterns they observed against a modern Indo-Malaysian archipelago which acted as a filter bridge for Asian immigrants. This seemingly continuous distribution, plus the prevailing taxonomy which included many widely dispersed grade taxa, tended to diminish both the perceived uniqueness of the Australian fauna and its antiquity. For example, Rawlinson (1974b) could write of the 'genus' *Leiolopisma* as being a widespread, Australian-Asian group which had 'radiated widely during the Quaternary'.

The acceptance of continental drift changed this viewpoint, but only partially. Several elements of the herpetofauna, with obvious South American affinities, (chelid turtles; hylid and leptodactyloid frogs) became accepted as Gondwanan relicts (Maxson, Sarich & Wilson 1975; Tyler 1979). The rest of the fauna was regarded as being more closely related to Asian taxa, but the initial palaeogeographic maps (for example, Colbert 1973) showed an extremely wide ocean gap between northern Australia and South-East Asia with no archipelagic connection until the Miocene or later. As a consequence, a northern origin for the fauna continued to be equated with a recent origin (for example, the review by Cogger & Heatwole 1981).

During the 1980s, revisions have been made of the origins and movements of plates and smaller continental fragments (terranes) between Australia and Asia. It is now becoming accepted that there has been a continuous rifting away of terranes from the leading, northern, edge of the Australian plate, so that much of the Indo-Malayan Archipelago and mainland South-East Asia is Gondwanan in origin. This implies that for Australian taxa showing 'Asian' connections, the common origin may be potentially much earlier than mid-Tertiary. It raises also the possibility that the relationship is not necessarily with Laurasian fauna, but may merely be with other Gondwanan elements that were isolated vicariantly on the rifted terranes.

The timing of the rifting of the various terranes is not yet well established (Fig. 26.9). For example, Audley-Charles (1987) suggested that the terrane now forming part of Thailand and the Malay Peninsula rifted during the Cretaceous, whereas Burrett *et al.* (1991) concluded that this terrane had already accreted onto the Asian landmass by the end of the Triassic. Also in doubt is the degree to which these terranes were actually exposed above sea level during their crossing of the Australia-Asia gap. As Burrett *et al.* (1991) pointed out, this exposure is absolutely crucial to terrestrial biogeographic reconstructions, but evidence for it may be very hard to detect during routine geological mapping. The area between Australia and Laurasian Asia thus may have been linked by a wide ocean gap or by various landmasses, although their composition and relative positions along the route would have changed constantly. The trend for land to leave Australia and join Asia invites the speculation that Australian fauna could have reached Asia via vicariance or dispersal, while Asian fauna could only disperse via island hopping to Australia.

It is hard to avoid the feeling that geology places few constraints on zoogeographic explanations and that a wide range of possible times, vicariant events and dispersal routes are possible. Rather, a strongly corroborated hypothesis of relationships for a group is likely to constrain the geologic setting. As pointed out above, such hypotheses are not generally available at present. Greer (1989) provided a pungent critique of the history of biogeographic speculation regarding Australian reptiles.

The following discussion summarises knowledge on the age of taxa in Australia, its likely nearest extralimital relatives and probable geographic origin. A common theme through this discussion is that Australian taxa, represented in recent fossil finds and/or subjected to molecular 'clock' studies, are now suggested to have originated or arrived in Australia by at least the early Tertiary.

Squamates in General

A supposed Permo-Triassic 'lizard', *Kudnu*, was described by Bartholomai (1979) from the *Lystrosaurus* Zone Rewan Formation of Queensland. This fragmentary specimen is probably not a paliguanid as originally proposed, and in any case, paliguanids, as discussed above, are not necessarily squamates. However, the find does show that primitive, possibly lepidosaurian diapsids, were present in Australia at a very early stage (Molnar 1985). The oldest undoubted squamate fossils in Australian are Cretaceous mosasaur fragments from Western Australia (Molnar 1985).

Outside Australia, the earliest fossil lizards (for example, bavarisaurs, paramacellodids; Estes 1983) in the strict sense are Jurassic and Laurasian, while the oldest snake, *Lapparentophis* (Lapparentophiidae), from the Lower Cretaceous of Algeria, is Gondwanan (Rage 1984). Evidently squamates were potentially worldwide in distribution well before the end of the Mesozoic.

Agamidae

The oldest Australian fossil records are from the Early Miocene of Queensland (Covacevich *et al.* 1990b), where the living genus *Physignathus* has been identified, along with an extinct genus, *Sulcatidens*, and numerous indeterminate fragments. Early fossils have yet to be associated explicitly with the amphiboluroid radiation. Apart from *Physignathus cocincinus* from South-East Asia, it is uncertain which extralimital taxa are the closest relatives of the Australian agamids. The profound biochemical divergence between Asian and Australian taxa (Baverstock & Donnellan 1990) implies that if any Asian-Australian exchange occurred it was probably long ago. The possibility raised by the MC'F data of an Australian-African relationship needs further evidence.

The three agamid lineages differ in distribution within Australia. *Physignathus* and *Hypsilurus* inhabit tropical and warm temperate, forested habitats along Australia's east coast, while the amphiboluroids inhabit virtually all environments except these wet forests, being particularly diverse in arid and wet-dry tropical environments. The diversity of the amphiboluroids could be a late Tertiary phenomenon, correlated with the recent development of widespread aridity in Australia (Bowler, Hope, Jennings, Singh & Walker 1976).

Gekkonidae

Gekkotan lizards are among the first, undoubted squamates known in the fossil record. The extinct families Ardeosauridae and Bavarisauridae from the Late Jurassic of Eurasia have been assigned to the Gekkota, based on general skull proportions and the presence of persistent intercentra and notochordal vertebrae (Estes 1983). Kluge (1987) believed that the bavarisaurs are reasonably interpreted as gekkonoids, but that the evidence for ardeosaur relationships is more ambiguous. Diplodactyline fossils are known from the Early Miocene of Queensland (Hutchinson pers. obs.), but Australian gekkonines are not known as fossils for certain.

Diplodactylines are known only from the Australian region, while gekkonines are worldwide, implying a local origin for the former, but suggesting no obvious pattern for the latter subfamily. Bauer's (1990) analysis simply posits the existence of diplodactylines (and pygopods) in Australia by the mid-Cretaceous; earlier authors assumed an Australian origin for both taxa. Subsequent differentiation within the Diplodactylinae was linked by Bauer to vicariant isolation of lineages on Australia, New Zealand and New Caledonia during the past 60 million years. Both subfamilies are widespread in Australia, although the much greater range of morphological variation and the greater taxonomic diversity of the diplodactylines, suggests a longer stay in Australia. Both taxa also show significant radiations in tropical and arid regions of Australia; temperate regions support lower diversity, due probably to the low nocturnal temperatures.

Pygopodidae

Pygopodids are known from the Early Miocene of Queensland (Hutchinson pers. obs.). The nearest relatives are the diplodactylines (Kluge 1987; King 1990) or all other gekkonids (Estes *et al.* 1988). If the former view is correct an Australian origin is very likely.

Within Australia, pygopods are most diverse in the southern third of the continent, especially in semi-arid to warm temperate heath and grass habitats. The north-west and tropical far north are relatively depauperate, with no endemic genera and only a few species. Densely forested and cool habitats in the east and south tend to lack pygopods altogether. This pattern contrasts with that of the elapid snakes, which are most numerous and diverse in the east and north. It has been suggested (Storr 1964a; Bustard 1970b) that elapids have displaced pygopods, but the two groups, at least today, seem to complement one another ecologically rather than compete.

Scincidae

Earliest Australian records are from the Oligo-Miocene of South Australia (Estes 1984) and Early Miocene of Queensland (Hutchinson 1992). These early records indicate that the fauna at that time was Australian in character, pushing the origin and differentiation of the Australian scincid lineages further back in time. Two of the three Australian skink lineages, the *Egernia* group and the *Eugongylus* group, are almost entirely confined to the Australian region (see above), implying possible origin here. The *Sphenomorphus* group is more widespread through Asia. South-East Asia supports a diverse but largely distinct lygosomine fauna, as well as relictual scincines, but apart from the identification of the Asian *Mabuya* as an ancestral form for lygosomines in general (for example, Greer 1974, 1979b, 1989), no relationship of any of the three Australian lineages to a particular extralimital taxon has yet been established. Within Australia, all three lineages are found throughout the continent, but with no clear biogeographic bias, emphasising their likely long period of evolution here.

Skinks occur throughout the Australian mainland and on virtually all adjacent islands. Greatest generic diversity is reached along the east coast, but all parts of Australia show significant local diversity and endemism.

Varanidae

The earliest definite Australian record is from the Oligo-Miocene of South Australia, as *Varanus* sp. (Estes 1984). Older varanid remains, of the extinct genus *Saniwa*, are known from the Early Tertiary of North America (Estes 1983). The new evidence from immunology and chromosomal analysis (King *et al.* 1991) emphasises the Australian nature of our varanid lizards. Merten's (1963) two Australian subgenera, *Odatria* and *Varanus*, can only be maintained if non-Australian species (*V. komodoensis* is a notable exception) are excluded. Even though the family is widespread across the Old World tropics, there is a distinct changeover from an Australian to a New Guinean to an Asian fauna north-west of the Australian mainland. In this, the varanid pattern of endemism matches the pattern seen in skinks and dragons and, to a lesser extent, in geckos and elapids.

The study of King *et al.* (1991) suggests that the species excluded from Merten's Australian subgenera (*V. salvator*, *V. indicus*, *V. carlschmidti* and *V. prasinus*), together with other more specialised South-East Asian genera, form a cluster of Asian-New Guinean species which are the sister group of the Australian species. The profound immunological divergence among Australian varanids and the generally primitive morphology of the Australian subgenus *Varanus* could be interpreted to mean that Australia was the point of origin not only of its own varanid fauna but also the New Guinean and Asian radiations.

Typhlopidae

Fossil typhlopids have been found in the Early Miocene of Queensland (Scanlon, cited in Archer, Godthelp, Hand & Merigan 1989). These are the oldest typhlopids, the next record being from the Middle Miocene of France (Rage 1984). There are no phylogenetic data on the relationships of Australian typhlopids, and no soundly based speculations on the origins of this globally distributed group.

Boidae (Pythoninae and Madtsoinae)

The pythonines *Montypythonoides riversleighensis* and *Morelia antiqua* have been described from the Miocene of Queensland and the Northern Territory, respectively (Smith & Plane 1985). *Montypythonoides* is close to, if not identical with *Morelia* (Scanlon, pers. comm.). *Morelia*, a distinctively Australian genus, was thus established by this time, but the relationship to extralimital pythonines (basically the genus *Python*) is rather distant (Schwaner & Dessauer 1981). Evidently the group has been in Australia since the early Tertiary, and its precise origins remain obscure.

Until Pleistocene times, Australia supported a second group of large snakes, the madtsoiines, first recorded when *Wonambi* was described from the Naracoorte Caves of southeastern South Australia (Smith 1976b). Recent finds (for example, *Yurlungurr*, Scanlon 1992) and restudy of *Wonambi* (Barrie 1990) have expanded the knowledge of these snakes, showing that they have been in Australia since the Eocene. McDowell (1985) and Scanlon (1992) suggested that the group deserves familial status. The oldest fossil regarded by Rage (1984) as a booid is *Madtsoia madagascariensis* from the Late Cretaceous of Madagascar. The primitive nature of Australian region boids, plus the presence of a second major lineage of boid-like madtsoiines, suggest that the entire booid group could be seen as having had a primarily Gondwanan, if not Australian, origin and differentiation, with only small scale invasions of the northern continents.

Acrochordidae

The living genus *Acrochordus* has been identified as a fossil from the Middle Miocene of Pakistan but the family is unknown in the Australian fossil record. Acrochordid relationships to other snakes are not well established. The three living species are found from tropical Asia to northern Australia and the family could have originated anywhere within its present range and subsequently dispersed readily because of its obligate aquatic, including littoral, habits. The two Australian species are confined to tropical freshwater and mangrove environments.

Elapidae (including Hydrophiidae)

The nearest relatives of Australia's elapids are Asian, but this relationship is not close (Cadle & Sarich 1981; McDowell 1967). The prevailing conclusion is that probably both groups of sea snakes, hydrophiines and *Laticauda*, share a common ancestry with or within the Australian proteroglyphs (McDowell 1969a; Mao *et al.* 1978; Cadle & Gorman 1981). This suggests a reasonably long period of evolution in Australia, especially in view of the wide dispersal and diversification undergone by hydrophiines.

Elapids are known from the Early Miocene of Queensland (Scanlon, cited in Archer *et al.* 1989), where cranial remains indicate species of Australian type (Scanlon pers. comm.). The oldest elapid fossils elsewhere in the world are from the Middle Miocene (*Palaeonaja*) of Europe. Immunological data (Schwaner *et al.* 1985a) suggested a Miocene origin for the Australian elapid–sea snake radiation. Fossil and biochemical data therefore provide a minimum age for the Australian elapid radiation (15 to 20 million years), but whether this represents the first arrival of the group in Australia, or simply the origin of the surviving lineages, remains to be seen.

Terrestrial elapids are most diverse in eastern tropical and warm temperate habitats, but nevertheless show significant diversity and endemism in cool temperate, semi-arid and arid environments. Elapids are one of only three reptile families to occur in Tasmania, possibly aided by the viviparity which characterises a major elapid lineage (Shine 1985c).

Colubridae

The oldest caenophidian, presumably colubrid, fossils are from the Late Eocene Quercy limestones of France (Rage 1984). The family is unknown in the Australian fossil record. As all Australian species are congeneric with Asiopapuan populations, their arrival in Australia was evidently from the north and very recent. Colubrids have successfully invaded arboreal and semiaquatic ecological niches only marginally exploited by elapids (Shine 1991c).

Concluding Remarks

The squamate fauna of Australia, with the single exception of the recently dispersed Colubridae, consists of families that probably have been present and differentiating within Australia through most of the Tertiary. Sister taxa of the Australian radiations are largely uncertain, apart from a general trend for an Asian relationship, and agamids are possibly exceptional in having African affinities. Australia is the centre of diversity for, and therefore possibly the point of origin of, diplodactylines, pygopodids, *Egernia* group and *Eugongylus* group scincids, the varanid subgenera *Varanus* and *Odatria*, pythonine boids, *Ramphotyphlops* blind snakes and hydrophiine sea snakes. All of these groups have dispersed to varying extents through the Australian region, but in most instances have made limited incursions into the Oriental region.

Future research on the evolutionary relationships of the Australian squamates should concentrate on the basal dichotomies and relationships between Australian and extralimital members of the same taxa. Reworking of existing morphological data sets, replacing intuitive or phenetic conclusions with cladistic analysis, must continue, as well as the development of new morphological data sets to augment the often analysed osteological and scutellation data sets (Kluge 1989). In the near future it will become increasingly easy to incorporate nucleotide sequence data sets in such analyses. Whether such molecular studies are used to test morphological hypotheses or included in 'total evidence' style studies, they should help considerably in clarifying phylogenetic relationships. Only then will biogeographic studies be likely to produce useful and soundly based scenarios explaining the origins and distributional patterns of Australia's squamate fauna.

27. FAMILY GEKKONIDAE

Max King & Paul Horner

DEFINITION AND GENERAL DESCRIPTION

Most members of the family Gekkonidae are distinguished from other lizards by the presence of large eyes which have a fixed transparent spectacle, or brille, and a pupil which appears as a narrow vertical slit (Fig. 27.1). The body is covered by a loose-fitting velvety skin which has small, juxtaposed scales on the dorsal surface.

The Gekkonidae comprises some 800 species, and is one of the largest vertebrate groups. The family is distributed circumglobally and species occupy an extensive array of habitat types; the variety of form and degree of specialisation of its members reflect a diversity of niches. Two of the four subfamilies of the Gekkonidae, the Diplodactylinae and Gekkoninae, occur in Australia. The Eublepharinae and Sphaerodactylinae are not found in this region.

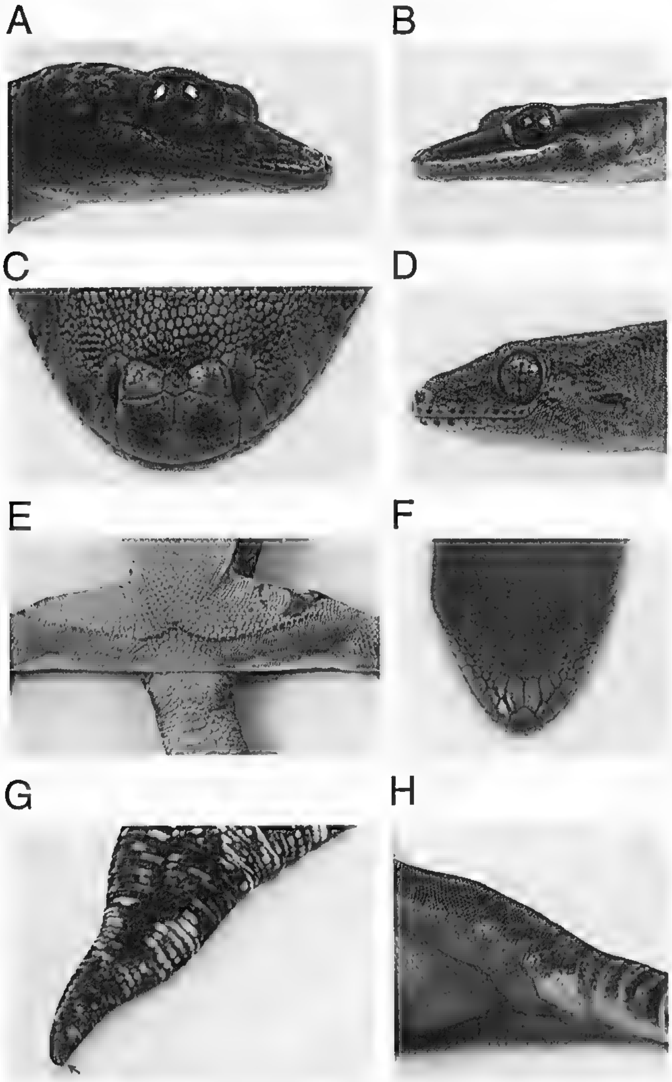

Figure 27.1 Selected morphological features of the Gekkonidae. **A**, head of *Oedura filicipoda* showing the large eye and shiny mouth scales; **B**, the depressed head, large elevated eyes and long snout of *Oedura gracilis*; **C**, scalation around nasal apertures and snout of *Gehyra membranacruralis*; **D**, lateral view of the robust head of *Gehyra membranacruralis*, showing the position of the ear aperture, and pupil shape; **E**, ventral view of the hind limbs of *Gehyra membranacruralis*, showing the distinct row of femoral pores and the skin folds on the back legs; **F**, glossy chin shields of *Gehyra australis*, in ventral view; **G**. spinose scales on the tip of the tail of *Oedura filicipoda* which permit the tail to operate as a 'fifth limb'; **H**, postero-lateral view of a male *Oedura gracilis* showing the enlarged hemipenial sacs and post-anal tubercles. [Photos by M. King & P. Horner]

Geckos of the subfamily Diplodactylinae are distinguished from other gekkonids by derived characters — an 'O'-shaped muscle that closes the external auditory meatus, and a thickened mid-portion of the tectorial membrane of the ear (Kluge 1987). The Diplodactylinae is subdivided into two tribes, the Carphodactylini and Diplodactylini. Males of the former tribe are distinguished by the presence of a large patch of pre-anal pores, which are usually arranged in multiple rows. This character has been modified secondarily in two of the genera, *Nephrurus* and *Phyllurus*, according to Bauer (1990), who also noted that co-ossification of the dermis with the underlying bones of the skull occurred in the Carphodactylini, but not in the Diplodactylini. The short, wide nasal process of the premaxilla in the Carphodactylini is diagnostic, as are the presence of an inner ceratohyoid process and the absence of autotomy planes in some caudal vertebrae (Kluge 1987). The Diplodactylini generally possess paired terminal toe pads, except in *Diplodactylus damaeus* where these may have been lost secondarily.

Fourteen genera of Diplodactylinae are recognised. Those in the tribe Diplodactylini (*Diplodactylus*, *Strophurus*, *Rhynchoedura* and *Crenadactylus*), are found only in Australia. Five of the ten genera of Carphodactylini occur in Australia (*Carphodactylus*, *Rhacodactylus* (including *Pseudothecadactylus)*, *Oedura*, *Phyllurus* and *Nephrurus*; Pl. 4.1, 4.3, 4.4, 4.5). *Naultinus*, *Hoplodactylus* and *Heteropholis* occur in New Zealand, and *Bavayia*, *Rhacodactylus* and *Eurydactylodes* occur in New Caledonia and the Loyalty Islands. This taxonomy emphasises the link between Australian and Pacific forms.

The subfamily Gekkoninae, which comprises 58 genera, is distinguished from other geckos by having a single centre of ossification in the ontogeny of the premaxilla. Two centres are present in the Eublepharinae and Diplodactylinae. Gekkonines have a pliable, calcium-shelled egg which hardens on exposure to air, unlike the parchment-shelled egg of diplodactylines, and the egg is more elliptical than those of other subfamilies. The endolymphatic system is expanded into a large sac on each side of the neck, in which calcium for egg shell formation is stored. Gekkonine autotomy planes occur along the length of the tail, whereas they are concentrated in the base of the tail in the Diplodactylinae (Greer 1989).

Only seven gekkonine genera are represented in Australia: *Gehyra*, *Heteronotia*, *Hemidactylus*, *Lepidodactylus*, *Cyrtodactylus*, *Nactus* and *Phyllodactylus* (Pl. 4.2, 4.6). Of these, certain species of *Lepidodactylus* and *Hemidactylus* appear to be recent introductions from Asia (Cogger 1992).

HISTORY OF DISCOVERY

The history of discovery of the Australian Gekkonidae can be divided broadly into five areas of exploration, systematic research, or technical application: the voyages of discovery and the analysis of specimens from Australia in British, French and other European museums, from 1790 to 1850; the expeditions to the interior between 1850 and 1920; modern systematics and museum exploration, from 1920 onwards; and the use of genetic and morphological analysis after 1970.

Intensive biological collecting accompanied the early British settlements at Sydney Cove in New South Wales (1788), and the subsequent isolated outposts of Fort Dundas on Melville Island (1824), at Raffles Bay (1827) and at Port Essington (1838) on Cobourg Peninsula in the Northern Territory. Most of this material was sent to Britain for analysis. The French government despatched the corvettes *Le Géographe*, *Le Naturaliste* and the goulette *Le Casuarina*, from which extensive collections were made in Western Australia between 1800 and 1804 and to a lesser extent along the eastern Australian coastline. Surprisingly, very few gekkonid species were described during this initial period, although *Phyllurus platurus* (White 1790) provided an interesting exception.

This burst of biological collecting provided the source material for the second period of activity which centred on the British Museum of Natural History in London and the Muséum National d'Histoire Naturelle in Paris. Eight of the major gekkonid genera were defined by J.E. Gray in London between 1825 and 1845 (*Hemidactylus*, *Cyrtodactylus*, *Phyllodactylus*, *Diplodactylus*, *Gehyra*, *Oedura*, *Crenadactylus* and *Heteronota*). Gray also described a suite of species, some of which have survived the rigours of synonymy (Cogger, Cameron & Cogger 1983a). In Paris, A.M.C. Duméril and G. Bibron described a series of species, many of which were collected at Shark Bay in Western Australia by French voyagers.

Expeditions throughout the interior and to the more remote areas of Australia in the mid to late 19th and early 20th century made significant collections of herpetological material. They included the *Chevert* expedition in 1877, the Horn Expedition to central Australia of 1896, the Elder exploring expedition in 1893 and Dr E. Mjöberg's Swedish Scientific expedition of 1910 to 1913. British maritime expeditions continued to be of significance, for example, those of HMS *Flying Fish* at Christmas Island, and of HMS *Erebus* and *Terror*. All added to the great number of specimens in British, European and more recently the Australian museums.

The British Museum continued to contribute to gekkonid systematics, and G.A. Boulenger and A. Günther described 13 Australian species between them from 1867 to 1897. A number of European taxonomists (Peters, Steindachner, Weigmann, Girard, Werner, Thominot, Lönnberg and Anderson) also contributed to the Australian faunal list before 1914. In the same period, an increasing number of Australian herpetologists, centred in each of the Australian state museums, were active in describing the Australian gekkonid fauna. They included C. de Vis (Queensland Museum), D. Fry (Western Australian Museum), A.H.S. Lucas and C. Frost (Museum of Victoria), J.D. Ogilby (Australian Museum) and E.C. Stirling and A. Zeitz (South Australian Museum).

From the 1960s, Australian systematists, largely museum-based, and international scientists interested in particular Australian gekkonid groups, made significant advances in describing this fauna. By far the greatest contribution was made by G. Storr of the Western Australian Museum who described 16 gecko species between 1963 and 1989. While working in Australia in 1962 and 1963, A.G. Kluge made a significant contribution to the higher taxonomy of the Diplodactylinae, and also described and reinstated a number of species. More recently, museum and university-based taxonomists have described some 17 species from remote regions in the north and interior of Australia.

In the 1970s population cytogenetics was introduced as a tool for analysing those species that are morphologically variable and taxonomically uncertain, and generally have very broad geographic distributions. Following chromosomal analysis of the *Diplodactylus vittatus* complex (King 1977a), *Diplodactylus polyopthalmus*, *D. furcosus* and *D. ornatus* were resurrected as species and *D. granariensis* was described (Storr 1979b). The chromosomal races described in the *Phyllodactylus marmoratus* complex (King & Rofe 1976; King & King 1977) led to the description of *P. marmoratus alexanderiz*, and those in the *Gehyra variegata-punctata* species complex (King 1979) resulted in the description of *G. minuta* and *G. montium*. A similar analysis of the *G. australis* species complex (King 1982b, 1983a) resulted in the resurrection of *G. dubia*, and the description of *G. pamela*, *G. borroloola*, *G. robusta* and *G. occidentalis*. Additional chromosomally distinct forms of *Gehyra* remain to be described.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Australian gekkonid species range from 25 mm to 130 mm snout-vent length and generally have a depressed body. However, some exceptional species show lateral compression. The body may have distinct lateral skin folds (Fig. 27.1E). Many species have loose, velvety skin made up of minute granular scales, whereas others have a dorsal surface with clusters of pronounced tubercles surrounded by smaller scales. Abdominal scales are often large, plate-like and imbricate. Geckos have well-developed, pentadactylic limbs with complex modifications to toe shape. Some rock-dwelling and arboreal species have pad-like toes with complex subdigital lamellae, although others retain primitive claw-like toes without laterally expanded pads. Some terrestrial forms also share lamellar specialisation, whereas others have simple toes. The individual lamellae are actually compound pads made up of microscopic projections or setae which take hold on the substratum (see Locomotion).

The tail is generally thick, but varies in its degree of specialisation and size. In rock-dwelling, and sometimes arboreal, species, such as *Rhacodactylus* (*Pseudothecadactylus*) *lindneri* (Pl. 4.3), the long tail, round in section, and with specialised pinose lamellae on the tip, is prehensile and is used as a fifth limb (Fig. 27.1G). The compound ejaculatory tail glands of members of the *Strophurus*

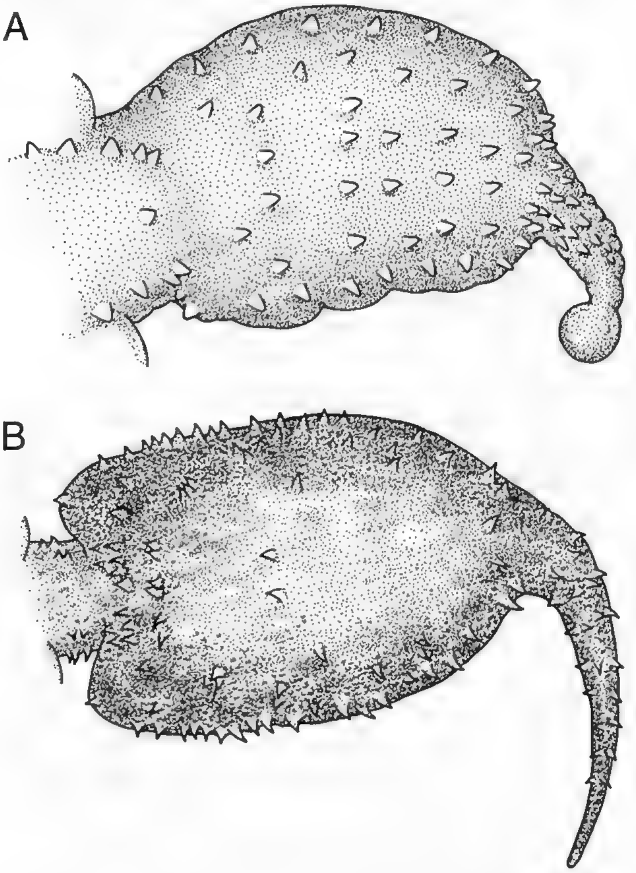

Figure 27.2 Tail shape in geckos. A, a knob-tailed gecko, *Nephrurus levis*; B, the southern leaf-tailed gecko, *Phyllurus platurus*. [M. Cilento]

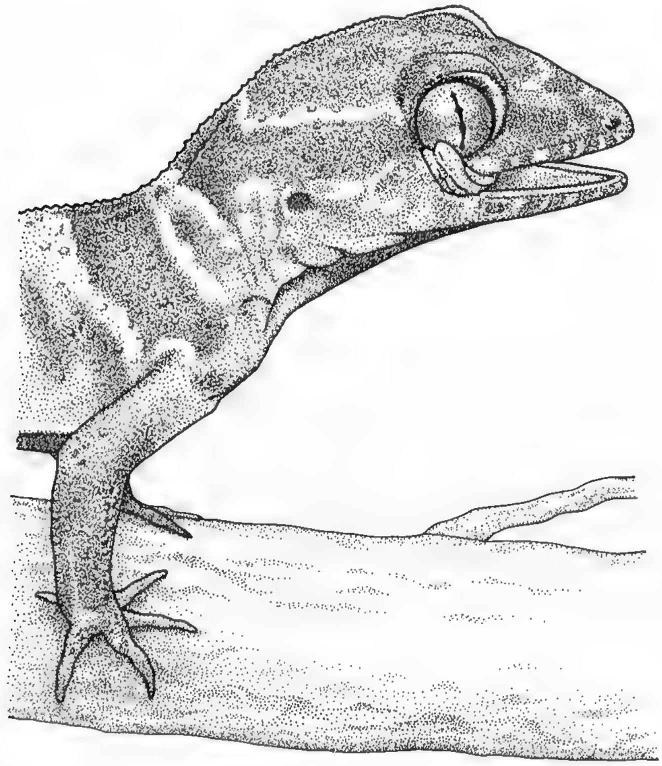

Figure 27.3 *Cyrtodactylus louisiadensis* using its tongue to wipe its face, a behaviour peculiar to the Gekkonidae and Pygopodidae. (After photo by Frithphoto/ANT)

[M. Cilento]

ciliaris complex can be used as a defence mechanism to squirt an irritant at predators. Many species can autotomise their tails along structural breakpoints when attacked. The writhing, distracting tail squirms on the ground, while the animal either lies motionless, slowly sneaks away, or flees. The tail regrows in time. Tails may also be large and function as fat reservoirs, as the round plug of a burrow entrance, as in *Diplodactylus conspicillatus*, or as leaf-like camouflage, as in most *Phyllurus* species (Fig. 27.2A; Pl. 4.7, 4.8). In the genus *Nephrurus*, most species have a tiny sensory ball on the end of a heart-shaped and otherwise pointed tail (Fig. 27.2B; Pl. 4.1; Russell & Bauer 1987).

The gekkonid head is generally robust, depressed and diamond-shaped and the snout is short and blunt (Fig. 27.1A, B, D). The large eyes are set laterally on a sloping forehead. Auditory openings are generally round to oval in shape. Large, hard, shiny nasal and chin shields cover the margins of the jaws and nasal area and contrast markedly with the dull and velvety head and body scales. The powerful jaws bear dorsal and ventral rows of uniformly short, peg-like teeth. The wide, flat tongue has a notch in its leading edge and is frequently used by the animal for licking its face and eyes (Fig. 27.3).

The back pattern colouration of geckos is often striking. *Strophurus elderi* has a grey-black background colouration with occasional raised tubercles which appear as white spots. *Oedura gemmata* has a velvet black back with lemon yellow spots and a white-banded black tail (see also Pl. 4.4). Heavily camouflaged species often have intricate back patterns of grey, brown, black, and buff. Some groups are able to change their skin colour from almost translucent pink to a marked pattern (for example, *Gehyra borroloola*), by the action of chromatophores in the cells of the skin. Longitudinal stripes on both the back and abdomen of some species which live in spinifex (for example, *Strophurus michaelseni*) provide camouflage.

The post-anal region of males is enlarged, to form two sac-like pouches at the base of the tail. These pouches appear to be associated with the internal housing of the twin hemipenes (Fig. 27.1H), and bear clusters of large caudal spurs on their postero-lateral surface.

Skeletal System

The Gekkota are amongst the oldest of the squamate groups. As such they have numerous ancestral characteristics, but also some specialised structural characteristics when compared to other squamate groups. The following is general description of the basic gekkonid skeletal system derived from Romer (1956) and Bauer (1990).

The skull is depressed and broad, and the dermal bones are thin. The pterygoid flange is well developed. The dentition is typically pleurodont and the teeth are numerous. Occasionally the stapes is perforated for the stapedial artery. The hyoid apparatus is usually nearly complete, but may be completely developed in some species. The hyoid and second epibranchial frequently make contact with the skull.

The typical gekkonid skull has several derived characters, including loss of the supratemporal arch and reduction of the jugal, which produces an incomplete post-orbital arch. A reduction in the bracing structures contributes to the internal mobility of the skull (Bauer 1990). Kluge (1967a) identified two patterns in the ontogeny of the premaxilla in the Gekkonidae which are most apparent at the egg-tooth stage. The Diplodactylinae and Eublepharinae have paired centres of ossification, whereas the Gekkoninae and Sphaerodactylinae have a single centre. In the Diplodactylinae, the premaxillae remain partially paired early in ontogeny, although in the Carphodactylini they fuse in the midline at the time of hatching in some genera, but remain paired throughout life in others (Bauer 1990). Co-ossification of the dermis to the underlying skull bone occurs in the Carphodactylini but not in the Diplodactylini (Bauer 1990). Moreover, the short wide basal process of the premaxilla in the Carphodactylini is a derived condition.

Gekkonid teeth are small, conical, homodont and pleurodont and occur on the dentary, maxilla and premaxilla. The anterior teeth are generally larger than the posterior teeth. Palatine teeth are absent. Bauer (1990) distinguished between tiny, extremely numerous teeth found in the carphodactyline genera *Nephrurus*, *Carphodactylus* and *Phyllurus*, and the moderately sized, blunt and distally compressed teeth found in other diplodactylines, and primitively in gekkonine and eublepharine geckos.

The hyoid apparatus of geckos is primitive, wherein all three cornua of the hyoid apparatus are well-developed as long slender structures (Fig. 27.4B). The hyoid and second epibranchial cornua frequently attach to the paraoccipital process dorsally, and the lingual process is long and slender. The epibranchial cartilage of the last arch is continuous with the second ceratobranchial beneath it.

A series of detailed comparative analyses has been made on the structure of the hyoid apparatus in gekkonids. Kluge (1983) distinguished a group of gekkonine genera, termed the Ptyodactylini, by the absence of the second ceratobranchial arch. Within the Diplodactylinae, certain carphodactyline genera share uniquely derived characters of hyoid structure, such as an inner proximal ceratohyal projection in *Nephrurus*, *Phyllurus*, *Naultinus* and *Carphodactylus* (Kluge 1967b). This projection is absent in the Diplodactylini.

There are usually 23 to 29 presacral vertebrae and up to 47 caudal vertebrae. Within the Diplodactylini there are 25 to 27 presacral vertebrae (Holder 1960), and from 24 to 27 in the Carphodactylini. Generally the vertebrae are amphicoelous (in which the intervertebral surface of each centrum is biconcave) with a continuous notochord and with small, free trunk intercentra, but are procoelous (in which the centra are concave anteriorly and convex posteriorly), with small condyles, in a few genera. Septa are present in caudal centra and the tail is short and fragile.

Amphicoely is peculiar to the Gekkonidae. It is regarded as a secondarily derived condition, and has generated considerable debate on its evolution and phylogenetic significance (Kluge 1987). Both amphicoely and procoely are encountered in the

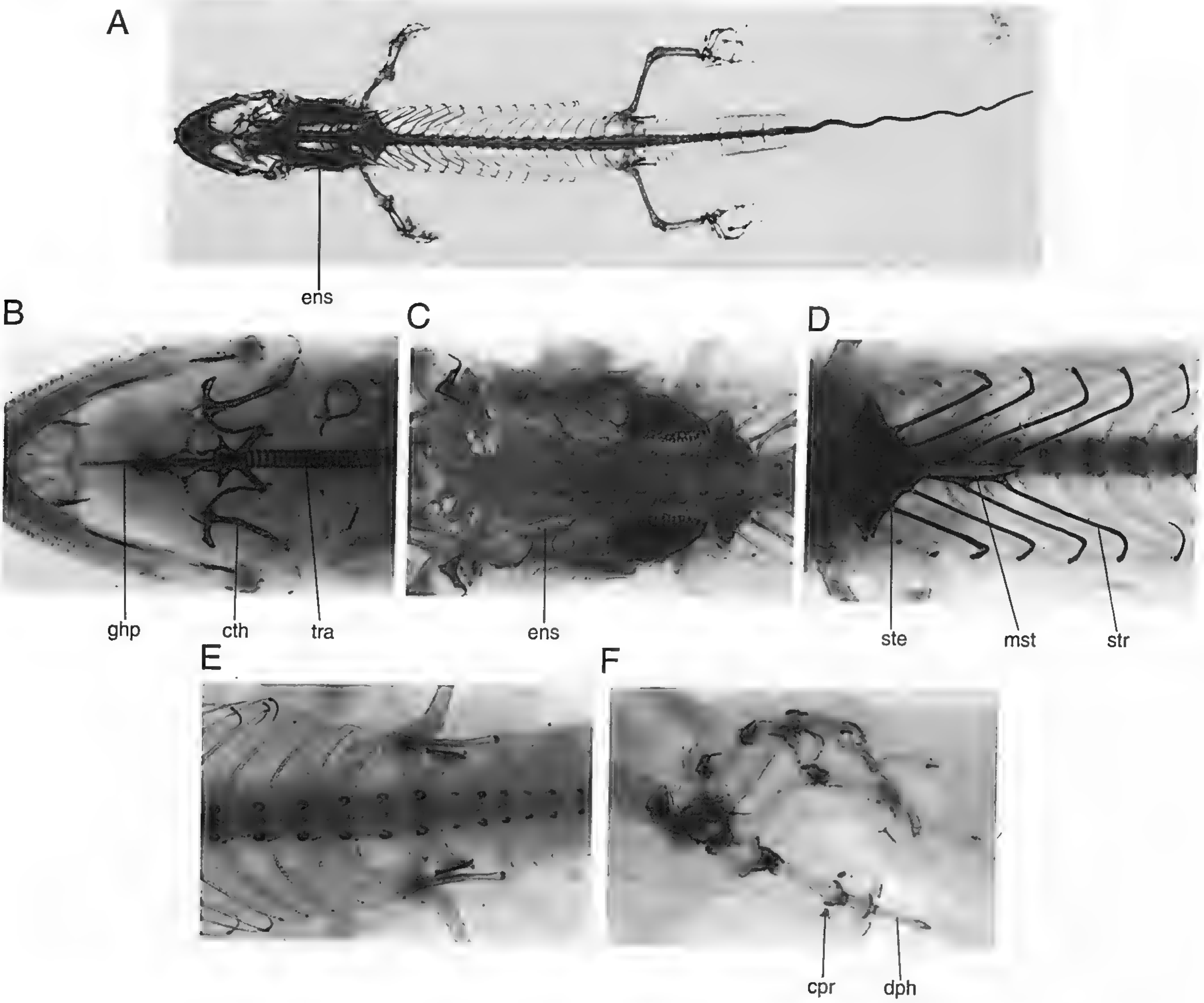

Figure 27.4 Alizarin preparation of an adult specimen of *Hemidactylus frenatus* showing the skeletal morphology of a typical gekkonid. Bone appears as grey material, except in the tail where the tissue is still visible, and cartilaginous tissue is black. **A**, dorsal aspect of the whole animal; **B**, ventral view of the hyoid apparatus, which is predominantly cartilaginous; **C**, dorsal view of the endolymphatic sacs anterior to the clavicles; **D**, ventral view of the sternum and sternal ribs; **E**, dorsal view of the pelvic girdle; **F**, foot. **cla**, clavicles; **cpr**, cartilaginous processes supporting the toe pad; **cth**, ceratohyal arch; **dph**, distal phalange with associated claw; **ens**, endolymphatic sacs; **ghp**, glossohyal process; **mst**, mesosternum; **ste**, sternum; **str**, sternal ribs; **tch**, trachea. [Photos by M. King & P. Horner]

geckos and the difficulty of attributing a derived or ancestral polarity to this condition remains. Kluge concluded that the primitive state of procoely was attained several times among gekkonoids and that amphicoely with a continuous notochordal canal, may have been aquired by paedomorphosis in early gekkotans (Gauthier 1981). Bauer (1990) viewed amphicoely as a primitive character within the Carphodactylinae and considered that procoely, which is found in certain species, is derived.

The eight cervical vertebrae of carphodactyline geckos are typically gekkonid and characterised by an association with persistent intercentra that lie ventral to the intervertebral discs, or with a persistent notochord (Bauer 1990). The intercentra are enlarged with ventral hypopophyses. The cervical intercentra are narrow. However, species of *Rhacodactylus* had broad intercentra with posteriorly directed hypopophyses.

The trunk vertebrae are relatively uniform. Bauer (1990) interpreted the high neural spines found in certain Carphodactylini as a derived character. In the Carphodactylini and Diplodactylini, one to three lumbar vertebrae (pre-sacral vertebrae which do not bear ribs) are typical; gekkonines have a single lumbar vertebra. Most geckos have two sacral vertebrae, although some carphodactylines have three or four (Bauer 1990). In the latter group, other vertebrae have been modified and included in the sacral complex (Fig. 27.4E). Moffat (1973) reported the absence of a sacral pleurapophyseal process in the Diplodactylinae. Her interpretation of this as a loss, and therefore a derived condition has been disputed by Bauer (1990) and Kluge (1987).

Not surprisingly, the geckos have a highly variable number of caudal vertebrae, a feature associated with the extreme variation in tail morphology. The number of caudal vertebrae ranges from 22 to 47 in the Carphodactylini (Bauer 1990). There is not always a direct correlation between caudal number and tail length, and *Phyllurus*, *Nephrurus* and *Carphodactylus* have greatly shortened centra compared to those of other Carphodactylini. Bauer (1990) regarded this as a derived state. In this group, many vertebrae are fused and all have reduced, or lack, transverse processes on the post-pygal caudal vertebrae (autotomising septum-bearing vertebrae). Tail autotomy is common throughout the Gekkonidae and is possible through any post-pygal vertebra in most Gekkoninae. While autotomy may be restricted to one or several autotomy planes in the Diplodactylini, only one or two vertebrae have autotomising septa in the Carphodactylini. *Nephrurus asper* lacks them altogether. The reduced number of autotomy sites is correlated with a loss of transverse processes, or caudal vertebra. The commonest site of the first autotomy plane is in the sixth caudal vertebra in both the Diplodactylinae and Gekkoninae (Bauer 1990) (also see Behaviour).

Ribs may be present on both cervical and trunk vertebrae (Fig. 27.4A, D, E). Each of the thoracic ribs consists of a vertebrocostal element, which is always present, an intermediate element composed of cartilage, and a sternal or mesosternal component. Abdominal ribs lack intermediate or mesosternal elements. Thoracic ribs may have a direct sternal attachment, or may be attached to a narrow band of cartilage which runs postero-ventrally from the sternum, termed the mesosternum (Fig. 27.4C). Parathoracic ribs, or parasternalia, which are posterior to the thoracic ribs, curve anteriorly, then fuse at the midline. Within the Carphodactylini, Bauer (1990) found between two and three sternal and mesosternal ribs and from none to seven parathoracic ribs. Kluge (1967b) proposed that an increased number of parathoracic ribs is correlated with arboreality in the genus *Diplodactylus* (which at that time included *Strophurus* species). Bauer (1990) found the same correlation in the Carphodactylini.

The sternum is a short, broad plate lying in a midventral position, posterior to the coracoids and superficially overlapped by the interclavicles (Fig. 27.4C). Sternal fontanelles are absent and a parasternum is sometimes present. Most carphodactyline species have a long and broad sternum, whereas in *Nephrurus* it is short and narrow (Bauer 1990). In *Naultinus*, the sternum remains unossified throughout ontogeny, thus recapitulating the primitive form.

In modern geckos the pectoral girdle lacks paired cleithra. The lower end of the clavicle is broadened and is either hook-shaped or perforated. It does not overlap with the interclavicle head. The interclavicle may be T-shaped, cruciform or rod-shaped (Romer 1956). The primitive clavicles in the Carphodactylini are longer than wide and bear a pair of laterally directed coracoid extensions. The interclavicle is primitively imperforate, although fenestrae are present in some genera. The primitive clavicle in this tribe is broadly expanded and fenestrated medially. Size and number of fenestrae vary within and between genera. They are absent in *Carphodactylus* and *Phyllurus*, whereas very large fenestrae occur in *Nephrurus* (Bauer 1990).

The second portion of the pectoral girdle, the scapulocoracoid, is an endochondral formation. The scapulocoracoids are paired and articulate with the leg bones. The scapula and coracoid form a compound element in which each component joins at right angles. Usually all four scapulocoracoid fenestrae are well developed and the two upper ones are emarginate. In the Carphodactylini, the primitive scapula is a broad, stout blade at its border with the suprascapula. It is narrow at its midpoint and expanded ventrally at the coracoid suture. However, the scapula of *Nephrurus* has a narrow shaft and an elongate blade (Bauer 1990).

The basic structure of the forelimb consists of a humerus, ulna, radius, carpals, metacarpals and phalanges. There is considerable variation in foot and toe structure, which has been accompanied by osteological divergence. Bauer (1990) found variation between carphodactyline genera in the size of the metacarpals and in phalangeal formula, and considerable phalangeal reduction in the Diplodactylini. The significance of the variation in toe structure is dealt with more extensively in the following section.

The pelvic girdle differs from the pectoral girdle in that it is an endochondral structure. The pubic bones of geckos are separated by a substantial epipubic cartilage (Romer 1956). The pubis is relatively narrow in most geckos and a pectineal tubercle is present. *Phyllurus* has a typically broad and robust pubis (Bauer 1990). The blade-like metischial process on each ischium is narrowly separated from the other in the Diplodactylini and New Zealand and New Caledonian Carphodactylini, whereas in the remaining Carphodactylini these processes are expanded postero-laterally and widely separated from each other. Geckos have a dagger-shaped hypoischium, which extends posteriorly to the metischial process. It is of variable length and form in different genera.

Overall, hind limb structure is relatively uniform within the Gekkonidae. As with the front limbs, considerable variation occurs in structure of the metatarsals and phalanges associated with highly derived foot and toe structure (Fig. 27.4F). Metatarsals are shortest in the Diplodactylini. Bauer (1990) recognised three groups of genera in the Carphodactylini which share a common pattern of metatarsal length (from shortest to longest): *Nephrurus* and *Naultinus*; *Phyllurus* and *Carphodactylus*; and the remaining Carphodactylini. The fifth metatarsal is short and broad, and medially receives a projecting spine from the fourth metatarsal (Romer 1956). The fifth metatarsal is strongly hooked in the genera with expanded toe pads, but only slightly hooked in the padless Australian genera. This structure permits the foot to grip the substrate and is analogous to the heel. Many of the characteristics of toe structure are also reflected in the osteology of gekkonid digits. Paraphalangeal elements are frequently present in the toes of species having adhesive pads.

Bauer & Russell (1989) described the ossified anal bones and other minor ossifications such as the supraorbital scales.

Locomotion

As in primitive reptiles, the Gekkonidae generally have larger hindlimbs than forelimbs. The body lies flat on the substratum at rest, but is cleared a short distance from the ground during movement. The limbs provide a wide trackway (Fig. 27.5).

Modifications in skeletal structure permit adjustment between the position of the tibia and tarsus to provide a laterally projecting hind foot, as is also true of the forearm and manus of the front foot. Such adaptations are important in the gekkonids with their highly specialised foot structures and surface attachment mechanisms, and permit geckos to run at great speed on a range of surfaces. King (1984a) observed a galloping gait in the diplodactyline, *Oedura filicipoda*.

Perhaps the most spectacular example of multiple convergence in form and function in the Gekkoninae, is the evolution of seven major patterns of foot morphology in response to selection for a more efficient climbing foot (Russell 1976) (Fig. 27.6). Similar patterns have evolved independently in the Diplodactylinae (Russell 1979). In both subfamilies, the shift in adaptive zone from terrestriality to arboreality has provided the selective medium in which these mechanisms have evolved. Russell (1979) proposed that each shift towards the development of adhesive subdigital pads from the primitive foot design, has been accompanied by restructuring of the foot. That the same pattern of change has arisen independently in a number of lineages is attributed to the similarity of selective pressures and the channelling of change in morphological complexity in a particular direction. Indeed, the integrated control mechanisms required for the efficient operation of a subdigital pad have arisen on several independent occasions and the structural differences between these mechanisms are a product of their different ancestry. There are many examples of the evolution of climbing feet from terrestrial ones and vice versa.

Primitive padless digits are found in both the Gekkoninae and Diplodactylinae (Fig. 27.6F). Russell (1979) identified three key features, as exemplified by the carphodactyline, *Carphodactylus laevis*. The double bellied extensor muscle to each digit gives rise to a single stout tendon which is tightly bound to all interphalangeal joints by strong ligaments. Secondly, the flexor musculature is simple and the flexor tendon traverses the phalanges mid-ventrally in a synovial sheath and inserts in the claw-bearing phalanx with a particularly high mechanical advantage. Lastly, the phalangeal formula is primitive and the joints between the phalanges overlap strongly both dorsally and ventrally, thus preventing hyperflexion or hyperextension of the digits.

These features permit grasping and climbing on rough surfaces, or trees, but pads or hyperextension are lacking (Fig. 27.6F; Russell

1979). Extensive radiations of primitive, padless *Nephrurus* (Carphodactylini) have abandoned rock-dwelling, or arboreal habits and demonstrate purely terrestrial adaptations of the primitive foot. These include adaptations of toe structure for life in a sandy environment, such as puffy feet with pinose scales, a reduction in size of the digits, and reduced phalangeal formula (Bauer & Russell 1991).

In the primitive foot pattern of the Gekkoninae, muscle masses do not traverse any of the phalanges on the dorsal surface of the toes and the phalanges articulate with double-headed joints which prevent hyperextension (Russell 1976). The genus *Cyrtodactylus* is typical of this type, but also demonstrates an evolutionary series in which pad formation has occurred in some species. Most species have long slender digits which exhibit a slight kink, beneath which are large, subdigital scales with microscopic hook-like outgrowths 2 to 3.5 µm long. These outgrowths are probably precursors of the microscopic hook-like setae which form adhesive toepads. Russell (1976) demonstrated an enlargement of subdigital scales associated with this kink in some *Cyrtodactylus* species, which include a lateral expansion of the scales into pads. These changes are accompanied by modification of the articulation of the phalanges that permits hyperextension. The dorsal musculature and tendons have also extended dorsally along the toe surfaces. Thus, there has been development of muscle, bone and tendons associated with toepads and setae.

Hyperextension is basic to the function of adhesive pads in the Gekkonidae. The thousands of microscopic setae present on the adhesive subdigital lamellae of the toes of geckos, can engage microscopic irregularities on the surface on which the animal is climbing, such that a pad makes contact and effectively hooks on to a surface. To remove the pad, the gecko must detach the pad in the opposite direction to which it was applied. To achieve release, blood is forced into sinuses within the toes, the muscles dilate and the phalanges disarticulate, thus changing the position of the setae. The toes can be curled back as the setae are effectively disengaged. This obligatory locomotory mode permits the gecko to walk on and adhere to smooth, vertical surfaces and even hang on the lower side of horizontal surfaces. It is noteworthy that the positioning of the feet obliquely to the body, plus the radiation of the toes on each foot, spanning over 200° of arc, provides all-round support for the animal and thus consolidates an otherwise precarious attachment.

Multiple evolutionary pathways of toepad form and function are evident within the different gekkonid lineages. Thus, while the genera *Gehyra*, *Hemidactylus* and *Lepidodactylus* of the Gekkoninae have very large toepads with multiple scansors and adhesive properties, in other genera only particular pads may be adhesive (Figs 24.2; 27.6A, B). In species of *Phyllodactylus*, *Diplodactylus*, *Crenadactylus* and *Rhynchoedura* only the paired, large terminal pads on each toe are adhesive.

The shift from terrestriality to arboreality has been considered to be the driving force in the specialisation and development of adhesive toe pads (Russell 1976). However, numerous species in different lineages have either secondarily lost these pads because of a new direction in habitat specialisation, or have acquired quite different morphological specialisation with other adaptations. While modification in toe structure from padless to padded may provide for a transposition to an arboreal habitat, it also allows sufficient plasticity to enable species to specialise secondarily in a rock-dwelling lifestyle, as has occurred in some Australian *Gehyra* (King 1984c), without the necessity for any substantial change in toepad structure. This is not true for those geckos which have reverted to a purely terrestrial existence, living on or in different soil types.

Russell (1979) proposed that pads were acquired once within the Diplodactylinae, and that the Carphodactylini and Diplodactylini exploited them in different ways. Since he regarded terminal pads as primitive and argued that they were associated with arboreality (as in the Gekkoninae), secondary terrestriality developed in association with the invasion of the Eremean floristic zone.

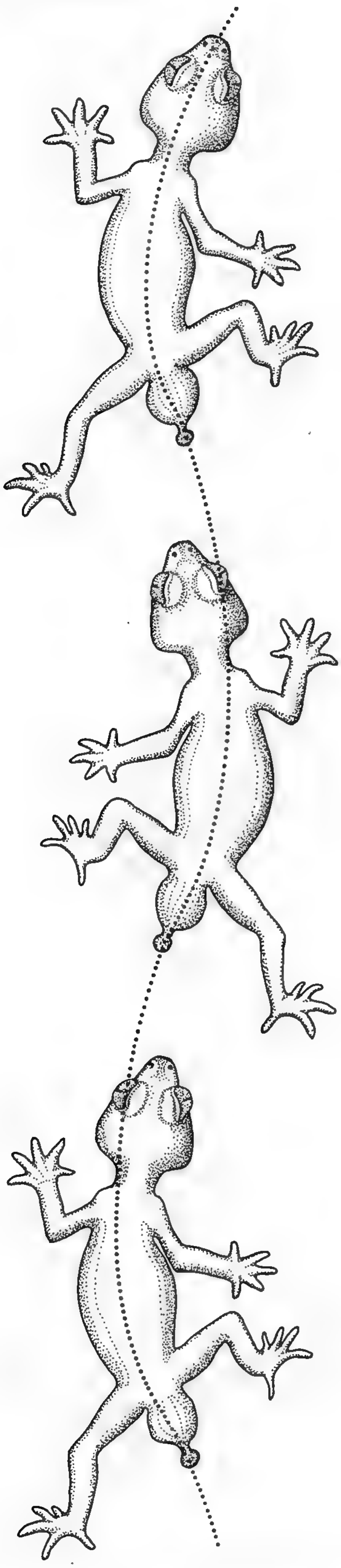

Figure 27.5 Locomotory movement in the Gekkonidae. The dotted line emphasizes the swimming motion of the spine. [M. Cilento]

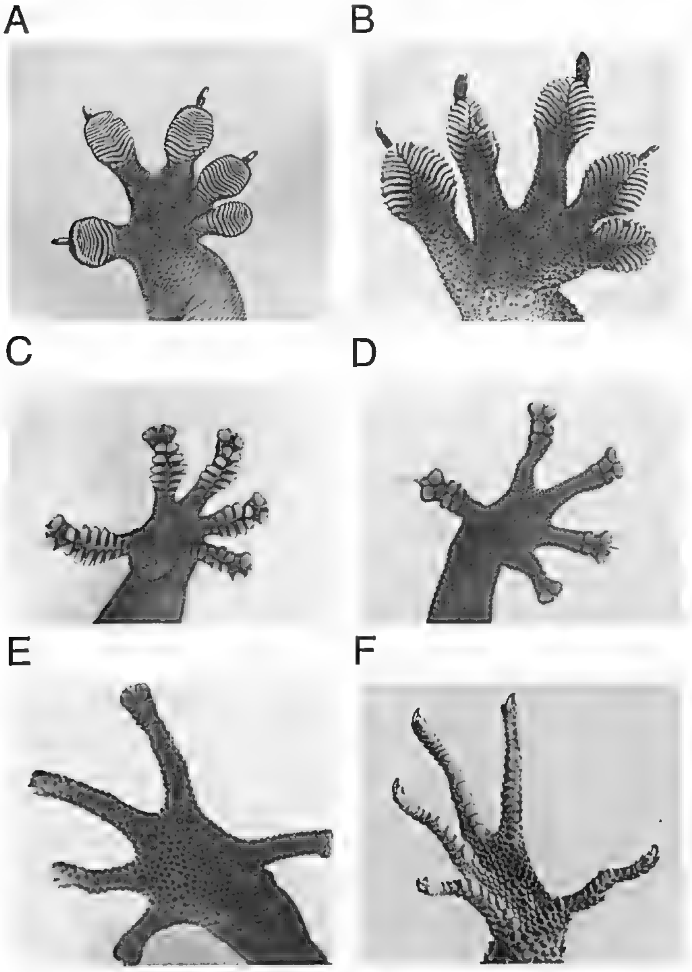

Figure 27.6 Ventral view of the hind feet of selected gekkonid species. **A**, dilated toepads and numerous subdigital lamellae of *Gehyra membranacruralis*, in which the claw on the fifth toe is absent; **B**, the wedge shaped group of rounded scales dividing the toepads increases the opposing angle between lamellae in *Gehyra xenopus* and large claws are present on digits 1 to 4; **C**, the large pair of terminal toepads and the very enlarged intermediate pads form each toe of *Oedura filicipoda* into one laterally divided adhesive surface; **D**, the enlarged pair of terminal toepads and two pairs of subterminal pads of *Oedura gracilis* are typical of this genus; **E**, the terminal adhesive toepads and other subterminal pads of *Diplodactylus occultus* are reduced in relation to toe length; **F**, adhesive pads are lacking in the primitive gekkonine condition shown by *Heteronotia binoei*
[Photos by M. King & P. Horner]

Supporting evidence for this view comes from the presence of mechanisms for hyperextension in terrestrial Diplodactylini which have very small pads, or no pads at all, and which do not hyperextend their toes (Fig. 27.6E). Terminal pads have been lost completely in *Diplodactylus damaeus* and yet musculature, sinuses and osteology associated with hyperextension remain. Other adaptations to a sandy substrate include the reduction in size of digital scales and their development into a spinose form (Bauer & Russell 1991).

A substantially different evolutionary course from most Diplodactylini (excluding *Strophurus*), has occurred in the Carphodactylini, in that basal, as well as terminal, adhesive toepads have developed. The arboreal and rock-dwelling *Strophurus* show this same development (Fig. 27.6C, D). In the Carphodactylini, the pair of terminal pads which characterise the Diplodactylini have been much reduced or lost in most groups. An exception is the genus *Oedura*, in which the terminal pads and the intermediate scales are enlarged. Highly developed basal toepads have also evolved in the Gekkoninae (for example, *Hemidactylus*), although by different pathways (Russell 1979). Operation of the toepads in the Carphodactylini involves a simpler internal mechanism than that of advanced gekkonines.

Complex locomotory adaptations resulting in complete changes in foot structure in terrestrial and arboreal species have been accompanied by a number of additional locomotory adaptations. Parallel adaptations to an arboreal existence are seen in the Carphodactylini and Gekkonini. Thus, *Gehyra membranacruralis* has a prehensile tail with a pinose scale tip, which it uses as a 'fifth limb' to hang from foliage. Species of the carphodactyline genera *Naultinus* (see Bauer 1990, Fig. 52) and *Rhacodactylus* have similar prehensile tails, although in *Rhacodactylus* (*Pseudothecadactylus*) *lindneri* the tail tip has a series of pinose scales (presumably with setae), which may act as an adhesive pad. Remarkably, the cavernicolous carphodactyline, *Oedura filicipoda*, has a similar prehensile tail with pinose scales on the tip (Fig. 27.1G), even though its tail is also used as a fat storage area.

Feeding and Digestive System

Three aspects of ingestive behaviour are considered: licking food, drinking water, and preying on other animals. Free-ranging and captive geckos use the same technique to lick food as they use for drinking. *Rhacodactylus lindneri* and *Phyllodactylus guentheri* lick nectar from blossoms on trees and *Gehyra australis* licks decaying, or pulpy fruit. Gekkonids generally lick water from the surface of leaves or rocks, but on occasion, captive *Gehyra* species have been observed drinking water from a glass petri dish. This involved partial submersion of the head and continuation of the lapping motion.

Geckos can be voracious predators and will actively pursue and kill their prey. Generally they attack moths and arthropods by running up to the animal, biting down on it and then beating the prey on the ground by shaking the head laterally. The geckos' head size governs the size of large insects which can be eaten. The prey is orientated longitudinally in the gecko's mouth, so that protrusions, such as an insect's legs, fold back, thus avoiding obstruction. The prey is swallowed with assistance from the tongue, muscular contractions in the neck and body, and by progressive biting and swallowing.

Sense Organs and Nervous System

Sensilla of supposed mechanoreceptive function are widespread among geckos, although their presence in Australian species has been poorly studied. They have been reported in a number of gekkonines, and are principally associated either with scales bordering the subdigital lamellae, with the labial scales, or with the body scales (Russell & Bauer 1987).

The possible function of the terminal caudal knob, which is characteristic of most members of *Nephrurus*, has long intrigued herpetologists (Fig. 27.2B; Pl. 4.1). This hard, rigid integumentary structure is richly supplied with vascular tissue and has numerous, regularly arranged sensilla on each of its surface scales (Russell & Bauer 1987). The caudal peduncle supporting the knob is well-muscled, permitting the knob to be moved freely, thereby suggesting that it may play an active role in sensory reception. Surface sensilla on the caudal knob probably monitor disturbance impinging directly on their exposed surfaces. Compared with other geckos, frequency of tail autotomy in *Nephrurus* is generally low (Bauer 1986a) and *N. asper* is the only gecko unable to autotomise any portion of its tail (Holder 1960). Russell & Bauer (1987) postulated that, apart from the mechanoreceptive function of the knob, its extensive vascularisation may also be an advantage in thermoregulation and heat exchange. They noted that the carphodactyline genus *Carphodactylus* has a similar, but much smaller, terminal knob on its tail.

Taste buds occur in the oral and pharyngeal epithelia of most vertebrates, but are generally considered to be unimportant to lizards (Schwenk 1985). Schwenk found that geckos have numerous taste buds in the oral epithelium, but virtually none on the tongue. However, Nonoyama (1936) recorded numerous taste buds on the tongue of *Gekko japonicus*, suggesting that taste bud numbers and distribution may be variable within the family;

concomitantly, the reliance placed on this chemosensory mode may also differ.

Endocrine and Exocrine Systems

Little is known of endocrine systems in Australian gekkonids, although endolymphatic sacs have been examined. In most lower vertebrates, the endolymphatic sacs are part of a calcium-filled system associated with the ear or organs of balance. In many gekkonine and sphaerodactyline species, the sacs are greatly enlarged and protrude from the cranial vault to lie along the surface of the peripheral lateral neck musculature (Fig. 27.4A, D; Kluge 1967a).

The function of the endolymphatic sacs in geckos is still unclear. The endolymphatic system may regulate pressure in the labyrinth by removing the endolymphatic fluid from the sacculus, thus aiding the transmission of sound waves from the skull into the ear, and also it may be a source of calcareous material for bone growth (Whiteside 1922). Additionally, as the paired endolymphatic sacs are larger in females (Greer 1989) and the size and density of the sacs increases before egg-laying, the system could provide calcium for egg shell production (Bustard 1968a). In support of this hypothesis, gekkonine species have a hard, relatively impermeable, calcareous shelled egg (Bustard 1968a) and possess prominent endolymphatic sacs, whilst the diplodactylines have relatively pliable, permeable egg shells (Greer 1989), and apparently lack enlarged endolymphatic sacs. Lymphatic sacs filled with calcium carbonate have not been detected in Eublepharinae, or in most Diplodactylinae. However, Bauer (1990) found aragonite accretions in sacs in the nuchal area of *Eurydactylodes* species. He concluded also that the accumulation of calcium carbonate is related to calcium stress in reproductive females.

Exocrine structures in geckos include 'escutcheon' scales and pre-anal organs. The latter are present in the males of most lizard groups. Pre-anal organs are tubular evaginations of the epidermis (Fig. 27.1E) and include femoral glands and similar structures in the posterior abdominal region (Kluge 1967b). Their external apertures, pre-anal pores, occur either in the centre of a scale, or at its posterior edge. Homologous scales in females are occasionally indented in a pattern that suggests the male pore arrangement. The pre-anal organs secrete an odourless, cellular material, or 'secretion plug', that arises from the basal layer of germinal cells, passes into the lumen and differentiates as it travels distally towards the pore (Cole 1966b; Maderson 1972); their function remains unclear (Cole 1966b; Kluge 1967b). Pre-anal organs are most heavily swollen with waxy cellular material during certain seasons, which are seemingly correlated with the sexual cycle (Kluge 1967b). Greenberg (1943) suggested that they function in some prelude to copulation in the gekkonid, *Coleonyx*, in which males were observed rubbing the wax cones from the pores transversely across the tail of the female. She responded by elevating her tail. Pheromone dispersal may be another possible function, as the epidermal glands are well placed for transfer of products to the substrate during locomotion (Maderson 1970a, 1972).

'Escutcheon' scales, or generation glands, are restricted to sphaerodactyline geckos and thus not found in Australian gekkonids (Maderson & Chiu 1970). They are thought to have evolved from pre-anal organs (Kluge 1967b; Bauer 1990). They are specialised, unpigmented glandular scales located on the abdominal, femoral and post-cloacal regions (Taylor & Leonard 1956). They are more pronounced in males and increase in number with age (Kluge 1967b).

The caudal glands in the genus *Strophurus* are used in defence. They secrete a sticky, black, or pale yellow, substance which has a distinct musty odour (Rosenberg, Russell & Kapoor 1984). The caudal secretions of *S. ciliaris*, *S. rankini* and *S. strophurus* are mainly proteinaceous, with at least one glycoprotein component present in the secretion of *S. strophurus* (Rosenberg *et al.* 1984). In active *Strophurus* species, the secretion can be ejected explosively from the dorsal surface of the tail to a distance of 300 mm or more (Bustard 1970b; Morrison 1950, 1951). Considerable quantities may be extruded, and the secretion can be directed by an appropriate curvature of the gecko's tail. Apart from being irritating to eyes (Morrison 1951), the secretion is non-toxic, at least to chicks (Rosenberg & Russell 1980) or rats (Richardson & Hinchliffe 1983), and the extreme stickiness of this exudate may be its most effective defensive property (Rosenberg *et al.* 1984). The gecko itself is not irritated by the secretion, as has been shown by observations of an individual licking residual secretion from its tail (Russell & Rosenberg 1981).

In *Strophurus*, the defensive glands are a longitudinal, paired series of caudal chambers that secrete and store the glandular products (Rosenberg & Russell 1980). They are located deep within the caudal musculature, adjacent to the caudal vertebrae, and muscular contraction ejects the secretion. The fluid leaves the tail through a mid-dorsal epidermal rupture zone located anteriorly in each caudal segment (Russell & Rosenberg 1981). Regenerated tails contain elongate unsegmented glands. Therefore individuals with regenerated tails retain the ability to extrude the defensive secretion, and ejection of the secretion occurs either at the junction of the old and new tail, or in rupture zones contained in any remaining segments of the original tail (Russell & Rosenberg 1981).

Reproduction

Like most other reptiles, gekkonids are generally bisexual, except for a few parthenogenetic forms. Several different reproductive strategies have been established. Generally the Gekkoninae and Sphaerodactylinae lay one or two calcium-shelled eggs per clutch, and the Diplodactylinae and Eublepharinae usually lay two parchment-shelled eggs. All Australian taxa are oviparous. However, species of the New Zealand genera *Naultinus* and *Hoplodactylus* are live bearers (viviparous), as is the New Caledonian *Rhacodactylus trachyrhynchus* (Bauer 1990). Other species of *Rhacodactylus* are oviparous. Viviparity has been derived independently in these temperate and tropical species. Apparently, viviparity is not necessarily a low temperature adaptation, but may be associated with the provision of an energy reservoir enhancing the survival of juveniles. Much foetal nourishment in live-bearing carphodactylines is derived from yolk. The choriovitelline placenta is used for food absorption (Bauer 1990). Viviparous species are generally slow-moving animals and the yolk may be a nutritional buffer for young which may not have immediate hunting success.

Calcium-shelled eggs of the Gekkoninae and Sphaerodactylinae are soft when first laid, but harden after exposure to air. The egg shells are made of calcite and provide resistance to desiccation. They are capable of withstanding exposure to sea water for prolonged periods while still remaining viable (Brown & Alcala 1957). In contrast, diplodactyline and eublepharine eggs fail to show any mineralisation and are sensitive to aridity and humidity changes (Kluge 1987).

Male gekkonids have a bilaterally symmetrical reproductive system. The testes are located deep within the body cavity and are attached by mesenteries to the dorsal peritoneal lining on either side of the spine. In certain spiny tailed diplodactylini (*Strophurus* spp.), which are active during daylight hours and exposed to the sun, the peritoneal lining and the tunica of the testes are black; this may be a means of reducing the mutagenic effects of solar radiation. Testes undergo substantial changes in size, as much as ten-fold, as a prelude to sperm production. The seasonality of these changes is dependent on the reproductive strategy adopted by the species. For example, in *Phyllodactylus marmoratus*, testis weights are at their greatest in January and February and decline during the less active winter months. Meiotic activity commences in the spring, reaches a peak in November and extends to February.

Female reproductive systems are also bilaterally symmetrical, and the pair of ovaries lies in the dorsal midline in a similar position to the testes. Because of the great size of gekkonid eggs (up to 30% of the body weight), substantial anatomical and physiological changes are associated with egg production. The uterine area of the oviduct is relatively compact in the non-breeding season. However, before ovulation the oviducts become massively enlarged and distorted. Fat is mobilised and converted to yolk and fat bodies are substantially reduced in size, particularly those of the tail. Thus, in *Gehyra variegata*, loss of the tail in a female can prevent egg production (Henle 1990b).

Reproductive strategies adopted by Australian gekkonids may be grouped into four categories, three of which occur in southern forms. Females of species such as *Heteronotia binoei* (southern populations) are inseminated by males during the spring and early summer (Bustard 1969a), and lay a clutch of two eggs between late November and early December. These hatch between late February and March. A second strategy has been adopted by *Gehyra variegata*, as shown for populations in the Pilliga scrub and at Kinchega, New South Wales(Bustard 1969d; Henle 1990b). Mating occurs from September to December. Females produce two single-egg clutches per year, the first in late November and early December, the second in early January. A first wave of hatchlings appears in February and a second in March.

The third strategy is seen in *Phyllodactylus marmoratus*. In this cold-adapted species, mating occurs in autumn after egg laying is completed (King 1977b). Sperm are stored in oviducal lamellae throughout the winter months and are available for immediate fertilisation when ovulation occurs. This strategy allows very early fertilisation when males may be less active because of lower temperatures. Early egg-laying and hatching ensure that the hatchlings will have an opportunity to accrue adequate food reserves before winter. A similar reproductive strategy is apparent in *Phyllurus platurus* (Green 1973).

In the tropical regions of Australia a fourth strategy appears to operate. Hatchlings of *Hemidactylus*, *Oedura* and *Gehyra* are commonly observed in the wet season when there is an abundance of insect life. *Hemidactylus frenatus* can breed throughout the year in other tropical environments. More southerly species of these genera have been observed to lay eggs in the dry season. Greer (1989) suggested that this may be because of poor egg survival in the wet season.

Morphologically distinguishable sex chromosomes are rare in the Gekkonidae, although they have been found in the gekkonines, *Phyllodactylus marmoratus* (King & Rofe 1976), *Gehyra australis* (King 1977c) and *Gehyra purpurascens* (Moritz 1984). Female heterogamety has been reported in all of these. Sex chromosomes are unknown in the Diplodactylinae. Parthenogenesis has been reported in *Lepidodactylus lugubris*, *Nactus pelagicus* and *Heteronotia binoei* (Moritz & King 1985).

Chromosomal variation within the Gekkonidae is extreme. The most recent summary was published by King (1987a, 1987b). In all groups, the ancestral karyotype is acrocentic. In the Diplodactylinae, the ancestral number is $2n=38$. In the polyphyletic Gekkoninae, clusters of species have different acrocentric numbers ranging from $2n=32$ to $2n=46$. In both subfamilies, individual species often have extensive karyotypic modifications as a result of structural rearrangements (also see Affinities with other Groups; Affinities within the Taxon).

NATURAL HISTORY

Life History

Little information is available on the longevity of gekkonids. Most accounts are drawn from captive animals. Personal observations suggests that geckos can be particularly long-lived. A specimen of *Oedura gemmata* which had been captured from the wild in 1980 and maintained in the laboratory, died in 1991 (King & Horner pers. obs.). This animal was an adult when captured and remained much the same size over the 11 years of its confinement. One of the few reports of longevity in the wild is for a New Zealand carphodactyline, *Hoplodactylus maculatus*, which had been monitored for 17 years (Anastasiadis & Whitaker 1987).

Other aspects of gekkonid life history support the view that these are long-lived species. Sexual maturity in *Gehyra variegata* occurs at two years and egg production commences when females are three years old (Henle 1990b). The same pattern was observed in *Oedura monilis* (Bustard 1971). In *Strophurus ciliaris*, sexual maturity occurs at three years, whereas female *S. spinigerus* are mature at 20 months (How, Dell & Wellington 1986). How & Kitchener (1983) found that *Oedura reticulata* females were reproductively mature after 4 years. Moreover, in most instances geckos only produce two eggs per annum, indicating a very low reproductive rate and suggesting that longevity is an important component of reproductive success.

Henle (1990b) calculated a life expectancy of 6.5 years for *Gehyra variegata* after the attainment of sexual maturity at 2 years in females. Mortality was particularly low for adults and there were no differences between males and females, or between adults and subadults. However, juveniles showed a considerably higher mortality. Similar results were obtained by Bustard (1969d) in his examination of *G. variegata* in the Pilliga scrub, although he did find a female-biased sex ratio. It is noteworthy that the arboreal preference of *G. variegata* is correlated with a low number of potential predators.

Ecology

Most geckos are dietary generalists which prey on various arthropods and occasionally small vertebrates, and eat some plant material. Pianka & Pianka (1976) determined that at least three Australian desert species, *Diplodactylus conspicillatus*, *D. pulcher* and *Rhynchoedura ornata*, are dietary specialists which feed almost exclusively on termites.

Behaviour

Of all reptiles, gekkonids appear to be the most vocal. Calls usually take two forms. In the first of these, gekkonine and diplodactyline geckos produce defensive or distress calls when threatened. In the Gekkoninae, these may be a simple chirp, or scream, such as heard in species of *Gehyra*, *Hemidactylus* and *Phyllodactylus* (Daniels, Flaherty & Simbotwe 1986). In the Diplodactylini, aggressive threat calls may be accompanied by back-arching, leg-extension and mouth-opening (Fig. 27.7). Numerous instances of these calls have been described for *Phyllurus* and *Nephrurus* (Bauer 1990) and one of us (King pers. obs.) has observed this in *Diplodactylus byrnei*. Calls of the second form are associated with contact in territoriality or mate attraction. These contact calls consist of multiple chirps and are known from a number of gekkonine genera including *Hemidactylus*, *Gekko*, *Phyllodactylus*, *Ptenopus*, *Ptychozoon*, *Cyrtopodion*, *Ptyodactylus* and *Thecadactylus* (Kluge 1987). Bustard (1969c) suggested that *Strophurus* species also make contact calls.

Three types of call were detected in Mexican populations of *Hemidactylus frenatus* (Marcellini 1977, 1978). A single chirp is given under stress. A multiple chirp call is made by both sexes, but more generally males, associated with feeding, defaecation, mating, or fighting between males. The third type of call consists of a very rapid burst of short chirps, made when males are preparing to fight.

Diplodactyline and gekkonine geckos have developed a series of unusual defensive mechanisms, in addition to vocalisation and defensive posture (Fig. 27.7). Some of the most spectacular of these adaptations are found in the Diplodactylinae. In *Strophurus*, the fourteen species are characterised by ejaculatory tail glands. The tail may be curled over the animal's back and aimed at a

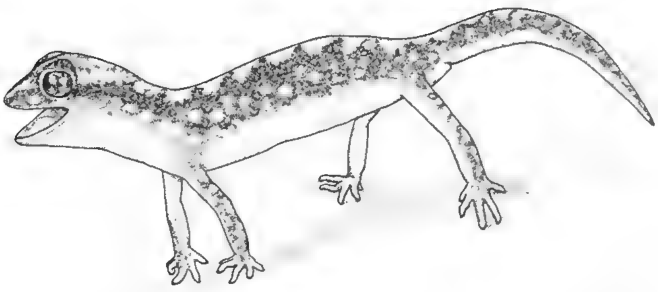

Figure 27.7 Defensive posture of *Diplodactylus damaemi.* (After photo by O. Rogge/ANT) [M. Cilento]

potential predator. A stream of sticky, viscous and irritating liquid is then fired at the target from one of the tail glands.

One of the more bizarre aspects of display adopted by members of *Strophurus,* involves flash colouration and is associated with typical defensive posture. *Strophurus spinigerus, S. intemedius, S. rankini, S. williamsi, S. strophurus* and certain populations of *S. ciliaris* have a bright blue mouth lining. This is revealed as part of their defensive posture, which involves stiffening the legs and arching the back. *Strophurus spinigerus* bulges its bright yellow eyeballs at the same time.

Diplodactyline and gekkonine geckos are able to drop their tails as a defensive strategy. This is used as a last resort, as it involves the loss of perhaps a third of the body weight, including valuable stored fat. Its loss may render females incapable of breeding in the following egg-laying season. While gekkonines are apparently able to economise in the degree of tail loss, since they have more numerous sheer points, diplodactylines tend to lose the whole tail. Generally, tail autotomy follows physical grasping of the tail by a predator. However, there is evidence to suggest that autotomy can occur as a result of shock alone (Greer 1989).

When geckos adopt their defensive posture, they often lash the tail from side to side. *Nephrurus* species temptingly sway the ball on the tail tip. Both behaviours may attract a potential attacker to the tail as a prelude to tail autotomy. However, in *Hemidactylus* and *Gehyra,* such tail lashing appears to be associated with aggression and territorial fighting.

Most Australian geckos are nocturnal, and avoid the extreme heat of the day by living either in spider holes or similar burrows. Some shelter under rock exfoliations, or under the bark of trees. Nevertheless, many of the arid-adapted gekkonine species are unable to avoid extreme temperatures in their particular habitat. *Gehyra variegata* remain active even when night-time temperatures reach 45°C (Henle 1990b). The critical thermal maximum for this species is 43.8°C (Spellerberg 1972a). Cloacal temperature was found to be more closely correlated with substrate temperature than with air temperature. Nevertheless, this does illustrate the very high temperatures these organisms can tolerate.

At Kinchega, New South Wales, *Gehyra variegata* are active at temperatures ranging from 7.5° to 45°C, during September to May (Henle 1990b). During the colder months, *Gehyra variegata* attempt to elevate body temperature by moving under the bark of trees or to the sunny side of fence posts (Bustard 1967). From June until August, *Gehyra variegata* remain inactive and do not feed. They are unable to digest food at the lower temperatures.

In most geckos that have been studied, there is a differential activity pattern during the night. At sunset they became active and start to hunt, but as the ambient temperature drops they reduce their activity and remain inactive until warmed by the morning sun. During the daylight hours they shelter from the heat, but are capable of making forays from their sheltered position to take prey. Certain species of *Strophurus* may actively bask in the sun to achieve their optimal operating temperature (Greer 1989). However, this behaviour is unusual and even atypical for that genus.

When stressed by temperatures approaching their critical thermal maximum, geckos open their mouths and pant. Heatwole, Firth & Stoddart (1975) also observed fluttering of the gular area, presumably increasing air flow and evaporative cooling efficiency. Nevertheless, most terrestrial diplodactylines attempt to avoid thermal stress by sheltering in burrows and only emerge in the cool of the evening.

Areas of gekkonid reproductive behaviour for which some data are available are copulation and communal egg-laying. A male *Hemidactylus frenatus* grasps the neck of the female from the back while holding her chest with his front feet. The pair then twist their bodies around so that one of the hemipenes enters the female laterally. After copulation, the pair repeat the procedure using the other hemipenis. This behaviour has been reported for a number of gekkonid species (Greer 1989). Communal egg-laying is common in species of *Phyllodactylus, Heteronotia, Lepidodactylus, Phyllurus* and *Oedura* (Greer 1989). King (pers. obs.) has observed communal sites containing up to thirty eggs of *Phyllodactylus marmoratus,* often in areas where there was an absence of sheltered sites, and where all females might lay their eggs under one log. In areas where adequate cover was available, communal egg-laying was not generally observed, at least in *P. marmoratus.*

BIOGEOGRAPHY AND PHYLOGENY

Distribution

The Gekkonidae are distributed throughout the mainland of Australia, except for the very south of Victoria, the Bass Strait islands and Tasmania. The seven genera of Gekkoninae within Australia can be subdivided into two groups. One group comprises genera that contain one or more endemic species: *Gehyra, Phyllodactylus, Heteronotia, Nactus* and *Cyrtodactylus.* The second contains the recently introduced Asian genera *Lepidodactylus* and *Hemidactylus.* Of the former group, *Gehyra* and *Heteronotia* are distributed throughout mainland Australia. *Cyrtodactylus* and *Nactus* occur as relic populations on Cape York Peninsula, presumably reflecting a Papua/New Guinean connection, whereas *Phyllodactylus* occurs in the far south of eastern and western Australia and on the Norfolk and Lord Howe island complexes. Both *Gehyra* and *Phyllodactylus* are well represented in other countries. *Gehyra* species occur in Madagascar, India, South-East Asia and the islands of the Pacific basin. *Phyllodactylus* is thought to be polyphyletic and occurs in Africa, South and North America and southern Europe. The Australian representatives of this genus have uncertain affinities. The genus *Cyrtodactylus* is one of the most successful and widespread gekkonines, and is found throughout south-eastern Europe, southern Asia and the Indo-Malayan Archipelago. *Heteronotia* is endemic to Australia and is morphologically very similar to *Cyrtodactylus* and *Nactus.*

The majority of gekkonine species are concentrated in the arid interior of the continent and in northern Australia. Generally, species within a genus are distributed allopatrically and occupy particular geographic regions defined by belts of mountain ranges, river systems, soil types or deserts. In some instances, species are distributed parapatrically and sympatry can occur between species which usually occupy different niches.

The Diplodactylini (*Diplodactylus, Rhynchoedura Strophurus* and *Crenadactylus*) are Australian endemics. Some genera in the Carphodactylini are found only in Australia (*Carphodactylus, Oedura, Nephrurus* and *Phyllurus*), some which are shared between Australia and other countries (*Rhacodactylus,* including *Pseudothecadactylus,* in Australia and in New Caledonia), and some which are found only in New Caledonia and the Loyalty Islands (*Eurydactylodes, Bavayia*) and New Zealand (*Naultinus, Hoplodactylus* and *Heteropholis*).

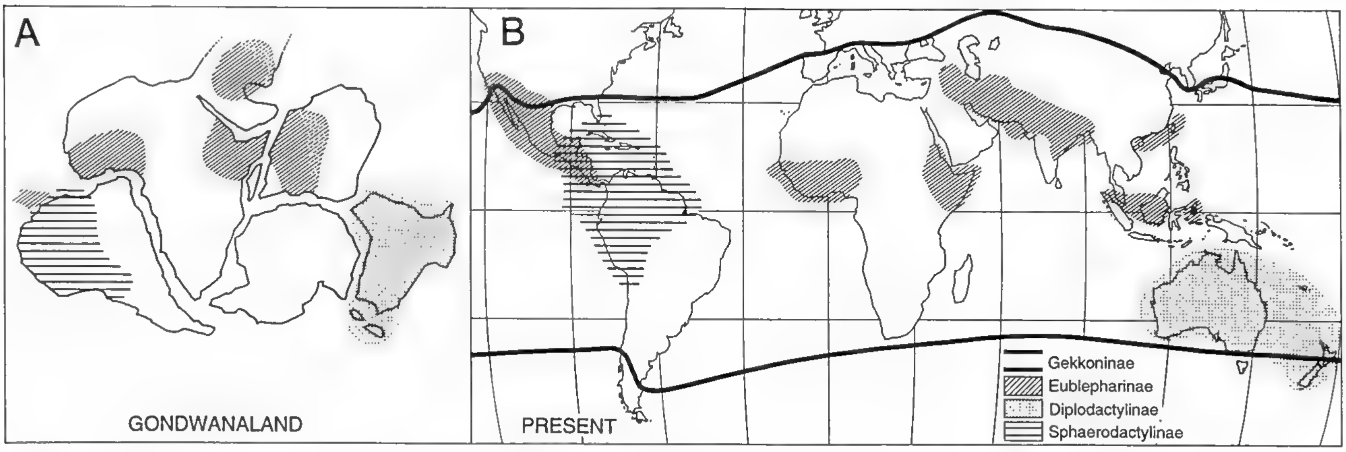

Figure 27.8 Distribution of the Gekkonidae. A, the presumptive Gondwanan distributions; B, present distributions. [W. Mumford]

Within the Diplodactylini, species of *Diplodactylus* are generally distributed allopatrically in relation to their closest relatives, and if not, are sympatric but isolated in specific habitat types, or specialised niches. The monotypic genus *Crenadactylus* is found in the western half of the continent, and *Rhynchoedura* occurs in the arid areas of Australia.

Species within the Carphodactylini are divided into two morphological groups. One group includes the tropical rainforest specialist, *Carphodactylus* and the northern rock-dwelling genus *Rhacodactylus* (*Pseudothecadactylus*), which occur across the tropical north of Australia. The arboreal, or rock-dwelling, members of *Oedura* also belong to this group and are generally found throughout the northern two thirds of Australia, although southern species are known. The second group comprises members of *Phyllurus* and *Nephrurus*. The leaf-tailed *Phyllurus* are found in a narrow belt along the eastern coast of Australia, where they live in the lush forests and associated ranges, on rock outcrops or on trees. *Nephrurus* (including *Underwoodisaurus*), encompasses a variety of burrowing terrestrial species which inhabit most of arid Australia and generally occur on the western side of the Great Dividing Range.

Affinities with Other Groups

The Gekkonidae is closely related to the Pygopodidae and there is considerable support for a sister group relationship between the Pygopodidae and the gekkonid subfamily Diplodactylinae (Chapters 26, 28). Indeed, chromosomal data suggest that the Pygopodidae diverged from the Carphodactylini (King & Mengden 1990).

Affinities within the Taxon

Because of the extensive and complex distributional patterns of the gekkonid subfamilies (Fig. 27.8), the phylogenetic origins and relationships between them have proved contentious. The Sphaerodactylinae occurs in Central America, whereas the Diplodactylinae is found in Australia, New Zealand, New Caledonia and the Loyalty Islands, and thus represent regionally intact distributions. In contrast, the Eublepharinae is found in western North America, pockets occur in eastern and western Africa, the Middle East, India, a Japanese/Chinese isolate and a small area in South-East Asia. The Gekkoninae occurs circumglobally. However, this tends to be misleading, since much of this distribution is occupied by a few, highly successful genera and many of the more primitive genera are restricted to Africa. Such a distribution, with independent lineages occurring in different zoogeographic regions, could support the polyphyletic nature of this taxon.

Numerous complex arguments have been used to explain the subfamilial distribution pattern, including rafting and substantial migrations and extinctions. However, the most reasonable explanation for the present day distribution is a Gondwanan origin (Cracraft 1974; King 1987c) (for an alternate view, see Greer 1989). All of the higher taxa are present on the components of the ancient supercontinent including the primitive Gekkoninae, the Diplodactylinae (in a unified land mass), the Eublepharinae (in a series of isolates), and most of the Sphaerodactylinae (Fig. 27.8). The non-Gondwanan components, such as the North American Eublepharinae and Sphaerodactylinae, can be accounted for by colonising radiations after contact between North and South America. This may equally apply to the Middle Eastern and Asian Sphaerodactylinae, which were probably established from colonising radiations of species subsequent to the contact of the Indian plate with the Asian land mass. This same argument could account for the distribution of the Gekkoninae in Europe and Asia after the contact of Africa with that region. Much of the world has been colonised by Kluge's (1967a) 'modern expanding dominants' such as the gekkonine genera *Gehyra*, *Hemidactylus*, *Cyrtodactylus* and *Lepidodactylus*. It is probable that the ranges of these species were expanded over much of their distribution by association with man's activities, rafting, or simply migration (Vanzolini 1968).

Storr's (1964a) view that *Gehyra* radiated throughout Australia from an Asian introduction, may be tempered by the highly complex distribution pattern of *Gehyra* within Australia, South-East Asia, the Pacific basin, India and Madagascar. Indeed, the greatest morphological and species diversity in this genus occurs within Australia and relatively few species of *Gehyra* are found in the other regions (King 1979, 1983a, 1984c; King & Horner 1989; Moritz 1986). The distributional evidence suggests that the ancestral *Gehyra* had a broad Australian distribution, before they were reduced to a series of relictual populations. Subsequent internal radiations of *Gehyra* recolonised the continent.

Similar arguments can be applied to *Cyrtodactylus*, *Heteronotia*, and *Phyllodactylus*. Thus, although *Phyllodactylus* is probably an artificial assemblage, it is worth considering that its distribution includes southern Africa, south-western North America, Central America and Norfolk Island. This distribution accords with a Gondwanan origin. Morphological similarity between Australian and Asian species of *Cyrtodactylus* and *Heteronotia* suggests a direct biogeographical relationship. The widespread Australian distribution of the complex clones of *Heteronotia*, and the considerable time required to establish these, suggests that this genus, too, may be a Gondwanan relict.

Chromosomal comparisons of the Gekkoninae (King 1987a) indicate that eight distinct chromosomal lineages are present in the 74 karyotyped species. Ancestral numbers in each group are 2n = 32, 34, 36, 38, 40, 42, 44 and 46 respectively. These data suggest that the Gekkoninae is a polyphyletic assemblage and group comparisons reveal some agreement with the morphogroups, based on toe structure, proposed by Russell

(1976). The species found within Australia have evolved from four independent ancestral karyomorph groups (King 1987a): *Hemidactylus* 2n = 46, *Gehyra* and *Lepidodactylus* 2n = 44, *Cyrtodactylus*, *Nactus* and *Heteronotia* 2n = 42 and *Phyllodactylus* 2n = 40, indicating a series of distinct evolutionary lineages within Australia. The division of the Gekkoninae into the tribes Gekkonini and Pytyodactylini on the basis of the presence or absence of a second ceratobranchial arch by Kluge (1987), cuts across the eight chromosomal groups of King (1987a) and the seven morphogroups which were defined on toe structure by Russell (1976, 1979), and adds weight to the inference that the Gekkoninae is polyphyletic.

The absence of Australian fossil material has precluded the confirmation of pre-Miocene Gekkoninae in this continent, although specimens dating back to the Cretaceous have been found in other regions (Estes 1970).

A Gondwanan origin for the Diplodactylinae has been confirmed by two types of evidence. First, a chromosomal analysis of the Diplodactylinae indicates that a highly derived karyomorph which has 19 fixed inversion differences is shared by members of the Carphodactylini in Australia (*Rhacodactylus*, including *Pseudothecadactylus*, and *Oedura*), in New Caledonia (*Rhacodactylus* and *Bavayia*), and New Zealand (*Hoplodactylus*). King (1987a, 1987c) argued that the most logical means by which the derived karyomorph could have established such an unusual distribution was when Australia, New Zealand and New Caledonia were in contact through Antarctica in the Gondwanan supercontinent 80 million years ago. Albumin immunological distances between species of *Phyllurus*, *Nephrurus*, *Oedura*, *Crenadactylus* and *Diplodactylus* also support a Gondwanan origin. The length of separation between the last three genera was estimated to be at least 66 million years (King 1987c), which predates the separation of Australia from Antarctica, and may be greater, but is beyond the resolution of the technique. The Diplodactylinae was thus established in Australia when it was part of the Gondwanan supercontinent (King 1987c).

Current understanding of the lower taxonomic categories of Australian Gekkonidae has been modified by analyses of population cytogenetics. A number of widely distributed and morphologically variable species have been recognised as species-complexes within the Gekkoninae and Diplodactylinae, although the impact has been far greater within the former.

Seven distinct chromosome races have been detected in the gekkonine species complex of *Gehyra australis* of northern and eastern Australia (Fig. 27.9; King 1983a, 1984c), four of which have been described as new species. A similar situation applies to the *Gehyra variegata-punctata* species-complex which is distributed throughout Australia. Twelve chromosome races have been detected (Fig. 27.9A; King 1979, 1984c; Moritz 1986). Many of these have been described as new species and some remain undescribed. These studies indicate that the earlier proposal by Storr (1964a) that *Gehyra* radiated through Australia after a relatively recent introduction from Asia is no longer appropriate, and that a Gondwanan origin is more likely.

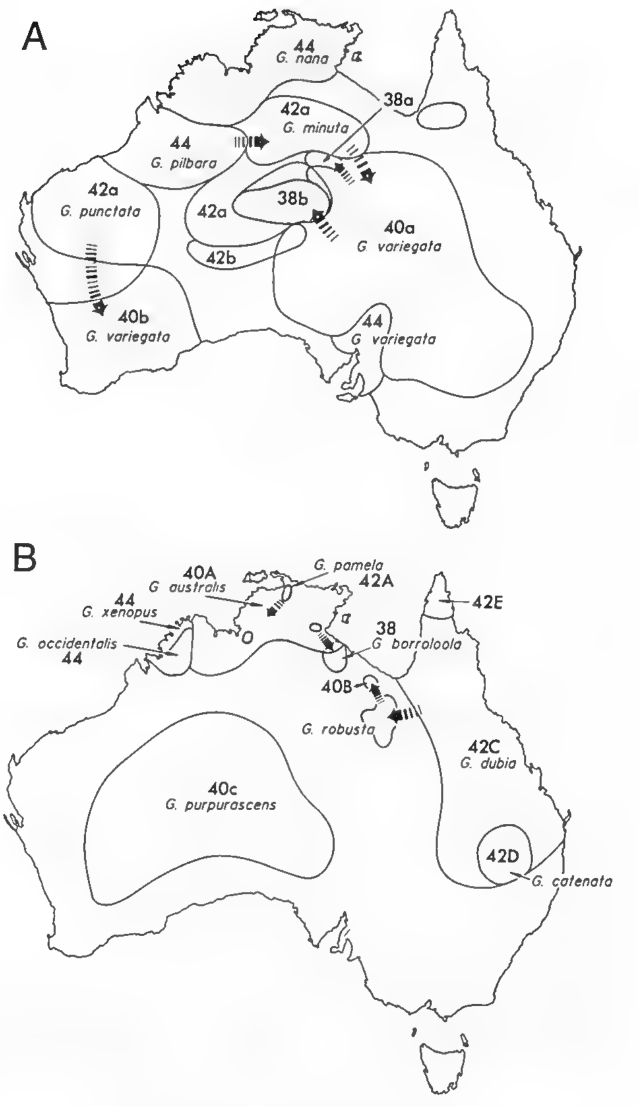

Figure 27.9 Distribution of chromosome races in *Gehyra*. A, the *Gehyra variegata-punctata* species complex: arrows indicate the probable direction of colonising radiations during speciation, and shading indicates the three regional distributions of *G. nana*; **B**, *Gehyra purpurascens*, and species and chromosome races of the *Gehyra australis* species complex. The three small shaded areas in the north refer to isolated populations of the 2n = 42A chromosome race. [W. Mumford]

Gehyra species with the ancestral 2n = 44 karyomorph have a disjunct distribution. Isolated relictual populations of *G. nana* are found in central, north-western and north-eastern Australia (Fig. 27.9A). Although separated by thousands of kilometres, these are morphologically, chromosomally and electrophoretically indistinguishable (King 1984c; Moritz 1986). To have such a widespread distribution, the species must at one time have been distributed continuously. In addition, a form of *G. variegata* with 2n = 44 occurs as an isolate in the Flinders ranges of South Australia. A number of species which share the ancestral karyomorph are found in the north-west of Western Australia (Fig. 27.9A, B). King (1984c) argued that this high density of species with 2n = 44 in the north, together with their relictual populations in central and southern Australia, reflect a once continuous 2n = 44 Australian distribution, which was broken up into a series of isolates (Fig. 27.9A). Species with lower chromosome numbers (2n = 42) appear to have colonised areas to the south of the northern 2n = 44 stronghold, whereas more recent radiations of 2n = 40 and 2n = 38 forms colonised areas further to the south, or had occupied particular mountain ranges in central Australia, thus recolonising most of the continent. A shift in habitat occurred away from the purely rock-dwelling 2n = 44 species, to arboreal forms and habitat generalists. In some instances, recently derived races have reverted back to specialist rock dwellers. No biochemical, molecular, or fossil data are available to provide an full perspective on the evolution of Australian *Gehyra*.

Phyllodactylus marmoratus is also a complex of chromosome races (King & Rofe 1976; King & King 1977). These include 2n = 36 ZZ/ZW, 2n = 36, 2n = 34 and 2n = 32 races which appear to have radiated into Western Australia from the east. Sequential chromosome fusions were established during the colonisation of Western Australia. The two Australian representatives of *Cyrtodactylus* are restricted in their distribution to Christmas Island and the northern area of Cape York Peninsula. Since two of the species are also found in New Guinea, these forms appear to be relics of population movements between New Guinea and Australia, which occurred when there was a land-bridge connection.

Species of *Heteronotia* are most similar in their morphology to *Cyrtodactylus* and *Nactus*, but are only found within Australia. Chromosomal, mitochondrial DNA and electrophoretic investigations of the *Heteronotia binoei* complex have revealed the presence of bisexual diploid chromosome races as well as triploid parthenogenetic forms (Moritz 1983; Moritz, Donnellan, Adams & Baverstock 1989a; Moritz, Brown, Densmore, Wright, Vyas, Donnellan *et al.* 1989b). Three $2n = 42$ diploid chromosome races were recognised in bisexual populations and were regarded as biological species. These could be further subdivided into eight karyomorph groups by comparing their chromosome banding patterns. The parthenogenetic triploid species ($2n = 63$) had 17 separate karyotypes, most of which were in three geographically widespread chromosomal forms. These were postulated to be the products of hybridisations between bisexuals. Two of the three parthenogens have very large central and western Australian distributions and appear to have actively colonised the area. The complexity of the situation is highlighted by the fact that 52 different genotypes are recognised within the triploid parthenogens (Moritz *et al.* 1989a).

The situation within the monophyletic Diplodactylinae contrasts with that in the gekkonine genera. Within the tribe Diplodactylini, Russell & Rosenberg (1981) separated a cluster of species groups in *Diplodactylus* (the *strophurus, michaelseni and elderi* groups) into the subgenus *Strophurus* on the basis of shared caudal-gland systems and the absence of certain osteological characters. This subgenus was elevated to generic status by Greer (1989). King (1987a) showed that the spiny-tailed members of *Strophurus* (*strophurus, ciliaris, intermedius, williamsi, taenicauda* and *spinigerus*) form a distinct cluster of chromosomally derived forms, distinguished by five pericentric inversions from the ancestral diplodactyline karyomorph. However, *S. elderi* is chromosomally divergent from this complex. The chromosomes of the *S. michaelseni* group are unknown. The members of *Strophurus* are generally arboreal species which are distributed allopatrically over the arid and tropical areas of Australia. Species of the *S. elderi* and *S. michaelseni* complexes are specialised for living in spinifex clumps (*Triodia* sp.).

The genus *Diplodactylus* includes a widely distributed group of purely terrestrial species which are found throughout Australia in a range of habitat types. They shelter either under rocks or in burrows. Their distributions are regionally restricted and are associated with deserts, or belts of particular soil or vegetation types. They are chromosomally similar and share an ancestral acrocentric $2n = 38$ karyotype, although some minor differences have been detected between species (King 1987a). An exception is the *Diplodactylus vittatus* complex which, like *Gehyra* and *Phyllodactylus*, was thought to be a widely distributed, morphologically variable species until King (1977a, 1987a) and Storr (1979b) identified a species complex, comprised of five allopatric chromosome races, some of which were subsequently described as species. *Rhynchoedura ornata* and *Crenadactylus occellatus* are widely distributed, arid-adapted species. It is probable that *C. ocellatus* is a species complex, since it appears to occupy different habitat types in various parts of its range.

Generic subdivisions and radiations of the Carphodactylini appear to have occurred over a considerable time span. Bauer (1990) proposed that the subdivision of the Carphodactylini into *Carphodactylus*, *Nephrurus*, and *Phyllurus* was associated with the orogenic activities which produced the Great Dividing Range some 53 million years ago, isolating the different ancestral forms in eastern and western Australia. Thus Eocene desertification was associated with speciation in the arid-adapted, knob-tailed *Nephrurus*; the knob-less *N. milii* and *N. sphyrurus* evolved independently, with the former attaining its extensive western distribution in the Miocene. Bauer (1990) reasoned that *Nephrurus* was isolated into northern and southern lineages by the central Australian continental lake system, which restricted *N. asper* and *N. wheeleri* to central, northern and north-western Australia. The smooth-skinned southern lineage of *Nephrurus* subsequently invaded the entire arid region of Australia.

Division of the *Phyllurus* and *Carphodactylus* lineages has been attributed to Pleistocene vegetational changes and the remnants of the continental lake system (Bauer 1990). The subdivision of *Phyllurus* species into a series of linear isolates is also attributed to post-Pleistocene changes in sea level and rain forest fragmentation.

The northern Australian *Rhacodactylus* (*Pseudothecadactylus*) provide some areas of contention. Bauer (1990) argued that these forms could not have been found in Australia before the opening of the Tasman sea (at least 80 million years ago), because they appear to be amongst the most recently derived forms in his cladistic analysis. He invoked the colonisation of northern Australia by late Tertiary rafting from New Caledonia to explain their presence in Australia. Bauer supposed that the subdivision of the Carphodactylini into padless and padded groups was associated with enforced isolation associated with the Tasman Sea. This is unnecessary if the padded Carphodactylini had radiated throughout Australia, New Zealand and New Caledonia when they were still a part of the Gondwanan supercontinent (Fig. 27.8). Moreover, the paucity of padded Carphodactylini within Australia can be explained by the fact that *Oedura* are in reality carphodactylines. Such an action reconciles the shared derived chromosomal similarity between *Oedura* species and *Rhacodactylus*, *Bavayia* and *Hoplodactylus* (King 1987a). It explains also the great similarity in osteology, musculature and form of the toepads in *Rhacodactyus*, *Oedura*, and *Bavayia* (Russell 1979). Kluge (1967a) separated the Carphodactylini from Diplodactylini by the presence of numerous rows of pre-anal pores in certain Carphodactylini. These have been extensively modified in *Nephrurus*, *Phyllurus* and *Bavayia sauvagei* (Bauer 1990), and cannot be construed as a reliable character. Indeed, they may have been lost secondarily in *Oedura*.

The genus *Oedura* comprises thirteen species and is distributed throughout Australia in discrete allopatric units. This genus has been placed in the Carphodactylini because of its great morphological and chromosomal similarity to the highly derived *Rhacodactylus* (*Pseudothecodactylus*). Species are either saxicoline or arboreal, and *O. filicipoda* is thought to be cavernicoline. If sympatric, *Oedura* species are generally separated by habitat specialisation. Kluge (1967b) suggested that *Oedura* was derived from a *Diplodactylus*-like terrestrial ancestor because of the similarity of digit structure. However, Russell (1979) argued that there is little justification for this claim, since the lamellae on the proximal portions of the digits are controlled by different mechanisms from those in *Diplodactylus*, suggesting an arboreal ancestor.

28. FAMILY PYGOPODIDAE

Glenn M. Shea

DEFINITION AND GENERAL DESCRIPTION

The Pygopodidae is a small family of 35 species, placed by most recent authors in eight genera. The family is endemic to Australia and New Guinea. All species are elongate, snake-like lizards (Fig. 28.1, Pls 4.9–4.12), with imbricate, or overlapping, body scales, hind limbs reduced to short scaly flaps without obvious toes (Fig. 28.2), and a tail which varies from slightly shorter to much longer than the body and is capable of being autotomised. There are no external traces of front limbs. The eyes have vertical pupils and are covered by a transparent spectacle.

The premaxilla is single in adults and lacks a median ventral process. The postorbital arch, temporal arch and parietal foramen are absent, and there are no palatine teeth. Osteoderms are also lacking. The vertebrae are procoelous, with a median constriction and prominent subcentral foramina. Post-cloacal bones are present.

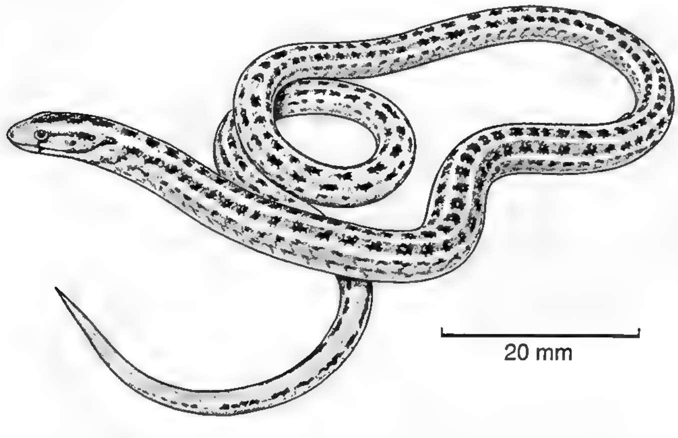

Figure 28.1 *Pygopus lepidopodus*, the most generally primitive pygopodid. [B. Jantulik]

HISTORY OF DISCOVERY

The first pygopodid to be described was *Pygopus lepidopodus*, which Lacépède (1804) named *Bipes lepidopodus* from six specimens collected by the Baudin Expedition of 1800–1804. No precise locality data are given in the description, and only one of the types can now be identified in the Muséum d'Histoire Naturelle, Paris.

The first of three genera and species described by John Gray was *Delma fraseri*, in 1831, probably from a single specimen lacking precise locality data collected by James Hunter. The name was subsequently applied to a species found only in southern Western Australia and South Australia (Kluge 1974). In 1835, Gray described *Lialis burtonis* (Pl. 4.10) from a single specimen collected by Dr Mair from New South Wales (as Nova Cambria Australi). The holotype can no longer be identified in the collection of the Natural History Museum (formerly British Museum of Natural History). In 1839, Gray described *Aprasia pulchella*, again from a single specimen, later stated to be from Western Australia (Gray 1845).

Between 1842 and 1884, a total of 16 new species and subspecies of pygopodids were described, almost all by European workers. Included amongst these was a fifth genus, *Pletholax*, from a single specimen from south-west Australia, collected by J.A.L. Preiss, and now in the National Museum of Natural History, Leiden.

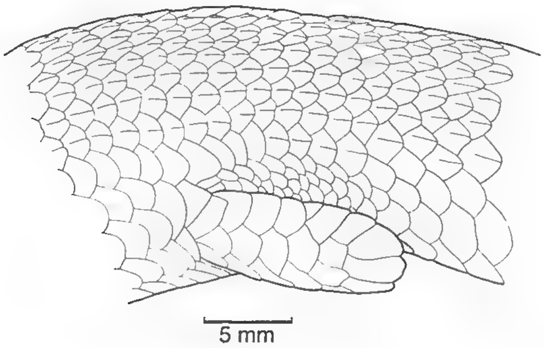

Figure 28.2 Hindlimb flap of *Pygopus lepidopodus*. [B. Jantulik]

Working on the extensive British Museum material, Boulenger (1884, 1885) placed all of the genera into a single family Pygopodidae. However, he was unable to make sense of the wide variation in colouration within the genera, particularly in *Lialis*, and placed most of the described species into synonymy, leaving six genera and eight species.

Between 1885 and 1914, an additional 12 species and subspecies of pygopodids were described, including *Ophidiocephalus taeniatus*, another monotypic genus. This species was known only from the holotype until its rediscovery by Ehmann & Metcalfe (1978).

In a checklist, Werner (1912) recognised eight genera and 16 species. Kinghorn (1923b, 1924, 1926) revised the family, recognised eight genera and 14 species, and erected the genus *Paradelma* for *Delma orientalis* Günther, 1876.

With the exception of a revision of *Aprasia* by Parker (1956) and a checklist by Wermuth (1965), pygopodid systematics remained almost untouched until Kluge (1974, 1976a) revised the family in two monographs and provided a cladistic analysis of intrafamilial relationships. In the first monograph, he recognised eight genera and thirty species, describing one genus (*Aclys*) and twelve species as new.

Since Kluge's revision, two new species of *Aprasia*, one new subspecies each of *Aclys* and *Pletholax*, and four new species and one subspecies of *Delma* have been described, although one of the *Delma* species has since been synonymised (Storr 1978a, 1979a, 1988; Shea 1987, 1991).

It is important to recognise that with the recent subdivision of *Delma* (1 species: Boulenger 1887; 3 species: Kinghorn 1926; 16 species: Kluge 1974 and subsequent authors), much of the pre-1974 literature on *Delma fraseri* is based on material which was probably misidentified and can now only be identified to genus.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Adult pygopodids range from 63 mm (*Delma torquata*) to 314 mm (*Lialis jicari*) snout-to-vent length, although *Aprasia* species are the

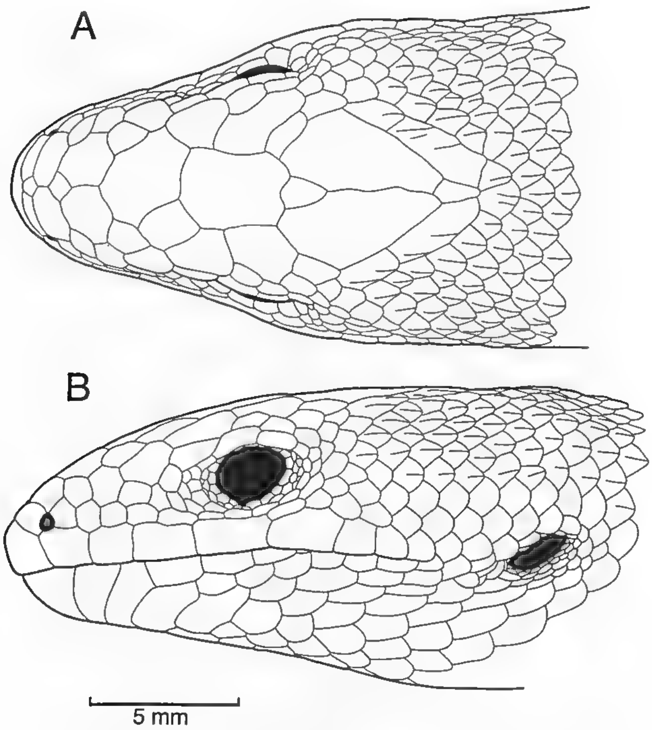

Figure 28.3 Head shields of *Pygopus lepidopodus*. **A**, dorsal view; **B**, lateral view. [B. Jantulik]

shortest in overall length, because their short tails are less than 92% of snout-vent length (Pl. 4.11). In other pygopodids, the tail is long, and may be up to 414% of snout-vent length in *Delma grayii*.

The head may be long and narrow, with snout pointed (*Aclys*, *Lialis*) to short and blunt (most *Aprasia*). Most species have a regular pattern of enlarged head shields (Fig. 28.3), although *Lialis* has small fragmented head shields.

Colour pattern, where present, typically involves stripes or longitudinal rows of spots on the body, which may continue onto the tail, or in a few species of *Delma* and *Pygopus*, be replaced by oblique bars converging distally on the tail dorsum. Several *Aprasia* species have a bright pink tail. Several *Delma* species and *Pygopus nigriceps* have a dark head which may or may not be interrupted by narrow pale bands. In these species, the side of the neck may also bear alternating light and dark bars. The undersurface in most species is white, grey or yellow. *Delma butleri* can change the intensity of the ventral colouration rapidly (Shea 1987b). *Lialis* is particularly variable in colouration, and several different colour patterns are often present at a single locality.

The dark heads of many *Delma* and *Pygopus* species tend to fade with age, while the prominent lateral markings of *Delma impar* develop with age (Greer 1989; Coulson 1990; Storr, Smith & Johnstone 1990; Shea 1991).

Body Wall

The body bears overlapping scales in a regular pattern of longitudinal rows. The pair of scale rows along the belly are much wider than other adjacent body scales in many species. Scales may be keeled (*Pygopus*, *Pletholax*) or smooth. The outer keratin layers of the epidermis are sloughed regularly.

The skin is tightly bound to the superficial musculature by connective tissue, with little subcutaneous fat present.

Aspects of the epaxial, ventral abdominal and pectoral and pelvic girdle musculature are described by Fürbringer (1870), Kluge (1976b) and Gasc (1981).

Skeletal System

The skull is similar to that of geckos. Bony elements present in the most generally primitive genus (*Pygopus*) (Fig. 28.4) are: premaxilla, nasal, frontal, parietal, maxilla, prefrontal, postfrontal, squamosal, jugal, quadrate, vomer, septomaxilla, palatine, pterygoid, ectopterygoid, epipterygoid, supraoccipital, prootic, otoccipital, basioccipital, basisphenoid, stapes, dentary, splenial, coronoid, surangular, prearticular and articular. The frontals are fused into a single element, as are the premaxillae in adults. In the mandible, the articular, prearticular and surangular are fused into a single element (possibly also incorporating the absent angular), although the prearticular and surangular remain distinct anteriorly. In the adult neurocranium, the supraoccipital, prootic, otoccipital, basioccipital and basisphenoid are fused.

Both the postorbital and upper temporal arches are incomplete (Fig. 28.4). The forebrain is partially enclosed by ventral flanges of the frontal and parietals. The palate is formed mainly by the

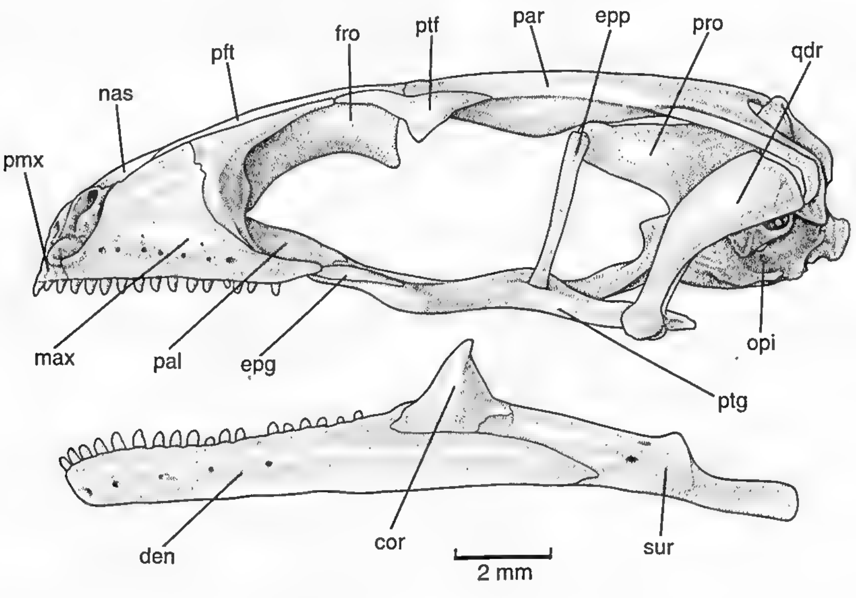

Figure 28.4 Skull of *Pygopus lepidopodus* in lateral view. **cor**, coronoid; **den**, dentary; **epg**, ectopterygoid; **epp**, epipterygoid; **fro**, frontal; **max**, maxilla; **nas**, nasal; **opi**, opisthotic; **pal**, palatine; **par**, parietal; **pft**, prefrontal; **pmx**, premaxilla; **pro**, prootic; **ptf**, postfrontal; **ptg**, pterygoid; **qdr**, quadrate; **sur**, surangular. [B. Jantulik]

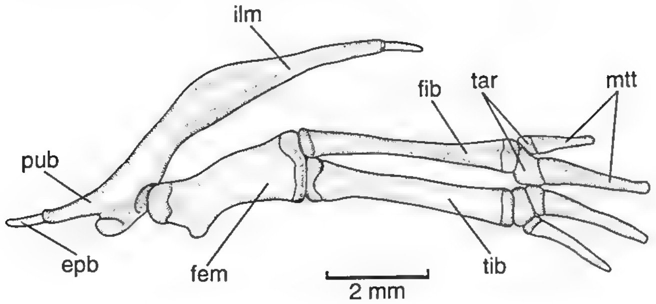

Figure 28.5 Pelvic girdle and hindlimb skeleton of *Pygopus lepidopodus*. **epb**, epipubis; **fem**, femur; **fib**, fibula; **ilm**, ilium; **mtt**, metatarsals; **pub**, pubis; **tar**, tarsals; **tib**, tibia. [B. Jantulik]

vomers. The palatines are narrow, widely separated, and form the caudal margin of the choanae (McDowell & Bogert 1954; Underwood 1957; Stephenson 1962; Rieppel 1984a; Kluge 1987).

In miniature burrowing genera (*Aprasia*, *Pletholax*), the postorbital regions of the skull are much elongated and the post-temporal fenestrae are either reduced or absent. The dentary of *Aprasia* is also very short (Stephenson 1962; Rieppel 1984a).

The skull of *Lialis* is elongate, particularly in the very narrow preocular region. The highly mobile fronto-parietal (mesokinetic) joint allows the snout to flex up to 40° from the horizontal. The parietals are fused, and the jugal is absent (Stephenson 1962; Patchell & Shine 1986a).

In all pygopodids, only the first ceratobranchial of the hyoid is osseous (Stephenson 1962).

The number of presacral vertebrae ranges from 44 to 110, and there are from 45 to 130 postsacral vertebrae (Greer 1989). The elements of the neural arch of the atlas are unfused in *Pygopus*, *Delma* and *Lialis*, but fused in *Aprasia* (Stokely 1947; Underwood 1957). The third vertebra in *Pygopus*, *Delma*, *Lialis*, or the fourth in *Aprasia*, bears the first ribs, and the number of cervical vertebrae is reduced to seven or fewer (Underwood 1957; Greer 1989). Postsacral vertebrae bear fracture planes immediately distal to the short transverse processes (Etheridge 1967). The ribs are unusual in possessing an antero-ventral process, but not a postero-dorsal process (Hoffstetter & Gasc 1969).

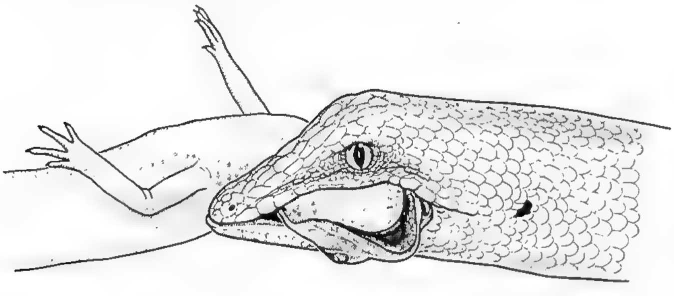

Figure 28.6 *Lialis burtonis* feeding on a skink. Note the flexion of the snout relative to the rest of the head. [B. Jantulik]

A pectoral girdle is present in all species, though there are no external vestiges of front limbs. The pectoral girdle of *Pygopus*, *Paradelma*, *Delma* and *Lialis* is represented by a sternum and paired clavicles, scapulocoracoids, epicoracoid cartilages and suprascapular cartilages. A humeral remnant is also present, though not in articulation with the scapula. A large interclavicle is present in *Pletholax* (Stephenson 1962). The pectoral girdle of *Aprasia* is modified and extremely reduced to a narrow, transverse rod composed of sternum, clavicles, scapulocoracoids and suprascapular cartilages (Stokely 1947; Stephenson 1962; Greer 1989).

The pelvic girdle consists of fused ilium, ischium and pubis (not fused in some *Aprasia*), and the ischium is often directed anteriorly rather than posteriorly. Ventrally, the two halves of the pelvis are widely separated. In *Pygopus*, *Delma* and *Lialis*, the pelvis is connected to the sacral vertebrae, but this connection has been lost in *Aprasia*. In the most complete state (*Pygopus*), the hindlimb consists of femur, tibia, fibula, tarsal elements and four digital elements (Fig. 28.5), while in the most reduced state (*Aprasia pulchella*), there is only a femoral remnant (Underwood 1957; Stephenson 1962; Greer 1989).

Post-cloacal bones are present in males of all species (Kluge 1974, 1982).

Locomotion

Pygopodids move by lateral undulations of body and tail. Surface-active species of the genera *Pygopus*, *Lialis* and *Delma* move through thick vegetation and litter, while the fossorial *Aprasia* and *Ophidiocephalus* use lateral undulations to burrow through loose soil, and crawl along narrow earth cracks and insect tunnels (Kluge 1974; Ehmann 1981; Greer 1989). Ehmann (1981) reported that *Ophidiocephalus* sometimes uses the head as a lever to pull the body through the substrate.

The hindlimb flaps are normally held tightly alongside the body when moving, although they may be extended when traversing rough terrain or climbing, or when stressed (Annable 1983; Greer 1989).

Feeding and Digestive System

The extensive cranial kinesis of *Lialis* allows it to grip firmly and subdue large prey. The tip of the snout bends down to contact the tip of the mandible in a pincer-like action, encircling the prey (Fig. 28.6; Greer 1989). *Pygopus* and *Delma* have been observed to disable large, potentially dangerous prey by rotating the body rapidly along the long axis (Kästle 1969; Philipp 1980).

Dentition is pleurodont, with the teeth of most taxa blunt and rounded, and firmly attached to bone. The teeth of *Lialis* species are narrow, recurved and hinged to bone, allowing them to fold posteriorly towards the jaws (Patchell & Shine 1986c). Apparently this is adaptive for feeding on skinks; it occurs convergently in several snake genera (Patchell & Shine 1986c). Teeth are present on the premaxilla, maxilla and dentary (except in *Aprasia*, where the maxilla is edentulous, as is the premaxilla in most juveniles and adult females; Parker 1956).

The gastrointestinal tract is simple, with few notable features. The oesophagus is straight and broad. The stomach lies dorso-sinistral to the liver, the cardia is at about mid snout-vent length, and the pylorus lies more posteriorly at about two-thirds of the snout-vent length, level with the gall bladder. The small intestine is divisible into an initial descending duodenum on the left, separated by a caudal flexure from an ascending duodenum. The latter is separated by a duodenojejunal flexure from a moderately convoluted jejunum on the right. The duodenal loop is short in *Pygopus* and long in *Lialis*. The small intestine opens eccentrically dextrally into the straight large intestine, the ileocolic ostium lying at about 80% of the body length in *Pygopus*.

The elongate liver is divided posteriorly into two lobes. The left lobe is the larger, and distally turns medially so that the interlobar fissure opens transversely and dextrally. This extension of the left lobe is least developed in *Lialis*. A gall bladder is present, lying between the lobes (Underwood 1957).

Circulatory System

The heart lies anteriorly within the body cavity, at about one quarter of the snout-vent length from the head. In *Lialis*, it is slightly elongate, and greatly so in *Aprasia* (Underwood 1957). Some aspects of the arteriovenous system have been described by Beddard (1904) and Underwood (1957). A ductus caroticus joins the carotid and systemic arches. In *Aprasia*, the common carotid bifurcates near the head, while in *Delma* and *Lialis*, the bifurcation is more posterior, near the carotid arch. Two (*Lialis*) or several (*Pygopus*) gastric arteries provide the gastric blood supply

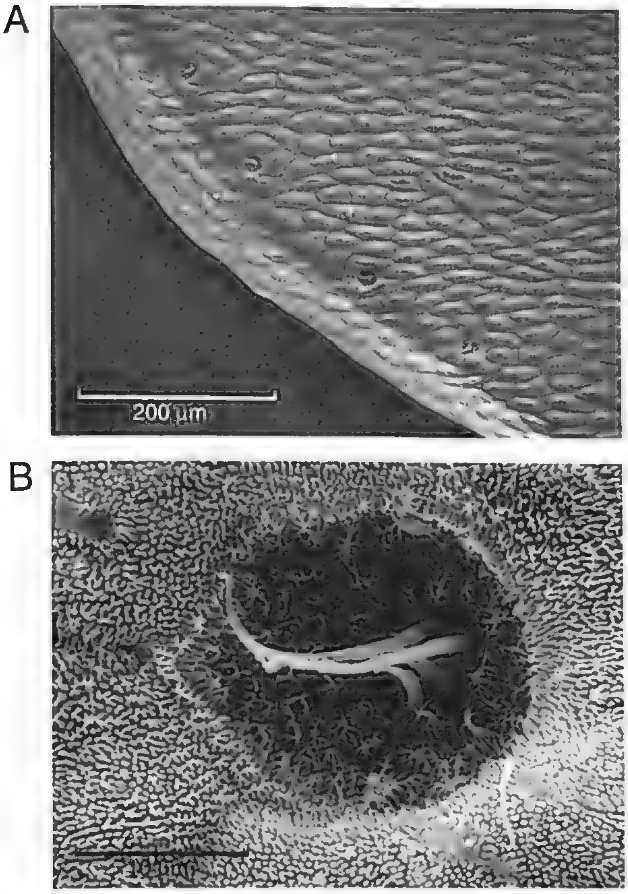

Figure 28.7 Scanning electron micrograph of cutaneous sensilla of a dorsal body scale of *Pygopus lepidopodus*. **A**, apical lateral quadrant of scale with several sensilla; **B**, detail of a single sensillum. [Photos by G. Avern]

from the coeliac trunk, although they may arise independently from the aorta. More distal visceral branches of the aorta may arise from intercostal arteries.

The spleen is small and rounded, and is associated with the posterior end of the liver and the pancreas (Underwood 1957).

Respiration

The paired lungs are asymmetrical, the left lung being much shorter than the right. The ratio of lengths range from 34 to 68% in the larger, less attenuate species, to 9 to 15% in *Aprasia* (Butler 1895; Underwood 1957; Greer 1989). Respiration involves active expiration by constriction of the thoracic region, followed by passive inspiration (Greer 1989).

Excretion

The paired kidneys lie posteriorly in the body cavity, reaching to the level of the vent (*Lialis*) or extending slightly beyond the cloaca (*Delma*, *Pygopus*). In *Lialis*, the right kidney is slightly longer than the left (Underwood 1957). The ureters are short and open via a pair of urinary papillae into the urodaeum. A bladder may be absent (*Delma*) or weakly developed (*Lialis*) (Gabe & Saint Girons 1965).

Sense Organs

The eye is well developed, even in burrowing forms, and is similar to that of geckos. It is covered by a spectacle. The pupil is vertical, and the outer segments of the visual cells are enlarged. Oil droplets in these cells, and a fovea are lacking (Underwood 1957).

An external auditory meatus is present in all pygopodids except *Aprasia aurita* and *Pletholax gracilis edelensis*. The auditory meatus is narrow and the tympanum deeply sunk. The stapes is short, and lacks a stapedial foramen and an internal process. In some of the earless *Aprasia*, the stapes attaches to the skin rather than to a tympanum; in others it is very reduced (Underwood 1957; Greer 1989). The inner ear is similar in most respects to that of geckos (Shute & Bellairs 1953; Wever 1974).

Cutaneous sensilla are present on head and body scales (Fig. 28.7). They are particularly prominent around the margins of scales, and may bear one or more central bristles (Underwood 1957).

Endocrine and Exocrine Systems

The hypophysis of *Delma* is similar to that of geckos. In *Lialis*, the neural and intermediate lobe complex lies caudal to the distal lobe, on a similar horizontal plane, and the posterior part of the *pars nervosa* is flattened. The median eminence is narrowly connected to the diencephalon. The intermediate lobe is well developed, and its internal layer tends to form cellular cords (Saint Girons 1970a).

The thyroid is variable in shape. In *Delma*, it is a bilobed body associated with the fork of the brachiocephalic trunk, and embraces the trachea ventrally. In *Lialis* and *Pygopus*, it is a flattened, unlobed structure (Lynn & Komorowski 1957; Underwood 1957). The parathyroid lies lateral to the origin of the internal carotid artery (Underwood 1957).

The pancreas is V-shaped, its apex directed posteriorly, with a transverse or anteriorly directed hepatic lobe extending towards the gall bladder, and an intestinal lobe lying along the small intestine as far as the pylorus. In *Aprasia*, *Delma* and *Pygopus*, a posteriorly directed splenic lobe extends from the anterior end of the intestinal lobe (Underwood 1957).

The adrenals are small and narrow, lying immediately postero-medial to the testes, or antero-medial to the ovaries, the right adrenal more anterior than the left.

Several cephalic exocrine glands have been reported from *Delma* and *Lialis* by Saint Girons (1988). They are the inferior labial, palatine, anterior sublingual, lingual, Harderian and nasal glands.

In *Pygopus*, *Paradelma* and *Lialis*, preanal glands are present subcutaneously. Each drains via a separate duct to open posteriorly at a pore located in the free margin of a scale (Underwood 1957; Greer 1989).

Reproduction

The gonads lie dorso-medially within the body cavity, on either side of the dorsal mesentery. The right gonad lies more anteriorly than the left. In male *Pygopus*, the anterior pole of the right testis lies level with the gall bladder, that of the left gonad level with the posterior end of the liver. The ductus deferens is straight and passes over the ventral midline of the kidney before entering the urodaeum. Paired hemipenes lie within the base of the tail when inverted, and are everted from the proctodaeum for intromission. Hemipenial morphology was described by Böhme (1988).

In the female, the gonads are more posterior than those of the male. The right ovary is level with the ileocolic ostium. Each oviduct is initially narrow and thin-walled, and lies dorso-lateral to its ovary. Distally, the oviducts are broader and thicker walled. The left oviduct is much the shorter.

Pygopodids are oviparous, with a normal clutch size of two. Temperate climate species appear to mate in spring and lay in summer. Known incubation periods range from 66 to 77 days. *Pygopus* and *Lialis* species have been reported to lay communally (Patchell & Shine 1986b; Greer 1989).

Karyotypic data are available for sixteen species of pygopodid, including representatives of the genera *Aprasia*, *Delma*, *Lialis*, *Ophidiocephalus* and *Pygopus* (Gorman & Gress 1970; Gorman 1973; King 1990). Diploid number ranges from 34 to 42, most commonly 2n = 38 and chromosomes are predominantly biarmed. Many species have sex chromosome systems based on male heterogamety, some (*Lialis*) with complex multiple sex chromosome systems.

NATURAL HISTORY

Life History

Almost nothing is known of the life history of pygopodids. Captives have lived for up to seven years (Mertens 1966; Greer 1989).

Ecology

Most pygopodids feed on arthropods. *Lialis*, however, feeds exclusively on other squamates, mostly lizards, and both species of *Pygopus* have specialised diets. *Pygopus lepidopodus* feeds primarily on spiders (Patchell & Shine 1986b) and *P. nigriceps* is a scorpion specialist (Pianka 1986). *Aprasia* may be myrmecophagous (Jenkins & Bartell 1980; Robertson, Bennett, Lumsden, Silveira, Johnson *et al.* 1989). Most species appear to search actively for prey, although *Lialis* is a sit-and-wait predator (Greer 1989; Murray, Bradshaw & Edward 1991).

Pygopodids inhabit a wide range of habitats and microhabitats. In arid areas, *Triodia* tussocks are a major microhabitat. *Aprasia* is fossorial, inhabiting ant tunnels and burrowing in sandy soils, as is *Ophidiocephalus* which burrows in loose sandy loams. *Pygopus*, *Paradelma*, *Lialis* and *Delma* are terrestrial surface dwellers, although some *Delma* species burrow in loose soil. *Pygopus* has been found up to 1.5 m above the ground in vegetation. *Aclys* and *Pletholax* are both surface active in low vegetation and are partly fossorial (Greer 1989).

Although usually encountered singly, and hence presumably solitary, occasional aggregations of pygopodids have been reported, possibly related to breeding (Bush 1981, 1986).

Predators of pygopodids include the diurnal raptors *Falco cenchroides* and *Hieraaetus morphnoides* (Morrison in Sedgwick 1949; Storr 1965b), elapid snakes of the genera *Cacophis*, *Cryptophis*, *Demansia*, *Neelaps*, *Pseudechis*, *Pseudonaja*, *Simoselaps*, *Suta* and *Unechis* (Shine 1980a, 1980d, 1984a, 1984b, 1987, 1988, 1989), goannas (Pianka 1968; King & Green 1979; Losos & Greene 1988) and feral cats and foxes (Martensz 1971; Brooker 1978). *Lialis* will also eat other pygopodids (Smith 1976a). In all instances, pygopodids are a minor dietary component.

The few parasites recorded from pygopodids include the trematode *Paradistoma crucifer*, the cestode *Acanthotaenia striata*, nematodes (*Abbreviata* sp., as *Physaloptera*) and other unidentified nematodes and linguatulids (Brongersma 1953; Ehmann 1981).

Behaviour

Four defensive behaviour patterns have been described. Long-tailed species (*Delma*, *Pletholax*) attempt to escape by leaping into the air (Bauer 1986a; Greer 1989). When disturbed, fossorial species (*Aprasia*, *Ophidiocephalus*) writhe the tail, which is often brightly coloured (Rankin 1976a; Ehmann 1981). *Pygopus* and *Paradelma* raise the forepart of the body from the ground and flicker the tongue, the former genus also compressing the neck and striking, apparently in mimicry of elapid snakes (Shea 1987c; Greer 1990). If restrained, pygopodids attempt to break free by twisting the body and bracing with the tail (Greer 1990).

The ambush predator *Lialis* is known to writhe its tail to attract potential prey lizards (Bradshaw, Gans & Saint Giron 1980; Murray *et al.* 1991).

Like geckos, pygopodids have a voice. A distinct high-pitched squeak is produced under stress, and sometimes emitted in social interactions (Weber & Werner 1977; Annable 1983; Greer 1989). Also like geckos, pygopodids use the tongue to wipe the face and spectacle (Greer 1989).

Captive *Pygopus* have been observed to excavate tunnels in soft soil by removing soil with the mouth and rotating the body to widen the tunnel (Husband 1980). Such tunnelling behaviour may allow the animal access to the burrowing spiders on which it feeds.

Economic Significance

All pygopodids are legally protected in the Australian states in which they occur. Six species with small geographic distributions, often close to major human populations (*Aprasia aurita*, *A. parapulchella*, *A. pseudopulchella*, *Delma impar*, *Ophidiocephalus taeniatus*, *Paradelma orientalis*) may be threatened by habitat loss (Ehmann & Cogger 1985; Jenkins 1985; Robertson *et al.* 1989; Coulson 1990).

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Pygopodids occur through most of Australia, with the exception of Tasmania, the extreme south-east of Australia, and the rainforests of the east coast. *Lialis* also occurs in the lowlands of New Guinea and New Britain. The most widespread species, *L. burtonis*, has an Australian distribution nearly covering that of all other pygopodids combined. *Pygopus*, with two species, and *Delma*, with 16 species, are similarly widespread. *Aprasia* (14 species) is predominantly southern Australian in distribution, extending north along the west coast. The monotypic *Aclys* and *Pletholax* are restricted to the lower west coast of Western Australia, while the monotypic *Ophidiocephalus* and *Paradelma* are restricted to deep-cracking sandy loams of northern South Australia and brigalow habitats of central eastern Queensland, respectively. The major centre of pygopodid diversity is the lower west coast of Western Australia, where up to ten species may occur together (Cogger & Heatwole 1981).

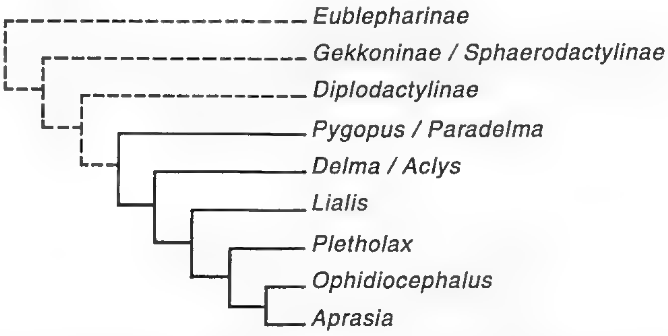

Figure 28.8 Hypothesised relationships between pygopodid genera, and with their nearest relatives. Solid lines indicate relationships within the family, broken lines with other gekkonid groups. (After Kluge 1976, 1987) [D. Wahl]

Affinities with other Groups

Pygopodids are closely related to geckos, sharing with them a large number of derived characters (Shute & Bellairs 1953; McDowell & Bogert 1954; Underwood 1957; Miller 1966; Wever 1974; Iordansky 1985; Kluge 1987). Of modern authors, only Camp (1923) has suggested an alternative relationship with anguinoids and helodermatids.

Most authors have assumed that the Pygopodidae and Gekkonidae are sister groups, derived independently from a common ancestor, and this traditional classification has been adopted here. However, Kluge (1987) examined the evidence critically for such a relationship and concluded that the pygopodids are the sister group of diplodactyline geckos, with the pygopodid-diplodactyline clade the sister group of gekkonine and sphaerodactyline geckos (Fig. 28.8). Hence he proposed the inclusion of diplodactyline geckos in an expanded family Pygopodidae. Kluge further suggested that pygopodids may be most closely related to certain genera of the tribe Diplodactylini.

Kluge's classification has yet to be accepted by most Australian herpetologists, and has been criticised (King 1990; King & Mengden 1990) on karyotypic evidence. However, the karyotypic evidence supports Kluge's hypothesis of a cladistic relationship between the pygopodids and diplodactylines, merely introducing uncertainty as to which group of diplodactylines (the tribe Diplodactylini or Carphodactylini) the pygopodids are most closely related. It is likely that the reluctance to accept Kluge's expanded Pygopodidae is because of the lack of any intermediary between the fully limbed diplodactylines and the nearly completely limbless pygopodids at such a low taxonomic level.

Affinities within the Pygopodidae

Of the eight genera of pygopodids recognised by Kluge (1974), four (*Aprasia*, *Ophidiocephalus*, *Pletholax* and *Lialis*) are well defined natural groups, successively more distantly related to each other (Fig. 28.8; Kluge 1976a). The relationships between the remaining, relatively primitive genera (*Delma*, *Aclys*, *Paradelma* and *Pygopus*) are less well defined. Although Kluge (1976a) recognised two groups among these genera (*Delma*/*Aclys* and *Pygopus*/*Paradelma*), his recognition of these two groups as genera (*Delma* and *Pygopus*) and his subfamilial classification have received little acceptance (Shea 1987a, 1987c; Böhme 1988; Greer 1989).

Fossil Record

No fossil material has yet been identified as being of pygopodid origin, probably due both to the fragile nature of the skeleton and the paucity of detailed data on pygopodid and gekkonid osteology.

COLLECTION AND PRESERVATION

Pygopodids are generally collected by hand from beneath ground debris, or in pitfall traps. *Pygopus nigriceps* (Pl. 4.12), *Lialis* and some *Delma* species are often found crossing roads on warm nights.

Pygopodids are best fixed in 10% formalin, injected into the body cavity and carefully into the tail, and stored in 70% ethanol. Due to the persistence of reflexes in the tail long after death, it may be necessary to delay injection of fixative into the tail for several hours post mortem if contortion and tail breakage are to be avoided. The keratin layer of the epidermis of preserved pygopodids is fragile and readily sloughs with handling.

29. FAMILY AGAMIDAE

Geoffrey J. Witten

DEFINITION AND GENERAL DESCRIPTION

The family Agamidae is one of three families belonging to the infraorder Iguania. Known as dragons in Australia, agamids are small to moderate-sized lizards at maturity, and vary from a snout-vent length less than 50 mm to nearly one metre. Most Australian agamids are terrestrial, a few are arboreal or semi-arboreal and one species is riparian. Some species are swift, while others depend on cryptic colours and shape to avoid predation. Some 62 species are known, placed in 13 genera.

Frost & Etheridge 1989) suggested that the Agamidae cannot be diagnosed as a monophyletic group, although the group containing the agamids and the chameleons can be diagnosed. These authors proposed to include the Agamidae within the Chamaeleonidae. However, as discussed in Affinities with Other Groups, until further supporting evidence is forthcoming, the traditional classification will be used here.

Agamids have acrodont teeth and, like most other lizard families, anterior pleurodont teeth (Fig. 29.1B). Acrodont teeth are fused to the superior part of the mandible and maxilla, and are not replaced once they are formed. As the animal grows, further teeth are added to the tooth row posteriorly (Cooper, Poole & Lawson 1970). The Chamaeleonidae is the only other lizard group in which acrodont teeth are known; this family also lacks pleurodont teeth (Fig. 29.1C). Pleurodont teeth are adherent to the inner aspect of the tooth-bearing bones and are replaced continuously through life. In most agamids the anterior pleurodont teeth are caniniform. The scales are rough and irregularly shaped in many species. Enlarged head scales are absent. The tongue is broad and flat, and all species have movable eyelids.

HISTORY OF DISCOVERY

The first dragon from Australia was described as *Lacerta muricata* by White in 1790. John Edward Gray named the three most distinctive Australian agamid genera: *Chlamydosaurus* (as *Clamydosaurus*), based on the frilled lizard, *C. kingii* in 1825 (Pl. 5.9); *Moloch*, based on the thorny devil, *Moloch horridus* in 1841 (Pl. 5.6); and finally in 1845, *Chelosania*, based on *C. brunnea*. By the time he wrote on the last of these, representatives of most Australian genera had been described.

Not long after Gray, Girard (1857) described *Oreodeira gracilipes*, based on a single female specimen supposedly collected in New South Wales by Charles Wilkes of the United States Exploring Expedition. The holotype was re-discovered by Moody (1988), and proved to be an *Agama* from Liberia in west Africa! The USNM received many specimens from west Africa during the 1840s as well as the results of the United States Exploring Expedition. Apparently the African *Agama* was tossed in with the Australian specimens, leading to Girard's later error (Moody 1988).

Boulenger (1885) consolidated much of the lizard taxonomy since Gray's (1845) catalogue, and rightly became the most authoritative worker of the day. Unfortunately, his coverage of the Australian agamids was not as complete as it should have been. Generic distinctions recognised by European taxonomists (for example, Fitzinger 1843) were ignored, and some of his own generic placements were puzzling.

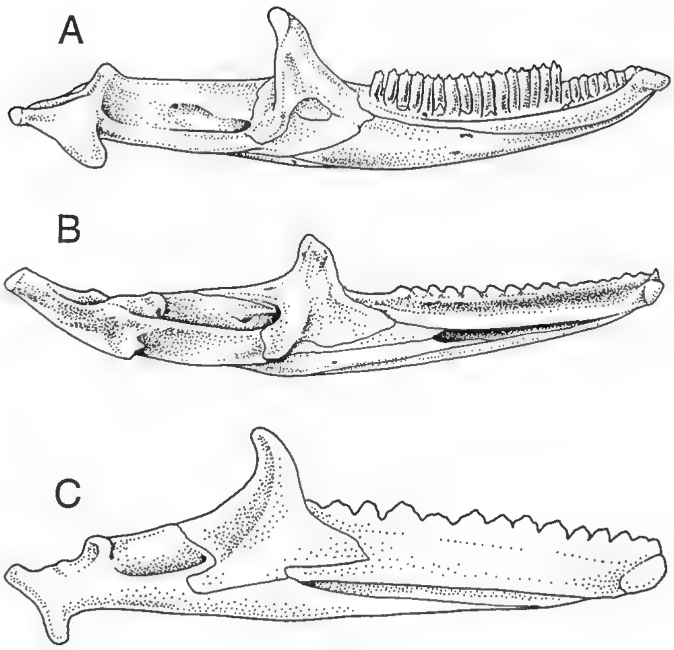

Figure 29.1 Mandible and teeth in the infraorder Iguania. A, the iguanid *Morunasaurus annularis*; B, the agamid *Pogona vitticeps*; C, the chamaeleonid *Brookesia stumpffi*. (After Estes *et al.* 1983) [R. Plant]

Lophognathus was first described in 1842 by Gray for *L. gilberti*. Boulenger (1883) described a further species in the genus, *L. longirostris* (Pl. 5.2), but in his catalogue placed all *Lophognathus* species in the very dissimilar *Physignathus*. This error was corrected formally by Cogger & Lindner (1974).

Houston (1978) synonymised *Lophognathus* with *Amphibolurus*, and was supported in this by Storr (1982), though Storr attempted to resurrect the long forgotten name of *Gemmatophora* for the combined genus. Witten (1985b) reinstated *Lophognathus*, based on body proportions, but this has not been followed in the latest major work on Australian lizards (Greer 1989). In contrast, *Diporiphora*, which also closely resembles the type species of *Amphibolurus*, retained its generic status. Boulenger (1885) placed all other Australian agamids without spectacular or obvious modification into the genus *Amphibolurus*. This large conglomerate presented a large task for any reviewer, and it remained untouched for almost a century.

Glenn Storr of the Western Australian Museum contributed greatly to agamid taxonomy. Most of his work was at the species level, but he described *Caimanops* (Storr 1974) and began to correct the generic disarray left by Boulenger (Storr 1982). He described the genus *Pogona* for the bearded dragons and resurrected *Ctenophorus* Fitzinger, 1843.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Typical agamid scales have a ridge or keel along the exposed surface, leading to a short posterior spine. In the more primitive genera, the scales are tubercular or granular and do not overlap; also they are relatively small and uniform in size, creating a surface like sandpaper. Many species have scattered enlarged scales over the dorsum. Head scales usually lack spines and are relatively smooth. Ventral scales commonly overlap (imbricate). Keels of ventral scales are often less prominent and are absent in some species.

Dorsal scales are modified greatly in some genera. The scales of *Moloch horridus* (Pl. 5.6) have a central spine instead of a keel. The mid-dorsal scales in species of *Pogona* are thickened towards their posterior margin, and are much larger than other dorsal scales. These form a rasp-like raised area along the back. In species of *Amphibolurus* the dorsal scales imbricate widely and are heterogeneous. The surface of agamid scales has a honeycomb micro-ornamentation (Maclean 1980). Modified skin helps *Moloch horridus* to take up water from rain or condensation. Interscalar channels carry water to the corners of the mouth where it can be swallowed (Bentley & Blumer 1962; Gans 1985a). Other agamids appear to lack this ability (Gans 1985a).

Agamid skin is rather loose and may form permanent folds. Most Australian agamids have a well-defined transverse, gular fold. This fold usually continues laterally into a 'scapular' fold. which passes above the insertion of the forelimb, and in some species, continues along the lateral border of the body to above the hind limb. The gular fold is very narrow mid-ventrally in *Chelosania brunnea*. It is absent in some *Diporiphora*, though the scapular fold persists in some species without its ventral continuation. In *C. brunnea*, the skin behind the tympanum is covered by tubercular scales arranged in five or six postero-dorsal rows. Each row is separated from the next by a deep fissure. This mobile skin presumably allows the neck to be distended, but its functional significance is unknown.

Femoral glands open through pores on the ventral surface of the thigh. These pores have been used extensively in the taxonomy of agamids. They are present in most Australian agamids, but are absent in *C. brunnea*, *Hypsilurus* species and *Moloch horridus*. The position of each pore relative to scales has received some attention. Humphries (1972) noted that pores of some species open between scales, while others are within a single scale. However, many apparently interscalar pores are in fact contained within the posterior margin of a scale (Witten 1982a). When ventral scales have a keel, the opening of a posterior intrascalar pore is hidden on the posterior surface of the pore-bearing scale. If the ventral scales are smooth, the opening of the pore is clearly on the exposed surface of the scale. An ontogenetic shift may occur in this character. Hatchlings with ventral intrascalar pores may develop posterior intrascalar pores as the glands become active and the secretion hides the posterior part of the scale, or the enlarged pore may obliterate the scale entirely, giving the appearance of an interscalar pore (Fig. 29.2D).

Most Australian agamids have posterior intrascalar pores (Fig. 29.2C). This type of pore is apparently the primitive condition as it occurs in the three most primitive agamid genera, *Uromastyx*, *Leiolepis* and *Physignathus*.

Two types of intrascalar pore, apparently derived, occur in Australian agamids. In most members of the *Amphibolurus* group the pore occurs on the ventral surface of the keeled ventral scales, thus interrupting the keel, rather than lying posterior to it. However, many *Diporiphora* species have posterior intrascalar pores (Fig. 29.2A). Some individuals have both pore types.

Interscalar pores (Fig. 29.2B) are present universally in *Tympanocryptis* species, and occasionally in some species of *Ctenophorus* and *Pogona*, but otherwise are rare (Witten 1982a). The ventral scales of these species imbricate more than those of most agamids, such that a pore is hidden unless the associated gland has produced considerable secretion. Females often have less active glands, which has led several authors to report, in error, an absence of pores in female *Tympanocryptis* (for example, Storr 1964b).

The tympanic membrane is superficial and obvious in most Australian agamids. It is sunken in some *Pogona*, particularly in larger specimens. Juvenile species of *Hypsilurus* have a few scales on the posterior part of the tympanum, which do not persist in adults. The tympanum is covered with scales in two groups. The scale-covered tympanum of *Ctenophorus maculatus* is functional and appears on the side of the head as a depression. The succession of conditions within *Tympanocryptis* probably indicates the direction of evolutionary change (Witten 1982b). *Tympanocryptis diemensis* has a naked tympanum, *T. adelaidensis* normally has a naked tympanum, but occasional specimens have a few scales on the tympanum, and *T. parviceps* has a reduced tympanum which is completely covered by scales. The other species in the genus lack a tympanum.

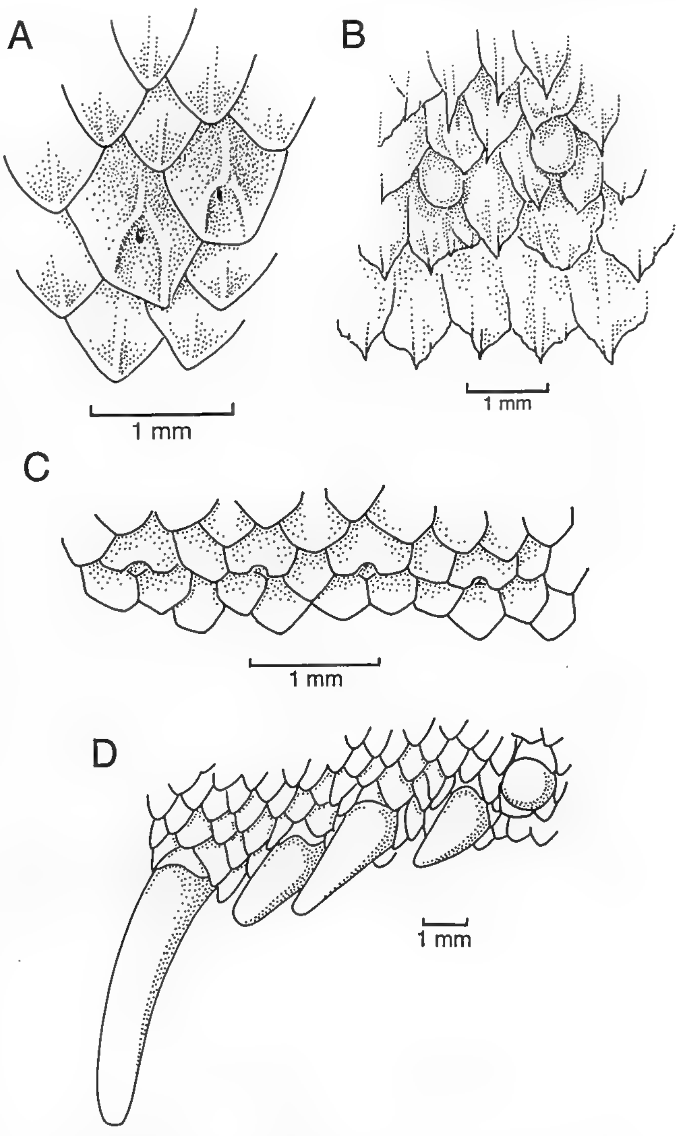

Figure 29.2 Inter- and intrascalar pores. **A**, ventral intrascalar pores in *Diporiphora australis*; **B**, interscalar pores in *Tympanocryptis diemensis*; **C**, **D**, posterior intrascalar pores in *Ctenophorus cristatus*; **C**, scales of a juvenile, before intrascalar glands become active; **D**, scales of adult male, showing elongate, spiniform secretions from the pores. [R. Plant]

Body Wall

The presence of a stiff outer coating on an animal creates the need for special sensory structures. The scales of agamids have epidermal sensory organs which resemble volcanic craters in shape. In *Pogona* species, these sensory organs occur on either side of the dorsal scales, just beneath the scale lip of the ventral scales, and are scattered over the larger head scales (Maclean 1980). The number on each head scale increases with age (pers. obs.). A dermal papilla, which extends into the base of these sensory organs, contains a nerve plexus with terminals in the cell layer immediately beneath the floor of the crater. The keratin is very thin in the floor of the crater, but the rim of the crater extends inwards to surround and support the dermal papilla (Maclean 1980).

Figure 29.3 Transverse section of mid-dorsal region of *Amphibolurus muricatus*. Within the large erectile body note the flattened veins and the arterioles surrounded by denser connective tissue. Inset **A** outlines three flattened veins; inset **B** encloses two arteries; **apo**, aponeurosis of forelimb muscle; **der**, dermis; **mus**, muscle; **she**, dense connective tissue sheath.
[Photo by B. Bowdern]

Large melanophores are prominent in the dermis of agamids. These cells consist of a large central body, from which numerous processes radiate. Dark pigment within the central body of the cell disperses into the processes under the influence of melanophore stimulating hormone, and causes the skin to become darker. Melanophore stimulating hormone is apparently produced by the pituitary gland or hypophysis. Removal of the hypophysis causes the lizard to remain permanently pale (Rice & Bradshaw 1980). Darker skin allows a lizard to absorb heat more rapidly. Thus, the activity of melanophores in the skin is important in the control of heat uptake and therefore in thermoregulation in lizards (Rice & Bradshaw 1980). Males defending territories also change colour in a way that highlights different patterns. The melanophores in the white lip stripe of *Lophognathus* species contain a pigment which transmits red light and may give the distinctive white colour typical of the group (Witten 1982a).

Some agamids are able to raise skin folds along their dorsal midline. Such crests are obvious and apparently permanent structures in species of *Hypsilurus*, but are transitory in *Lophognathus* and *Ctenophorus*.

In all Australian genera, except *Moloch*, a sheet of connective tissue passes from the neural processes of the trunk vertebrae to the skin of the midline. Over the anterior part of the trunk, this fascia receives aponeuroses from muscles of the pectoral girdle and forms a thickening about halfway between the neural spines and the skin. This rhomboidal connective tissue block provides a thick sheath around vascular tissue in many species. The vascular tissue is mainly loose connective tissue with numerous veins and some arteries. The arteries are surrounded by thicker connective tissue (Fig. 29.3); the lumina of most of the veins in the non-erectile vascular tissue are flattened dorso-ventrally (Witten 1982a).

Vascular blocks are largest in males of *Lophognathus*, *Amphibolurus* and *Diporiphora*. They are either lacking or poorly developed in females of these genera. In *Ctenophorus* species the vascular block is relatively less dense, with fewer blood vessels (Witten 1982a). This variation may be related to differences in the way crests are erected in the two groups. In *Lophognathus* and its relatives, raising of the crest takes several minutes; it remains erect for long periods. In *Ctenophorus*, the crest is a much more transitory structure, and is raised and lowered during territorial displays (Pl. 5.4; Gibbons 1979).

The hyoid apparatus of the bearded dragon, *Pogona barbata*, is modified to support its 'beard' (Pl. 5.8). The second ceratobranchial, a posteriorly projecting, medial element has been lost, and the relatively broad body of the hyoid is placed anteriorly. The entoglossal process at the anterior point of the hyoid extends further forward through the tongue than in other lizards, and actually emerges from the tissue of the tongue to lie in

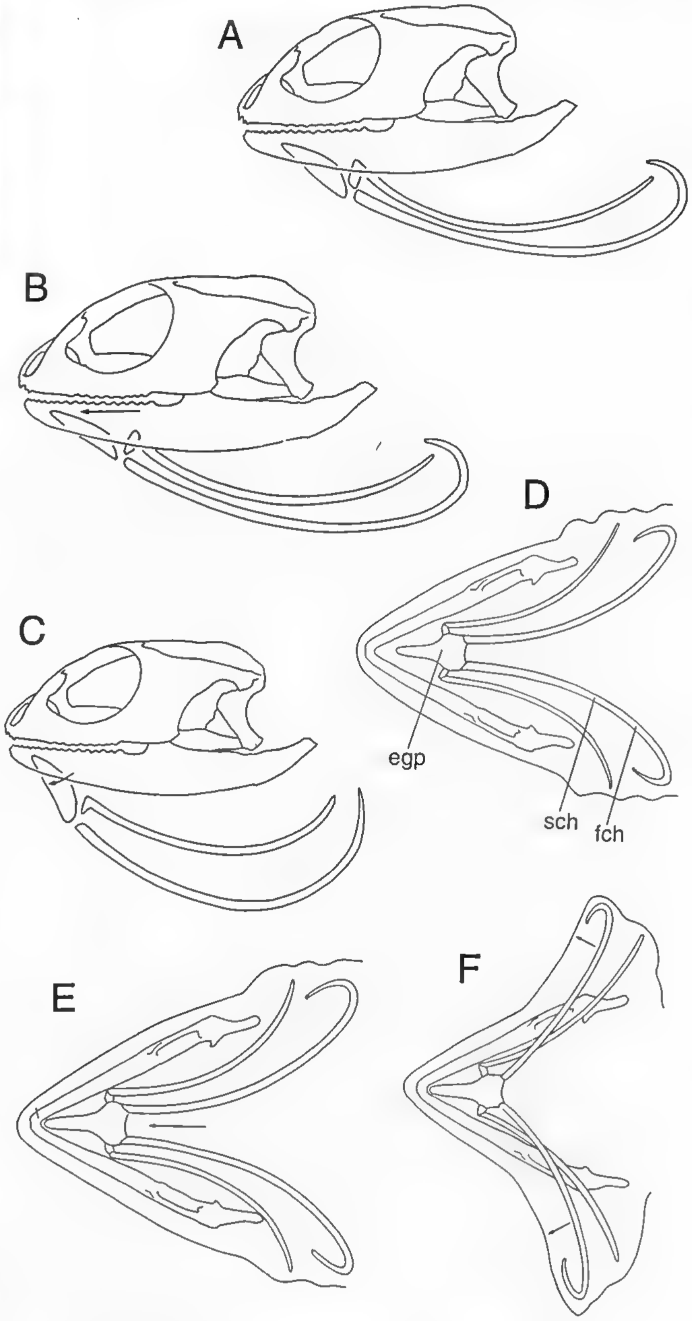

Figure 29.4 Erection mechanism of beard of *Pogona barbata*. **A–C**, in lateral view; **D–F**, in ventral view. **A**, **D**, beard in relaxed position; **B**, **E**, forward movement after initial contraction of anterior mandibular muscles, and contact of the entoglossal process with the mandibular symphysis; **C**, **F**, full contraction of mandibular muscles, outward and downward rotation of hyoid, resulting in full erection of beard. **epg**, entoglossal process; **fch**, first ceratohyal; **sch**, second ceratohyal. (After Throckmorton *et al.* 1985)
[R. Plant]

a mucous membrane sheath on the floor of the mouth. The hyoid apparatus is suspended in a sling of muscles passing from the inner mandible to bones of the pectoral girdle, with an attachment to the elongate first ceratobranchial. In frill erection, the muscles anterior to the ceratobranchial contract and pull the whole hyoid apparatus forward (Fig. 29.4B, E). The entoglossal process quickly abuts the mandibular symphysis, preventing further forward movement of the body of the hyoid. With continued muscle activity the hyoid rotates ventrally, and the ceratobranchials swing laterally and ventrally to support the overlying skin as the beard (Fig. 29.4C, F). While all *Pogona* are known as bearded dragons, it seems the degree of specialisation in *P. barbata* has been a recent development, as most members of the genus retain the second ceratobranchials (Badham 1976). The entoglossal process also passes forward from the tissue of the tongue in the related *Amphibolurus muricatus*, but not in other lizards (Throckmorton, de Bavay, Chaffey, Merrotsy, Noske *et al.* 1985).

Camp (1923) distinguished three parts of the *m. rectus abdominis* muscle: *m. rectus abdominis pyramidalis*, *m. rectus abdominis medialis* and *m. rectus abdominis lateralis*. Camp reported the *m. rectus abdominis lateralis* in some primitive agamids, but Moody (1983) demonstrated that the observed muscle was a cutaneous slip of the pectoral muscle. Its nerve supply comes from the brachial plexus in a nerve also distributed to the pectoral muscle. Spinal segmental nerves supply the *m. rectus abdominis*. The *m. rectus abdominis medialis* has no attachment to the skin. It extends from the pubis to the xiphisternum (Moody 1983).

Physignathus is the only Australian genus having a cutaneous slip of the *m. pectoralis*. It is present also in *Uromastyx*, *Leiolepis* and in one of seven specimens of *Hydrosaurus* examined by Moody (1983). This cutaneous muscle is apparently a primitive feature which has been lost in other agamids. Though this muscle may have been present in the ancestor of all lizards, there is no evidence for its presence in either the chameleons or iguanids (Moody 1983), so it is probably best considered as peculiar to agamids.

SKELETAL SYSTEM

The agamid skeleton is very conservative. The skull is typical of primitive lizards and there is little variation between taxa. Differences in skull shape which might be used to infer relationships between genera are generally less than occur in the development of an individual.

Skull shape can vary ontogenetically as a result of the differential, or allometric, growth of some elements. The skull of most juvenile agamids is much shorter than that of the adult. The parietal bone contributes greatly to this elongation. In hatchling *Chlamydosaurus*, the parietal is roughly quadrangular. In adults, this bone bears large postero-lateral processes (Cogger 1960). Such allometric changes have made differences between species difficult to define.

Allometric changes are minimal in *Ctenophorus fordi*, a small species. This diminution of size reflects maturation at an earlier stage of development, a process referred to as neoteny, and adult *C. fordi* closely resemble juveniles of similar size from larger related species (Cogger 1960).

The lacrimal bone is one element of the skull which does vary between a number of Australian taxa. This element persists only in *Physignathus*, *Hypsilurus*, and *Chelosania*. Its loss in all other Australian genera coincides with the palatine extending further laterally in the floor of the orbit. In some specimens this lateral process intrudes into the lower margin of the orbit. The lacrimal of *Physignathus* and *Hypsilurus* (Fig. 29.5B, C) occupies the antero-inferior corner of the orbit, including the anterior part of the lower margin. In *Chelosania* the lacrimal is reduced to a small element in the anterior margin of the orbit (Cogger pers. comm.). *Moloch* lacks the supratemporal bone (Moody 1980).

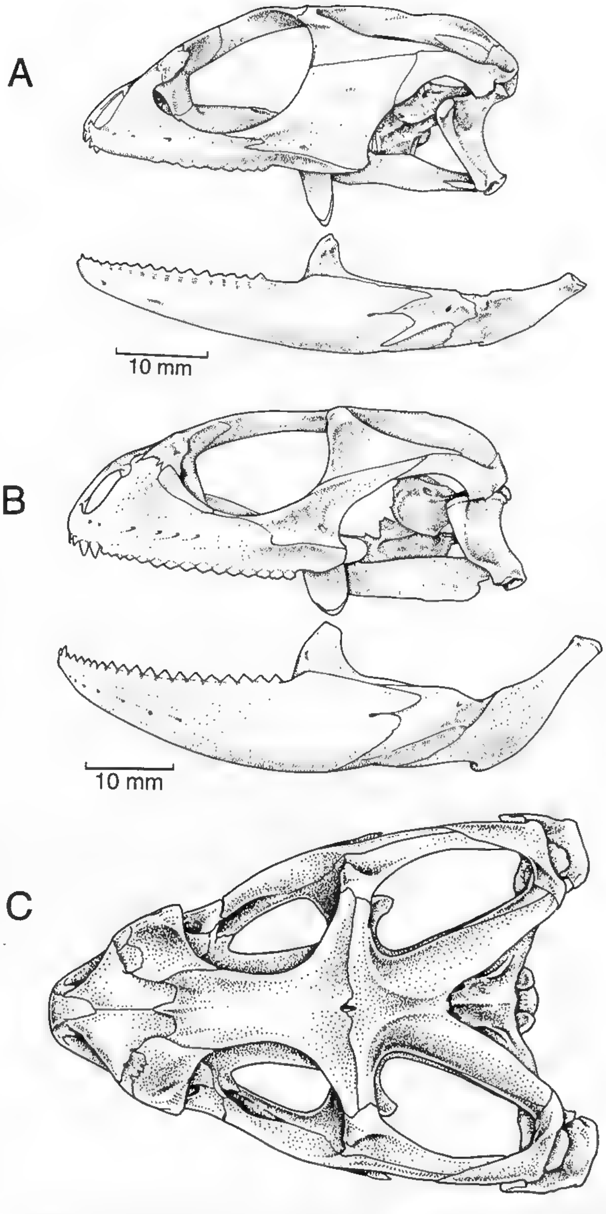

Figure 29.5 Skull of agamids. A, *Pogona barbata*, in lateral view, in which the lacrimal forms no part of the orbital margin; B, *Hypsilurus boydii* in lateral view, showing anterior pleurodont caniniform teeth and the large lacrimal in the lower anterior orbital margin; C, *Hypsilurus boydii*, in dorsal view. [R. Plant]

The pleurodont teeth of Australian agamids are generally caniniform, and tend to be relatively larger in adults. They are particularly prominent in *Chlamydosaurus kingii*, but relative to size are most prominent in species of *Tympanocryptis*. They are generally not as well developed in the genus *Ctenophorus*.

The maxillary teeth of *Moloch horridus* project medially from the inner edge of the bone (Cogger 1960). The tricuspid mandibular teeth (Cogger 1960) have an elongate central cusp and two lateral 'shoulders'. Each mandibular tooth slopes outwards, such that the central cusp fits between two maxillary teeth. This forms a shearing apparatus, which may be related to *Moloch*'s diet of hard-bodied ants. *Moloch horridus* has lost the anterior pleurodont teeth which, in other agamids, are presumably used in seizing prey; their loss in *M. horridus* may reflect the method of prey capture using only the tongue (Robinson 1976).

The number of presacral vertebrae is usually 22 or 23, except in *Pogona* species and *Chelosania brunnea* which have one more and *Moloch horridus* which has one less (Greer 1989). There is no adaptive alteration in the number of presacral vertebrae as is found in the skinks, for example. The number of postsacral vertebrae varies with the length of the tail, from 22 in *M. horridus* to 79 in *Lophognathus longirostris* (Greer 1989).

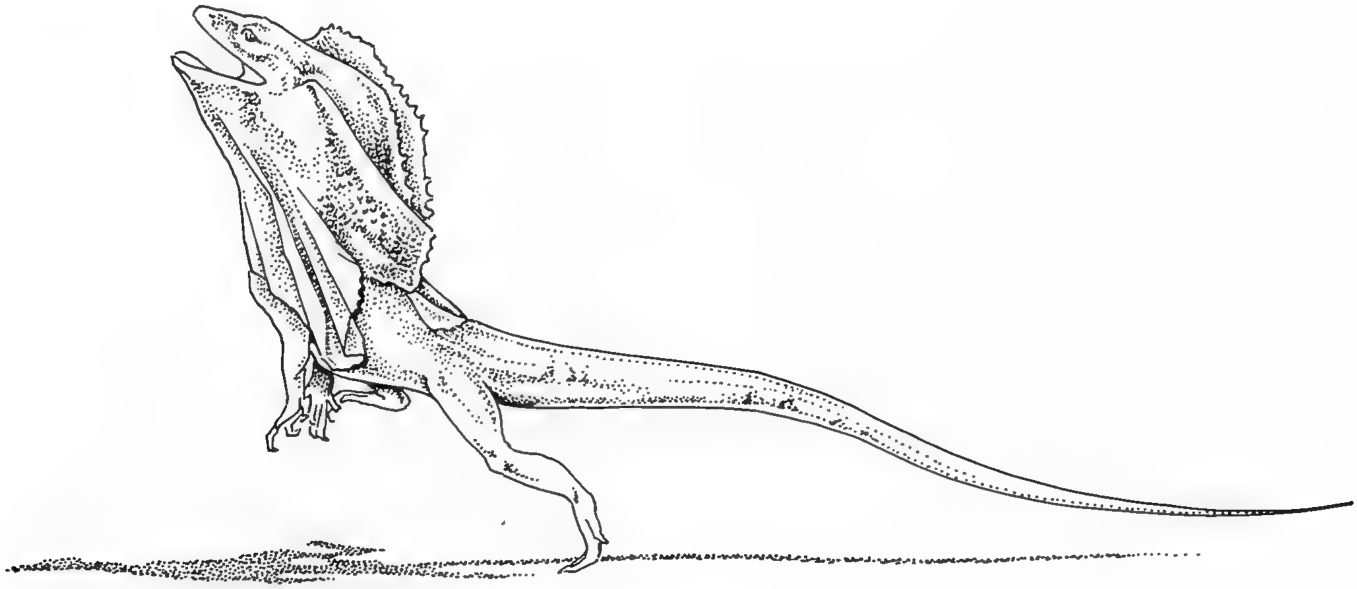

Figure 29.6 Bipedal running gait of *Chlamydosaurus kingii*. (After photo by J. Weigel/ANT) [R. Plant]

Most Australian agamids retain the ancestral phalangeal formula of 2.3.4.5.3/2.3.4.5.4. Each number represents the number of bones (phalanges) in each digit of the hand (manus) and foot (pes) respectively. The advanced *Tympanocryptis* species, which lack a functional tympanum, have lost one phalanx of the fifth toe (Cogger 1960; Mitchell 1965). A small percentage of *T. diemensis* have also lost this bone (7 of 94 digits; Kent 1987). Most *Ctenophorus clayi* have lost one phalanx of the same digit (Greer 1987b), to give a pes formula equal to that of the manus. Over most of its range, *Moloch horridus*, has a much reduced phalangeal formula of 2.2.3.3.2 for both manus and pes (Cogger 1960). However, the more primitive formula of 2.3.4.4.3 is found in a population from central Western Australia (Greer 1989). This loss of only three phalanges instead of the more widespread 11 is remarkable. It is not yet known whether the two populations are distinct species or whether there is a gradual change between populations with the different formulae (Greer 1989).

Locomotion

Most agamids move by quadrupedal walking or running, but some species typically adopt a bipedal gait at high speed. *Chlamydosaurus kingii* tucks its front legs against its chest in bipedal movement, with the great frill covering its chest (Fig. 29.6). *Moloch horridus* moves with a deliberate action, in which the body rocks back and forth as the animal makes slow forward progress.

Little work has been done on the relative speeds of locomotion in Australian lizards. The relative lengths of limbs varies widely among the Australian agamids, both interspecifically and during growth (Witten 1985b). Garland (1985) found that differences in sprint speed between individuals were not related to different limb proportions or sex in *Ctenophorus nuchalis*. The highest speed recorded was 13.5 km/h, achieved within 3 m of the start.

Feeding and Digestive System

Agamids are 'sit-and-wait', or ambush, predators. Some species will change position regularly, but they generally do not seek prey from within cover. When a prey item comes within range the lizard lunges forward and either grasps it with its jaws directly, or uses the tongue to pick up the prey.

Dragons are probably opportunistic rather than selective feeders. They eat a large number of ants, especially in comparison with the members of other lizard families, but this probably reflects prey availability. Other lizards tend to avoid ants. Some of the larger species also eat plant material (Greer 1989). Movements of the jaw and tongue ensure a secure hold on the prey and assist in moving it backward into the throat (see Chapter 24; Throckmorton & Clarke 1981). The alimentary tract has not been studied in any detail. The distinct stomach lies to the left of the midline. The pancreas lies to the left of the midline, as does the spleen. The pancreas extends from left to right across the peritoneum.

Circulatory System

The heart is typical of squamates, as described in Chapter 24 (see also Webb 1972). The heart itself is supplied by a single coronary artery and an apical artery (MacKinnon & Heatwole 1981). The coronary artery arises from the left systemic arch in *Pogona barbata* and *Amphibolurus muricatus*, but from the right systemic arch in *Physignathus lesueurii*. This difference in origin may be an adaptation to diving, as the right systemic arch normally receives more highly oxygenated blood. Agamids retain a gubernaculum cordis, a fibrous band joining the apex of the heart to the pericardium. An apical artery runs along this structure to reach the apex of the heart. The apical artery comes from the anterior epigastric artery, referred to inappropriately as the internal mammary by some authors (MacKinnon & Heatwole 1981).

Respiratory System

The lungs are two vascularised sacs occupying the thorax. The main area for respiratory exchange is arranged around the periphery of a large central cavity, and resembles a netting bag suspended within a balloon. Layers of tissue link the strands of netting to the outer wall of the lung, forming many parallel tubular cavities called faveoli (McGregor & Daniels 1990).

The relatively simple sac-like lungs of lizards are inflated by virtue of their attachment to the body wall of the thorax (McGregor pers. comm.). During inflation the faveoli are pulled open. The walls of the faveoli tend to collapse when the lungs are deflated, and are prevented from sticking to each other by large amounts of surfactant on the lung surface (McGregor & Daniels 1990).

Excretion

The kidney of reptiles produces urine which is not hyperosmotic. In agamids urine flows to the cloaca and then back into the colon. The wall of the colon extracts water and salts, thereby preventing excessive water loss. In *Ctenophorus ornatus* up to 98% of water may be reabsorbed before the urine is voided (Bradshaw 1975).

Sense Organs and Nervous System

Agamids rely heavily on sight for feeding and detection of predators. The retina of *Pogona* species has a well-defined central specialisation with some foveation (Rowe pers. comm.). This morphology is typical of an animal with acute vision. Whether it is typical of all agamids is not known. In the Asian genus *Calotes*, olfaction appears to play little, if any, role in prey detection (Cooper 1989). The same is probably true of Australian agamids, and indeed, possibly of the Iguania generally (Cooper 1989).

Endocrine and Exocrine Systems

Overall colour change has been demonstrated to be under the control of the hypophysis (pituitary gland). Removal of the hypophysis leads to a general paleness, presumably because of the absence of melanophore stimulating hormone (Rice & Bradshaw 1980). The mechanism of control of the second form of metachromatism in agamids, that of pattern changes, is unknown (Bradshaw & Main 1968).

The control of kidney function and the rate at which water is reabsorbed by the colon are influenced by hormones. The hypothalamus reacts to increased salt intake by reducing the rate at which urine is produced by the kidney. This is achieved by production of arginine vasotocin (AVT), which acts as an antidiuretic hormone (Bradshaw 1975). The control of colonic reabsorption is apparently influenced by adrenal corticosteroids in a way which is broadly parallel with the mechanism found in mammals. Bradshaw (1975) reported some dramatic differences between *Ctenophorus ornatus* and *C. nuchalis* in the levels of circulating corticosteroids. In *C. ornatus* the correlation between salt levels and corticosteroids was high when salt levels increased during dry weather. The same was not true of *C. nuchalis*, and adrenal failure was postulated as a causative factor in the high mortality rate of *C. nuchalis* (Bradshaw 1975).

The parietal organ has been implicated in the control of panting in *Amphibolurus muricatus* through its influence on the activity of the pineal gland (Firth & Heatwole 1976).

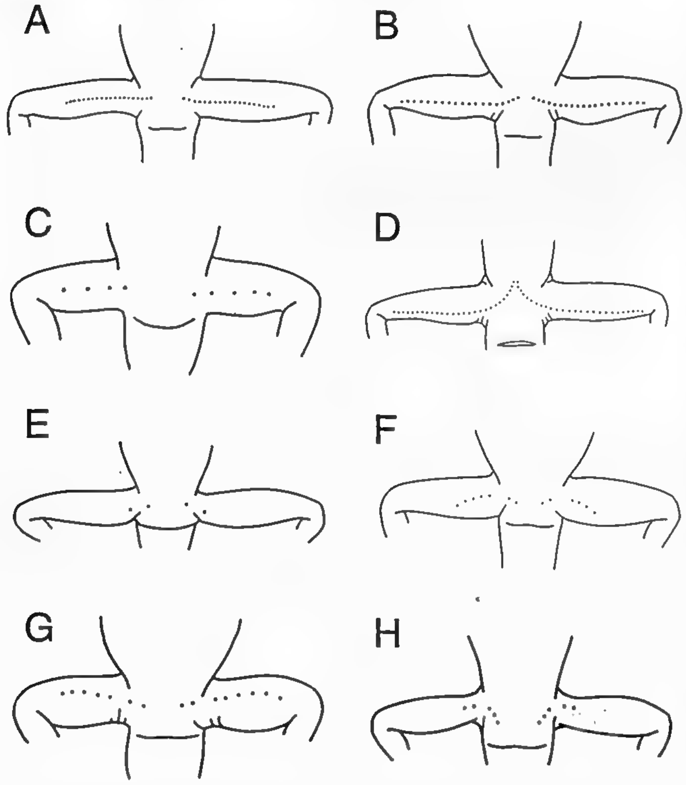

Figure 29.7 Femoral pore arrangements in agamids. **A**, *Physignathus lesueurii*; **B**, *Ctenophorus decresii*; **C**, *C. maculosus*; **D**, *C. isolepis*; **E**, *Tympanocryptis tetraporophora*; **F**, *Chlamydosaurus kingii*; **G**, *Ctenophorus nuchalis*; **H**, *Amphibolurus nobbi*. [R. Plant]

Most Australian agamids possess femoral glands. They are apparently a primitive feature of lizards, as they occur in a wide range of families, but their function is unclear. Cole (1966a) looked at the structure of femoral glands in iguanids, but was unable to demonstrate a clear function. He made the observation that they are more active in males, particularly in the breeding season, and on that basis suggested they might be used in territorial defence or marking. The same is true for Australian agamids, but the only evidence again is circumstantial. Cogger (1978) failed to find any volatile compound in the secretion which might have indicated a scent or pheromone function, and no compounds were present in one sex but not the other. More recently Alberts (1991) noted intraspecific variation in two iguanid genera which may allow individual or sex recognition. She also found that the pores of males were active all season, but only unmated females had active pores.

The arrangement of femoral glands, as indicated by their external pores, is a useful taxonomic character. The primitive arrangement is that found in *Physignathus*. Femoral pores on the under side of the thigh extend medially into the preanal region in a continuous series (Fig. 29.7A). The widely separated left and right side pores (in the preanal region) is presumed to be the primitive condition because it is shared by *Leiolepis*, a primitive Asian agamid, as well as the more distantly related iguanid genera of the Americas (for example, *Sceloporus*; Cole 1983). A slightly different arrangement is found in most *Ctenophorus* (Fig. 29.7B–D), in which the preanal pores extend almost to the midline. A further minor modification is found in *C. isolepis* (Fig. 29.7D) and *C. scutulatus* where the medial end of the pore series arches strongly forward. The more primitive *Tympanocryptis* species, including *T. parviceps*, also have the primitive *Ctenophorus* arrangement. The more advanced *Tympanocryptis* have a reduced number of glands, with only two preanal and two femoral pores (Fig. 29.7E), or two preanal pores only.

Two other derived pore arrangements are present in Australian agamids. The fewer and more widely spaced pores of *Ctenophorus nuchalis* (Fig. 29.7G) form an arch, an arrangement shared by the genus *Pogona* (Witten 1982b). In the *Amphibolorus* group, there are separate preanal and femoral pore series. The more medial preanal pores are more posteriorly placed, usually on adjacent scales. The femoral series, where present, tends to be crowded onto the medial end of the thigh (Fig. 29.7H). The arrangement in *Chlamydosaurus* has similarities to both of these derived states. The preanal pores, although usually separate, are not always in the neat postero-medial series typical of *Lophognathus* (Fig. 29.7F).

Reproduction

There are two primary karyotypes in the Australian agamids. The large arid-adapted radiation has 12 metacentric macrochromosomes and 20 microchromosomes (King 1981; Witten 1983). *Physignathus* and *Hypsilurus* have 24 microchromosomes, but are otherwise similar to the arid-adapted species (Witten 1983). *Lophognathus gilberti* from northern New South Wales and from near Broome apparently have undergone fission of most of the macrochromosome complement (Witten 1983), resulting in a mixture of telocentric and metacentric macrochromosomes totalling 20. However, another population from the Gulf of Carpentaria retains the more common karyotype (King 1985).

All Australian agamids are oviparous. Clutch size is apparently related to body size, at least interspecifically (Fig. 25.6). The smaller species (for example, *Ctenophorus fordi*), lay as few as two eggs per clutch (Cogger 1978). The clutch may be as high as 35 in the larger *Pogona* (Fig. 29.8; Smith & Schwaner 1981). Most agamids lay between 4 and 10 eggs (Greer 1989).

Gonadal cycles of *Ctenophorus fordi* have been described in detail by Cogger (1978). Briefly, in males, spermatocytogenesis (proliferation of sperm-creating cells) begins in late autumn (May)

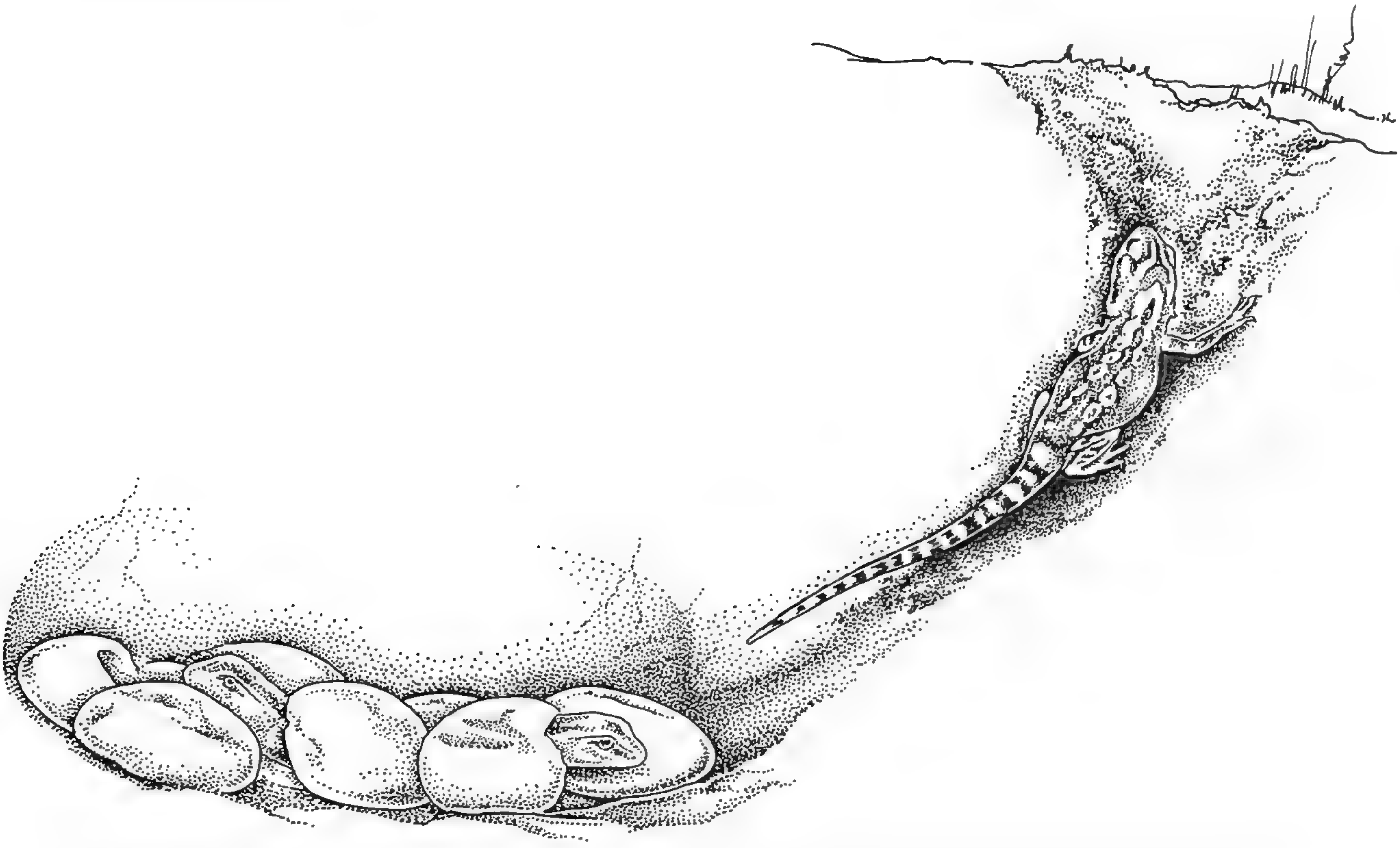

Figure 29.8 Young of *Pogona barbata* emerging from burrow. The young have to re-excavate the tunnel before they can emerge. (After photo by J. Weigel/ANT)
[R. Plant]

and continues through winter into spring. By early September the testes are fully functional and continue to be so until early December. At this stage, testicular function may continue, or the testes diminish in size. In animals with regressing testes the inguinal fat bodies increase rapidly in size. Most males die in January; exceptions are those having regressed testes. Ovarian follicles begin to develop in September and ovulation occurs during October. Corpora lutea develop on the ovary at ovulation and remain until egg laying, which begins towards the end of October. Further follicular enlargement occurs commonly in females with oviducal eggs indicating that second clutches often occur. There is a minimum period of about six weeks between clutches, and a third clutch is theoretically possible. Females, like males, suffer high mortality at the end of December. Females still alive at the end of January also have enlarged inguinal fat bodies, and regressed ovaries. This general scheme fits well with the information available for other Australian agamids.

NATURAL HISTORY

Life History

Ctenophorus ornatus is associated with rock outcrops in Western Australia. Its life history has been well documented and, so far as is known, is typical of agamids.

Adult *C. ornatus* engage in mating behaviour in November. Each female lays two or three eggs during December. Some females may lay a second clutch as the first eggs hatch in January, so that hatchlings may continue to emerge until the end of March. Groups of juveniles are restricted to certain parts of the outcrop soon after their emergence. Apparently harassment by territorial males is one factor that keeps the juveniles together. Harassment and the influx of adults from outlying areas drive most of the juveniles away from their hatching site to the marginal habitats from which the other adults have returned. Although *C. ornatus* is one of the larger species of *Ctenophorus*, some individuals achieve sexual maturity within their first year. Other individuals take two or three years to mature. Males become sexually mature at a snout-vent length (SVL) of 75 mm, and females at 69 mm (Bradshaw 1971).

Bradshaw (1971) classified individual *C. ornatus* as either fast or slow growers on the basis of the time it took them to reach sexual maturity. He found that slow growers were more resistant to drought, but more susceptible to severe winters. The resistance to drought is apparently due to a greater resistance to hypernatraemia (salt loading) in slow growing individuals. Hypernatraemia leads to increased urinary and evaporative heat loss which in turn causes loss of body weight (Baverstock 1975). Slow growers are susceptible to frost because they are forced to take refuge in less favourable retreats than larger animals (Baverstock 1978).

Many of the smaller *Ctenophorus* species are apparently 'annuals' (Storr 1965a, 1967a). There is variation in the timing and length of the breeding season, but it appears that for many populations very few if any adults survived to a second summer. It is possible for adults to be eliminated locally on an annual basis, with the species being represented only by eggs in the ground. Under conditions of low food availability, animals grow far more slowly and live much longer (Cogger 1974). The rapid growth typical of smaller species of *Ctenophorus* has also been recorded in one of the larger species, *C. nuchalis*. These relatively large animals reached sexual maturity in 9 or 10 months, and very few survive for a second summer (Bradshaw 1975).

Ecology

The smaller species of agamids are mainly insectivorous. This is probably more a result of insects being the most common prey available than any deliberate selection by the lizards. *Moloch horridus* eats small ants of the genus *Iridomyrmex* almost exclusively (Greer 1989). At least some of the larger species are omnivorous. *Pogona* species will eat dandelion flowers, and *Physignathus* are also omnivorous as adults (Greer 1989).

Only two Australian agamid genera inhabit forests. *Hypsilurus* is restricted to closed canopy forest, and *Physignathus* occurs along streams in a variety of vegetation communities. Most other species of agamids are found in arid parts of southern Australia. The few species found in the wetter parts of the continent are associated with heaths and open forests. Often these habitats are on poor soils where comparatively short periods without rain create effective desert conditions (Witten 1982b).

Amphibolurus nobbi nobbi in northern New South Wales is unusual in several aspects of its biology. Most individuals congregate in specific localities in autumn, where they hibernate. In spring males emerge first, as in *Ctenophorus maculosus* (Mitchell 1973). Females then emerge, mate and lay a clutch of eggs, after which all adults leave the breeding area. Hatchlings begin to emerge in January and disperse without pressure from larger individuals. Some females returning in autumn are gravid, and presumably lay an autumn clutch. Some hatchlings emerge in October, apparently from over-wintering eggs (Witten 1974).

Behaviour

Most agamids are territorial. Particularly in spring, males take up prominent positions from which they defend territories. The perching site varies between species and even within species. Species of *Lophognathus*, *Amphibolurus* and *Pogona* most commonly defend territories atop vegetation such as a shrub or small tree, or man-made perches such as fence posts and roadside dirt mounds. The more terrestrial species, such as small *Ctenophorus* and *Tympanocryptis*, tend to defend their territories from rocks or termite mounds. For example, on unsealed roads in central Queensland, a male *Tympanocryptis* may be seen every two or three metres sitting atop a dirt lump (pers. obs.).

The defence of territory is visually based in agamids. Use of colour and movement provide two very different methods of signalling to a rival.

Males in prominent positions are in full regalia. Male *Lophognathus gilberti*, for example, are commonly patterned in shades of grey but become black over most of their dorsal surface, with a brilliant contrast of white lips, and a light dorso-lateral stripe. Most males of the *Ctenophorus* group have permanent ventral patterns which are characteristic of the species. Some species become flushed with more spectacular colours. Male *Amphibolurus nobbi* are mainly grey with lemon dorso-lateral stripes and a red-tinted tail base for most of the year. In the breeding season the yellow and red colours become much more intense. The red-barred dragon *Ctenophorus vadnappa* (Pl. 5.4) takes its common name from a series of vertical red stripes on its lateral surface. This species combines brilliant colour with a complex display, which consists of three phases. The first involves orientation towards the intruder, so as to present a lateral view. The gular region is lowered, the trunk laterally compressed, and usually the front leg of either side is circumducted (rotated around in an overarm movement, but with the elbow bent). The second phase consists of a number of hind leg push-ups, during which the tail is coiled and the nuchal and vertebral crests raised. Coiling of the tail may be associated with showing the red or orange ventral surface to the rival, as this colour intensifies during the display. The third phase consists of a head-bobbing sequence (Gibbons 1979).

Circumduction is part of the behavioural repertoire of many agamids. *Lophognathus gilberti* do it so regularly that people interpret the display as bidding farewell, an impression accentuated because circumduction often follows a short sprint. At least some species of *Diporiphora* include circumduction in displays. *Ctenophorus fordi* also circumducts, often after running, but in this species it is not obviously related to territorial or social behaviour (Cogger 1978). Circumduction in *Ctenophorus maculosus* was interpreted by Mitchell (1973) as a deterrent to males by unreceptive females.

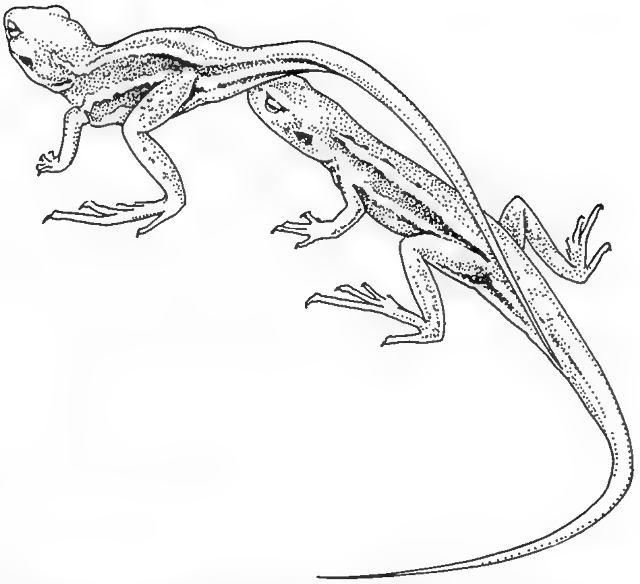
Figure 29.9 Rejection posture of female *Ctenophorus fordi*. [R. Plant]

Many lizards communicate by head-bobbing. This display is apparently useful in species recognition, as the speed and timing of the display is different for most species. Analysis of these displays has led to the definition of a 'display action pattern' which can be used to characterise a particular species (Carpenter 1967). Head-bobbing was elicited in *C. fordi* by the presence of other dragons but it did not respond to skinks in the same manner (Cogger 1978). Head-bobbing may be combined with front leg push-ups. Raising of the anterior part of the body displays the ventral surface of the lizard to a rival or prospective mate. The permanent ventral patterns of some species may be used in this way for species identification.

Copulation, where known, is relatively brief. The male grasps the female by the neck and one hemipenis is inserted for less than half a minute (12 to 23 seconds in *Ctenophorus fordi*; Cogger 1978; about 25 seconds in *C. maculosus*; Mitchell 1973). Copulation was not preceded by any display in *C. fordi* (Cogger 1978). In *C. maculosus* an approaching male 'undertakes a series of energetic head-bobs' (Mitchell 1973).

Ctenophorus fordi performs an extraordinary behavioural act after the main mating season (Cogger 1978). Between October and December, a female responds to the presence of a male by raising her hindquarters to present the cloacal region to the male. The male either ignores her or approaches and 'tastes' her hindquarters (Fig. 29.9), before both lizards move off. This behaviour is apparently not courtship, as mating has never been observed after this interaction. It could constitute a 'rejection posture', signalling to the male that she is not receptive (Cogger 1978). Another 'rejection posture' has been reported in *Ctenophorus maculosus*. In this species the female simply rolls onto her back (Mitchell 1973).

Two agamids apparently lack territorial behaviour — *Ctenophorus fordi* (Cogger 1978) and *Amphibolurus nobbi nobbi* (Witten 1974). Both are smaller than their nearest relatives, and their lack of territoriality may be a neotenic condition (Cogger 1978).

Agamids generally rely on crypsis to escape detection by predators (Pl. 5.1). Once detected, however, they may flee or display aggressively. *Pogona barbata*, for example, opens the mouth to expose its yellow lining and erects the gular region as a 'beard' (Pl. 5.8; Throckmorton, De Bavay, Chaffey, Merrotsky, Noske & Noske 1985). A similar display is given by *Pogona vitticeps* when under attack by a snake (Fig. 29.10).

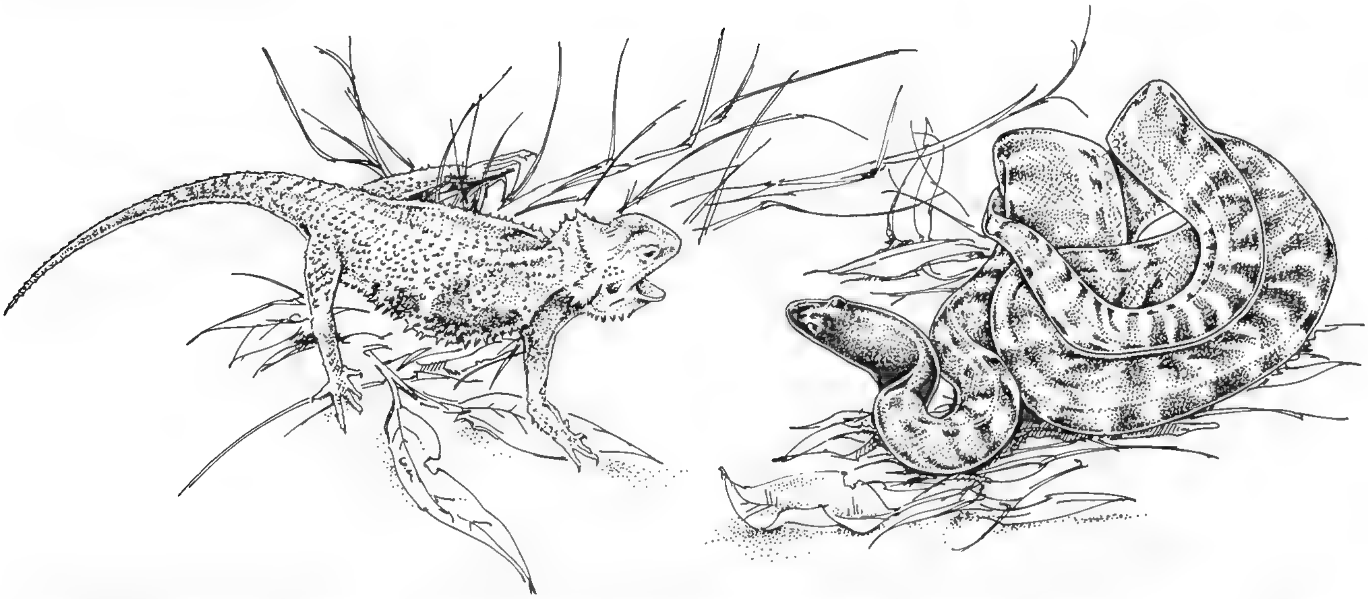

Figure 29.10 Threat display of *Pogona vitticeps*, in response to threatened attack by *Aspidites melanocephalus*. (After photo by D. Stammer) [R. Plant]

Most lizards when active maintain a relatively constant temperature. Most Australian agamids are heliotherms, deriving their heat primarily from the sun. Given the opportunity, as in a laboratory thermal gradient, they will maintain a temperature within a narrow range, and the mean is referred to as the preferred temperature. That of Australian agamids falls in the range 35.5° to 38.2°C (Fig. 25.4), except for *Physignathus*, which is only 30.1°C (Heatwole & Taylor 1987). Preferred temperatures are often a useful indicator of phylogeny (Bogert 1949), so the result for *Physignathus* is remarkable. *Hypsilurus* species are also exceptional. Observations on *H. spinipes* in the field suggest that it makes little or no attempt to regulate its temperature, and field temperatures ranged between 15.5° and 25.1°C (Manning & Ehmann 1991).

In the field, conditions often will not allow regulation of body temperature at the preferred level, so it is more realistic to look at a temperature range over which the animals are normally active. This varies considerably between species, and even within species at different times. For example, Cogger (1974) found that even mild starvation caused *Ctenophorus fordi* to operate at lower activity temperatures.

Different temperatures may also be acceptable under differing physiological conditions. Most preferred temperature determinations have been carried out using animals that have not fed recently. The preferred temperature is higher following feeding, and may be depressed for a variety of reasons apart from starvation (Witten & Heatwole 1978).

Daily activity patterns have been well documented for a number of arid-adapted Australian dragons (Bradshaw & Main 1968; *Ctenophorus nuchalis*, Heatwole 1970; *Ctenophorus fordi*, Cogger 1974; Fig. 24.15), and many features are common to the behaviour of these species. Before commencing normal activity, the lizards bask. During this phase the skin is darker, the body is dorso-ventrally flattened, and is oriented towards the sun thereby facilitating heat uptake. Once warm enough, the lizards begin normal activities, such as foraging or territorial defence. In deserts, temperatures in the middle of the day usually exceed those tolerated by lizards, and different behavioural patterns appear in response to rising temperatures. At first the lizards orient their bodies toward the sun thereby reducing heat uptake, and they seek shade intermittently. If temperatures continue to rise, shelter is sought, often in a burrow or vegetation. As temperatures begin to fall in the afternoon, activity is resumed. Lizards often press their bodies against a warm substrate as the sun recedes and prolong the period of elevated temperature.

One heat avoidance behaviour seen in desert species is 'stilting' (Bradshaw & Main 1968) in which the body is raised as high above the substrate as possible and is supported only on the front toes and the heels of the feet.

In the laboratory, lizards heated to above their preferred range will gape or pant. This behaviour has been observed in the field (Pl. 5.4), but is not common (Heatwole 1970). The level at which panting begins is raised in *Pogona* species by dehydration, but not in *Amphibolurus* (Parmenter & Heatwole 1975).

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Agamids occur in much of the Old World with major centres of diversity in Australia and Asia. Of 33 agamid genera listed by Wermuth (1967) many are endemic to India and Sri Lanka (nine) and the northern part of the Indo-Australian archipelago (five). Others are more widespread in Asia, with a few genera extending westwards into the Middle East. Though two genera extend into Africa (Wermuth 1967), no genus is endemic there.

The areas of highest agamid species diversity are in the southern part of the central Australian deserts and an area of the central coast of Western Australia (Witten 1982b). The wetter areas in the south-west of Western Australia and along the eastern coast have relatively few agamid species. This distributional pattern demonstrates the arid-adapted nature of most Australian agamid genera. A few species from arid genera have penetrated the wetter areas, but these are restricted to habitats with poor soils supporting heaths or open forests. Tasmania has only one agamid species, *Tympanocryptis diemensis*.

Physignathus lesueurii (Pl. 5.3) is riparian in habit, occurring near streams along the entire east coast. Another species occurs in South-East Asia. Presumably the ancestors of *Physignathus* have been displaced in the intervening islands by the related, but more derived, *Hydrosaurus*. *Hypsilurus* has at least two species in Australia, and a further 12 species in New Guinea (Moody 1980). The Australian species are restricted to forests of the east coast.

Affinities with other Groups

The Agamidae, Iguanidae and Chamaeleonidae form the infraorder Iguania (Camp, 1923). The Iguania is apparently the first 'branch' on the squamate evolutionary 'tree', with all other lizards placed in the Scleroglossa (Estes *et al.* 1988), and almost certainly contains the most primitive extant lizards (Camp 1923). It is clearly Gondwanan (Cracraft 1974), as it is not represented in Laurasian fossils until just before the Cainozoic. The iguanids arose in South America (Estes 1983b), although some species in

Madagascar may represent a separate Gondwanan relict (Moody 1980). The Chamaeleonidae evolved in Africa and are still largely restricted to that continent and Madagascar. Only one species occurs on the Indian subcontinent (Welch, Cooke & Wright 1990), and another extends into southern Europe. Agamids are apparently the East Gondwanan representatives of the Iguania. This land mass split to form the modern Antarctica, Australia and the Indian subcontinent (Powell, Johnson & Veevers 1980). The latter two land masses still retain large endemic agamid radiations.

Evidence confirming this hypothesis comes from the fossil record of Europe and Asia. Agamids do not appear in this fossil record until the late Cretaceous or early Cainozoic (see below). Many other lizard fossils are present before this, and all are assignable to families belonging to more derived groups than agamids (Estes 1983b). Presumably agamids had been evolving elsewhere, and invaded Europe and Asia, as there are no obvious ancestors in earlier Laurasian fossils. They almost certainly were passengers on Greater India, a tectonic plate from part of Gondwana. Unfortunately the Gondwanan fossil record for the entire Mesozoic is poor, and the absence of lizard fossils for the period is not surprising.

The Chamaeleonidae are usually assumed to have been derived from the Agamidae (Camp 1923). This has been so widely accepted that Frost & Hillis (1990) used the Agamidae as an example of a paraphyletic group because the Agamidae continues to be recognised as a separate family while presumed descendants (chameleons) are recognised at the same taxonomic level. It is clear that the chameleons arose in Africa (Estes 1983b). The agamids now in Africa are recent immigrants (Moody 1980); there is no genus of agamid endemic to Africa. If the agamids gave rise to the chameleons then they probably did so from a Gondwanan source. Most modern families were in existence by the late Cretaceous (Estes 1983b). The agamids and chameleons belong to the most primitive subdivision of lizards (Iguania), and are assumed to have developed before more derived lizard families. Faunal exchange between Africa and Laurasian land masses would not have occurred early enough to allow the evolution of chameleons from Asian agamids.

A different opinion of agamid origins was recently published by Greer (1989). He suggested that agamids arose 'on the northern landmass and entered southern continents ... relatively late in their history'. He wrote this before Early Miocene *Physignathus* was described (Covacevich, Couper, Molnar, Witten & Young 1990), and would find the statement more difficult to justify now. Moody (1980) also favoured this origin for Australian agamids. He discarded a number of characters because they 'influenced the prediction of common ancestry of the highly derived Australian agamids (*Moloch* and *Chelosania*) and the terrestrial and saxicolous agamid radiation of Africa and Asia'. Moody thus disregarded data which did not fit the accepted Asian origin for agamids and retained data which did. Preliminary biochemical data indicates the Australian radiation is closer to the terrestrial agamids of Asia and Africa than to the arboreal South-East Asian agamids that Moody and Greer considered to be ancestral to the Australian agamids (Baverstock & Donnellan 1990). This is possibly the result of a faster rate of biochemical evolution in the Asian arboreal radiation (Joger 1991). However, chromosome morphology of Asian *Gonocephalus* (Ota, Matsui, Hikida & Mori 1992) indicates that these are unrelated to Australian lizards once placed in the same genus, and confirms the biochemical data.

The proposal to include the Agamidae within the Chamaeleonidae by Frost & Etheridge (1989) is rejected here for three reasons. First, the main feature linking the two groups is their dentition, with both families possessing acrodont teeth (Camp 1923). However, the nearest relative of the Squamata, the Sphenodontida represented by the tuatara *Sphenodon* of New Zealand (Gauthier, Estes & de Queiroz 1988), also possesses acrodont teeth (Robinson 1986) and therefore the character may prove to be ancestral and no more diagnostic of close relationship than any other feature shared by early lepidosaurs. There are fossil sphenodontids with dentition essentially identical to agamids, including the possession of anterior pleurodont teeth (Whiteside 1986). While *Sphenodon* has anterior successional teeth (Robinson 1976), these are no longer pleurodont 'except perhaps for the premaxillary teeth ... where the distinction of pleurodonty and acrodonty becomes somewhat blurred' (Rieppel 1992). It is probable that the first lizards had a similar dentition. This suggestion is not new. Cope (1900) considered acrodont dentition primitive (*fide* Camp 1923). The alternative, that agamids evolved a dentition identical to one already in existence, is much less plausible. If the ancestor of the Iguania had agamid-like dentition then the evolution of the three modern families is simplified. Agamids retained the ancestral condition (29.1B), chameleons lost the pleurodont teeth (29.1C), while the iguanids lost the acrodonts (Fig. 29.1A).

Other differences between the dentition of agamids and chameleons include: the lack of anterior pleurodont teeth in the chameleons (Fig. 29.1C) but presence in at least juveniles of all extant agamids; a gap between adjacent teeth and a smooth lingual tooth in chameleons surface, unlike the swollen inner surface of agamid teeth; and the teeth of chameleons firmly ankylosed to the outer margin of the tooth-bearing bone, not slightly on the inner surface (Moody & Rocek 1980).

Further, even if Agamidae and Chamaeleonidae are shown to be monophyletic, they differ in so many other features that their continued recognition as full families is easy to justify. Estes *et al* (1988) list 85 apomorphies for the Chamaeleonidae, yet only three features unique to the combined taxon 'Acrodonta'. Finally, taxonomists have a responsibility to maintain a stable nomenclature. Changes, particularly at higher levels should only be made with overwhelming evidence. Chamaeleonidae and Agamidae are long established and well-defined groups, and there is simply not enough evidence to overturn them. For the same reason the counter suggestion of Lazell (1992) to include the Agamidae within the Iguanidae is rejected.

Apart from dentition, several characters indicate a closer relationship between the agamids and chameleons than with the rest of the Iguania. One is the meeting of the maxillae between the premaxillae and vomers in the palate (Borsuk-Bialynicka & Moody 1984). Again, 'it is difficult to say if [it is] symplesiomorphic or homoplastic' (= separately derived) (Borsuk-Bialynicka & Moody 1984). This shared character does not appear to be plesiomorphic for lizards as the maxillae in sphenodontids are separated anteriorly by the premaxilla (Gauthier *et al.* 1988). In chameleons the premaxilla is reduced in size, and this reduction, rather than an expansion of the maxillae, may have resulted in the anterior meeting of the maxillae. The explanation for this reduction is logical. Chameleons have lost pleurodont teeth. Premaxillary teeth in both agamids and sphenodontids are pleurodont, and as the ancestors of modern chameleons reduced, then lost, their pleurodont teeth the premaxilla may have been reduced in the process.

The possession of reticular papillae on the tongue is another possible character linking agamids and chameleons (Schwenk 1988). This feature is shared with anoles, and its strength as a phylogenetic indicator is unknown. However, anoles have a similar microstructure of the scales and mechanoreceptors to chameleons (Peterson 1984; Ananjeva, Dilmuchamedov & Matveyeva 1991), but not to agamids or most other iguanids. The phylogeny of the anoles, then, is also uncertain. The honeycomb micro-ornamentation of agamid scales is shared with some iguanids, probably indicating common ancestry (Peterson 1984). Some evidence therefore indicates that agamids may be closer to some iguanids than to chameleons.

Affinities within the Agamidae

The most primitive agamids include *Physignathus* and the Asian genera *Leiolepis* and *Uromastyx* (Moody 1980). The latter two genera have been placed in a separate family, the Uromastycidae, by some (for example, Moody 1983), but more recently have been placed within the Agamidae as a subfamily (Borsuk-Bialynicka & Moody 1984). These genera, including *Physignathus*, have femoral glands in the primitive arrangement with pores opening on the posterior margin of a scale. They possess small tubercular scales which overlap little if at all, and tend to form transverse whorls around the tail. They have smooth labial scales. These genera also possess only lentiform epidermal sensors, a character shared with all Australian agamids, but not other agamids, which have scale sensors with 'hairs' (Ananjeva *et al.* 1991). Another character suggesting this group may form a phyletic group is the possession of a straight ventral suture between the maxilla and palatine bone, parallel to the tooth row; the same suture is angled sharply antero-medially in the main Asian agamid radiation (Moody 1980). If the subfamily Uromastycinae (or Leiolepidinae; Frost & Etheridge 1989) is recognised it should include the Australian agamids as well as *Uromastyx* and *Leiolepis*.

Australian agamids form two distinct groups: the mesic-adapted *Physignathus* and *Hypsilurus* in one, and the larger radiation of arid-adapted species including the large genus *Ctenophorus*. *Ctenophorus* is more derived than *Physignathus* only in the absence of a lacrimal bone. *Chelosania* is not clearly related to either group, but is discussed below with the mesic-adapted group.

Mesic-adapted agamids. *Physignathus* is the most primitive member of this group. With certainty only two other genera, *Hypsilurus* and *Hydrosaurus*, belong in the group. *Hypsilurus* is best represented in New Guinea; only two species occur in Australia. *Hydrosaurus* is restricted to Indonesia and the Philippines. The neural processes of the trunk vertebrae of all members are elongate, enlarge ontogenetically and are better developed in adult males than adult females.

Biochemical data indicate that *Hypsilurus* and *Physignathus* may be more distantly related to the arid-adapted radiation than is *Physignathus* (Baverstock & Donnellan 1990). This is not reflected in the morphology. Morphological features shared by *Physignathus* and *Hypsilurus* could have been present in the common ancestor of all Australian agamids and lost in the arid-adapted radiation. Alternatively, *Hypsilurus* could have undergone more rapid biochemical change since its divergence from *Physignathus*. More data are needed to decide which is more likely. However, *Physignathus* has changed little since the Miocene (Covacevich *et al.* 1990), so the biochemical data could be seen as uncovering old differences masked by morphological conservatism.

The riparian genus *Physignathus* has one Australian species and another in Asia. The lacrimal bone is retained and femoral glands are in the primitive arrangement. The dorso-lateral scales are small, tubercular, and tend to form transverse series, although their keels are aligned in postero-medial series. There are scattered enlarged tubercles which also tend to align in transverse series. The trailing edges of toes have a series of flattened scales which may assist the animal when swimming. This feature is shared with *Hydrosaurus*, in which the scales have developed into a distinct 'web'.

For most of this century *Hypsilurus* was considered part of the Asian genus, *Gonocephalus*. Recent evidence suggests it may be more closely related to all other agamids than to the group containing *Gonocephalus* (Baverstock & Donnellan 1990; Ota *et al.* 1992). It was placed in *Gonocephalus* on the basis of characters developed as arboreal adaptations. The body is laterally compressed, and there are distinctive nuchal and gular skin folds used as visual signalling devices. Femoral glands have been lost, but the lacrimal bone is retained, as it has been in the Asian *Gonocephalus*. The enlarged neural spines of trunk and proximal caudal vertebrae support spectacular crests in some species. This feature is shared with *Physignathus* and *Hydrosaurus*, but not *Gonocephalus* (Moody 1980). The labial scales are smooth and dramatically enlarged in some species, including the Australian *H. boydii* (Pl. 5.7), which also has other enlarged flattened scales on its cheeks.

Chelosania is a monotypic genus confined to northern and north-western Australia. The lacrimal bone is retained, but is smaller than in *Physignathus*. The genus lacks the enlarged neural spines of *Physignathus* and *Hypsilurus*, but the body is laterally compressed. There are five or six skin folds behind the tympanum, each with a row of tubercular scales. The primitive tubercular scales of the trunk are arranged in postero-lateral rows. Nuchal and vertebral scale ridges are present, but femoral glands are lacking. Though very distinctive, its relationships are unclear.

Arid-adapted agamids. These are characterised as a group by the loss of the lacrimal bone (Cogger 1960), and a karyotype with only 20 microchromosomes (Witten 1983). In the absence of a lacrimal, the palatine bone of some species has extended into the lower margin of the orbit where the lower posterior part of the lacrimal would be expected. In some *Pogona* and *Chlamydosaurus* skulls this lateral process of the palatine contributes very little to the orbital margin, if at all. In other genera it contributes an obvious elongate piece of bone. This has been well illustrated by Greer (1989, Fig. 9) for '*Amphibolurus*' *temporalis*, though identified there as the lacrimal. If this is a separate bone, it is likely to have been formed from the palatine process, as *Lophognathus* is apparently highly derived among Australian agamids (see below). As well as the 20 microchromosomes, most members of the group have 12 macrochromosomes. Only some populations of *Lophognathus gilberti* have 20 macrochromosomes (Witten 1983).

Australian arid-adapted agamids form three groups: a large group containing *Ctenophorus* and a number of derived genera; the *Tympanocryptis* group; and the monotypic *Moloch*. The following discussion of phylogenetic relationships is based on a comparison of morphological characters. The group has not been subjected to a formal phylogenetic analysis.

Ctenophorus and derived genera: *Ctenophorus*, containing a number of species groups, includes the least derived species in the arid-adapted group. Perhaps the least specialised species group in *Ctenophorus* is formed by *C. cristatus* and the closely related *C. caudicinctus*. The two species are quite dissimilar in habit. *C. cristatus* is a widespread inhabitant of the mallee across the southern part of the continent. It depends on extreme speed to avoid predation. *C. caudicinctus* is a rock-dweller of the northern half of the continent which, while also a rapid runner, retreats to rocky outcrops for shelter. Both species have relatively large, somewhat heterogeneous dorsal scalation, rather than the primitive tubercular form. There is a tendency towards interscalar pores in both species, and the relative proportions of limbs and tail in both are similar, despite the disparate ecological niches occupied by the two species. Most individuals of both species retain the nuchal and vertebral scale ridges. However, the nuchal scale ridge of *C. cristatus* is both distinctive and unique among the terrestrial Australian agamids. A similar nuchal crest is found in some *Hypsilurus*. In juveniles of both genera a discontinuous nuchal scale row becomes contiguous in adults.

The rock-dwelling *C. decresii* and its relatives are depressed as an adaptation to living beneath rocks; two species are burrowers (*C. pictus* and *C. salinarum*). Most are very brightly coloured animals with pronounced sexual dichromatism. The species-group is probably relatively primitive within the genus. The vertebral scale series is retained in most species, at least in some individuals, and the scales are small and tubercular. The lower eyelid has a denticulate appearance.

Most of the running lizards of the *C. isolepis* group are associated with sandy deserts. The nuchal and vertebral scale ridges are retained and prominent in some species, but have been totally lost in some others. There is pronounced sexual dichromatism in most species, and most males have permanent black ventral markings.

The burrowing *C. reticulatus* group have stout limbs, a relatively deep head and body, and a denticulate fringe on the lower eyelid. Some members of the group have derived pore arrangements. *C. maculosus* has a reduced number of pores, which tend to be concentrated on the medial part of the thigh. *C. nuchalis* has another derived pore arrangement where the femoral pores arch forward on the thigh (Fig. 29.7G). *C. clayi* has a similar arrangement, but the number of pores is reduced. Permanent black markings of males are retained in most members of the group.

Cryptagama contains one small species originally described in the genus *Tympanocryptis* because of its similarity to *Tympanocryptis cephalus* (Pl. 5.1). These similarities are almost certainly independently derived in adapting to a ground-hugging cryptozoic habit. *Cryptagama* retains the primitive arrangement of femoral glands, although the number is reduced. The scales are much smaller in this species than in all other Australian agamids, with the possible exception of *C. clayi*. *Cryptagama* has clear affinities with *Ctenophorus* (Witten 1984).

Pogona shares a derived pore arrangement with *Ctenophorus nuchalis*, as well as the eyelid fringe, and is clearly related to the *C. reticulatus* species group (Witten 1982b). It includes five species referred to as bearded dragons. All species have an expanded gular pouch, and most have some indication of a series of spinose scales across the throat which forms a 'beard'. One or more rows of spinose scales occur along the side of the trunk. All species have strongly heterogeneous dorsal scalation which tends to break up the outline of the lizard and contribute to camouflage. The vertebral scale row has been lost.

Some specimens of *P. minor* from the west of the continent have a pore arrangement similar to that of *Amphibolurus*, with the more medial preanal pores more posteriorly placed, and an inguinal gap in the pore series. It seems probable that both *Chlamydosaurus* and the *Amphibolurus* group share an ancestor with *Pogona*.

Four genera form the *Amphibolurus* group: *Amphibolurus*, *Diporiphora*, *Caimanops* and *Lophognathus*. They are not strongly differentiated, and further study may lead to the species within these genera being included in *Amphibolurus*. The *Amphibolurus* group has lost the primitive gland arrangement; all members have the medial preanal glands more posteriorly placed, and the femoral glands, if present, form a separate series (Fig. 29.7H). The group also has ridged labials, presumably a derived feature. No member of the group has retained transverse whorls of scales on the tail. The phylogeny within the group is not clear. Presumably *Diporiphora*, the largest genus of the group, is the most derived because most species have lost femoral pores and the midline scale ridge. *Lophognathus* is distinguished by a brilliant white lip stripe and is more arboreal than most other arid-adapted agamids. *Caimanops* lacks femoral pores, which leaves *Amphibolurus* as the least derived genus of the group.

Diporiphora superba (Pl. 5.5) deserves special comment as the single truly arboreal species of the arid-adapted radiation of Australian agamids. It is green in colour and is so slender it gives the impression of being badly emaciated. It also has an extraordinarily long tail, sometimes in excess of four times the snout-vent length. A species of *Diporiphora* is the most heat resistant Australian dragon recorded (Bradshaw & Main 1968).

The frilled lizard *Chlamydosaurus* has usually been placed within the *Amphibolurus* group (Cogger 1960; Witten 1982a, 1982b). The arrangement of preanal glands is similar, but the condition is not as regular as in the other genera of the group. Other characters shared with the *Amphibolurus* group such as a relatively long tail may represent adaptations to an arboreal habit. *Chlamydosaurus* and *Pogona* share a narrow premaxilla and an expanded gular pouch, features not present in *Amphibolurus*, and both have lost a vertebral scale ridge. It is likely that *Chlamydosaurus* and *Amphibolurus* both descended from a *Pogona*-like ancestor, but independently.

Tympanocryptis group: members of this group are all small cryptic terrestrial species, typified by the possession of interscalar pores and heterogeneous dorsal scales. Some members retain the primitive gland arrangement, but the scalation of all members is modified from the presumed primitive condition. All members possess ridged labials, which is probably another derived condition. Ridged labials occur in the *Amphibolurus* group, but no member of that group retains the primitive pore arrangement. The *Tympanocryptis* group is therefore not closely related to any other member of the arid-adapted group. However, the phylogeny within this group is clear. *Tympanocryptis adelaidensis* and *T. diemensis* are the most primitive members of the genus. Each has a tympanic membrane and has prominent spines on the base of the tail. The arrangement of preanal and femoral glands is also primitive. Both species often have a nuchal scale ridge. *Tympanocryptis parviceps* is intermediate between the *T. adelaidensis* species group and the *T. lineata* species group. This species retains the primitive arrangement of their preanal and femoral glands, but has lost a functional tympanum. One phalanx from the pes is variable in occurrence, being present in some individuals (Moody 1980), but lost in most (Greer 1987a). The advanced *Tympanocryptis* have lost a functional tympanum and one phalanx of the pes. The number of preanal and femoral glands is reduced to either two or four. Because of the interscalar emergence of these pores they are often not visible in small specimens or females, but reflection of the skin allows the glands to be seen clearly.

Moloch: the single species in this genus is the most dramatically modified Australian agamid (Pl. 5.6). It is extremely spiny, with even the ventral surface having some strongly spinose scales. There is a distinctive nuchal hump on the neck which may serve as a decoy to distract predators from the diminutive head. The digits are very short, the number of phalanges being reduced relative to other Australian agamids. All scales are tubercular, abutting adjacent scales without overlapping. Femoral glands are absent. The acrodont teeth are oblique and the pleurodont teeth have been lost. Despite the extreme morphological changes, biochemical data suggest *Moloch* is a relatively recent derivative from within the arid-adapted radiation (Baverstock & Donnellan 1990).

Fossil Record

The earliest agamid fossils are from the upper Cretaceous of Mongolia, and have been placed in the subfamily Priscagaminae (Borsuk-Bialynicka & Moody 1984). This group includes the genera (*Priscagama* and *Pleurodontagama*) and *Mimeosaurus crassus*. Originally *M. crassus* was referred to the Chamaeleonidae (Gilmore 1943). The Priscagaminae comes from a deposit containing many fossils originally referred to the Agamidae but later transferred to other families. Gilmore (1943) described *Macrocephalosaurus* and *Conicodontosaurus* as agamids. *Macrocephalosaurus* was later transferred to its own family, the Macrocephalosauridae (Sulimski 1975), and Moody (1980) considered that *Conicodontosaurus* belonged in the same family within the Scincomorpha. Sulimski (1972) described *Adamisaurus* in the Agamidae, but later (1978) transferred it to its own family. These fossils have a dentition which resembles the acrodont condition, but is, in fact, a pleurodont dentition modified so that the teeth are placed higher on the tooth-bearing bone (Sulimski, 1978). *Pleurodontagama* lacks the most diagnostic characteristic of agamids. The inclusion of the Priscagaminae in the Agamidae may prove correct, but should be carefully assessed in the light of its associated fauna.

When describing *Pleurodontagama*, Borsuk-Bialynicka & Moody (1984) suggested it may be one of the last agamids to retain an all pleuront dentition. As modern agamids retain anterior pleurodont teeth it could equally be argued that *Pleurodontagama* has lost the ancestral mixed dentition. Carroll's (1988b) argument that streptostyly may have favoured pleurodont dentition in most lizards supports the latter idea.

The earliest undoubted fossil agamid, *Tinosaurus*, is common in Eocene deposits of both North America and Asia (Hecht 1959; Hoffstetter 1962). *Palaeochamaeleo* of the late Eocene of Europe is referable to the modern genus *Uromastyx* (Moody 1980; Estes 1983b). Agamids, some of them relatively modern, thus make a sudden appearance in the Eocene.

29. FAMILY AGAMIDAE

Until the last few years all agamid fossils reported from Australia were relatively recent, from the Pliocene or later (Molnar 1982a). Research on the extensive Riversleigh fauna has yielded several agamids from the Miocene including apparently modern *Physignathus* (Covacevich *et al.* 1990). Another genus from Riversleigh, *Sulcatidens*, is now extinct.

The Riversleigh fauna is mainly of Miocene age, with a few deposits extending back into the late Oligocene (Tyler, Hand & Ward 1990). Miocene *Physignathus* has so far only been identified from jaw bones, both upper and lower, which carry the distinctive acrodont teeth of agamids. *Sulcatidens* takes its name from its modified dentition. The four posterior teeth of the maxilla are notched anteriorly so that the tooth in front is partly enclosed. Such posterior teeth are almost square in shape, and distinct from the triangular shape of most other agamids. Apart from *Physignathus* and *Sulcatidens*, other agamid fragments have not been assigned to any genus (Covacevich *et al.* 1990). These fragments suggest quite an extensive agamid fauna present in the Miocene, and may well represent ancestors of the large modern arid-adapted radiation. The presence of Miocene *Physignathus* which are very similar to the modern form should not be surprising, since it is one of the world's most primitive lizards.

The existence of modern genera in the Australian Miocene and the European Eocene (*Uromastyx*: Moody 1980; Estes 1983b) highlights the extraordinary conservatism of agamids as a group. This is further emphasised by the fact that *Uromastyx*, which almost certainly evolved on the Indian tectonic plate, has its centre of greatest diversity in north-western India (Moody 1980).

30. FAMILY VARANIDAE

Dennis King & Brian Green

GENERAL DESCRIPTION AND DEFINITION

Australian varanids have long and slender necks, long bodies with strong, muscular tails, and well-developed, pentadactyl limbs with a strong claw on each digit. Autotomy does not occur. The whole body is covered with thick, loose-fitting skin with small, juxtaposed scales. The scales on the head are small. The eyelids are movable, and the tongue is extremely long, slender and deeply forked at the tip.

Approximately 40 species are known, all included in the single genus *Varanus*. At least 25 of these occur in Australia, where they are known as goannas. They are medium to large in size and are active, diurnal hunters (Pl. 5).

HISTORY OF DISCOVERY

The Nile Monitor, *Varanus niloticus*, was the first varanid named by Linnaeus in 1758, as *Lacerta monitor*. White (1790) described the first Australian species, *Varanus varius* (as *Lacerta varia*), from a specimen probably collected near Botany Bay, New South Wales. The holotype is presumed to be lost. *Varanus varius* was next referred to by Daudin (1802), and a designated holotype, from Sydney, New South Wales, is held in the Museum National d'Histoire Naturelle in Paris. Merrem first used the generic name *Varanus* in 1820.

Other Australian species were named during the remainder of the 19th and throughout the 20th century, as more of the continent became accessible to scientists. Thus up to 1869, all of the described species had coastal distributions, but more species were named from specimens collected on several of the major explorations into the deserts of central Australia between 1885 and 1903. Most new species described since 1942 were from northern Australia, or were named during revisions of previously described species. Several species that are currently recognised within Australia are still undescribed.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

The snout is elongate, the nares range in position from near the tip of the snout to close to the eyes (Bellairs 1949). The long, forked tongue fits into a sheath on the floor of the mouth (Smith 1986). The tail is round or laterally flattened in cross section, and its length in relation to the snout-vent length (SVL) is variable, ranging from approximately 100 to 220% in Australian species (Cogger 1975a). *Varanus* shows the widest size range of any vertebrate genus; adults of the smallest species (*V. brevicauda*) weigh approximately 17 g and reach a total length of 200 mm (James pers. comm.; Pl. 5.13), while adults of the largest species (*V. komodoensis*) can exceed 70 kg and are reported to reach a total length of 3.5 m (Auffenberg 1981). *Varanus salvator* and *V. giganteus*, respectively are the next largest species in terms of body mass. It is reported that *V. salvadorii* can reach a total length of over 4 m because it has an exceptionally long tail, but no specimens of that length have been documented.

Body Wall

The skin is loose and is covered by small, juxtaposed scales, and the scales on top of the head are small and fragmented (Cogger 1975a). There is a distinct, clear parietal scale on the top of the head.

Skeletal System

Cranial kinesis occurs in varanids, whereby the upper jaw can move independently of the rest of the skull (Rieppel 1979). This facilitates the functioning of the dentition and the swallowing of prey. The teeth are recurved and laterally compressed, and have serrated edges in some species (Greer 1989). The hyoid apparatus has greater mobility than in most lizards (Smith 1986), which assists in the movement of prey into the oesophagus. The roof of the nasal capsule is covered only by skin and connective tissue, unlike other lizards (Bellairs 1949).

Varanids have one cervical vertebra additional to those found in other lizards and the vertebrae are elongated. There is little variation in the number of pre-sacral vertebrae (27 to 32), and the number of post-sacral vertebrae varies from 56 to 139 in Australian species (Greer 1989).

The hemipenes contain ossified hemibaculae, and differences in the morphology of these structures have been used in constructing phylogenies of varanids (Branch 1982; Böhme 1988).

Locomotion

Terrestrial locomotion is generally quadrupedal, with a slow, swinging gait. A large varanid ambling through the bush in an almost arrogant manner, with its tongue flickering through the air, is very impressive.

Occasionally varanids raise the body and forelimbs from the normal position and run bipedally. Many species are arboreal as adults, particularly the smaller species. Some of the larger species, such as *V. tristis* and *V. varius*, also climb trees, and arboreal habits are common in the young of some of the larger species, including *V. komodoensis* (Auffenberg 1981) and *V. varius* (Weavers 1983). *Varanus varius*, *V. tristis*, *V. scalaris*, *V. gilleni* and *V. caudolineatus* often use tree holes and loose bark as shelters, and *V. prasinus* is aided by its prehensile tail when climbing (Greene 1986). Species such as *V. glauerti* (Pl. 5.11), *V. glebopalma* and *V. kingorum* are primarily saxicolous.

Several species (*V. indicus*, *V. mertensi*, *V. niloticus*, *V. salvator*, *V. semiremex*) are amphibious and most species, including some from Australian deserts, can swim well. When swimming, the limbs are held loosely alongside the body and horizontal strokes of the tail and undulations of the whole body are the main means of propulsion (Cowles 1930). Amphibious forms have a dorso-ventrally flattened tail, apparently to assist in swimming and, in *V. mertensi* (Hermes 1981) and *V. salvator*, to assist in hunting aquatic prey.

Feeding and Digestive System

Varanids possess large Jacobson's organs which are located in the front of the nasal capsules in the roof of the mouth. They augment the nose, and appear to play a major role in detecting prey by smell

(Bellairs 1949). They are connected by ducts to the nasal sacs and enable the lizard to detect scent particles which have been collected from the air by the tongue and delivered to the roof of the mouth near the openings to the Jacobson's organs. A flickering tongue is highly characteristic of a foraging varanid (Pianka 1986). The tips of the deeply incised tongue move separately, thereby increasing the volume of air they sample and the scent particles they collect (Smith 1986). When the tongues of varanids are extended, they can increase in length by 70 to 90% (Smith 1986).

The tongue plays no part in manipulating prey (Smith 1986). Varanids use inertial feeding, movements of the neck, and the hyoid apparatus to force the prey down the throat and into the simple stomach. Small prey are swallowed whole. Large prey or carrion are dismembered by holding them with the forefeet and using the sharp teeth and jerking movements of the head to tear off pieces of the carcass (Auffenberg 1981). The tongue is protected in its sheath on the floor of the mouth during feeding (Smith 1986) and when the food has reached the throat, the hyoid apparatus moves it back into the oesophagus (Smith 1986). The neck is then twisted from side to side to help move the food further down the throat. Sometimes large food items are forced down the throat by ramming; the lizard places the food item against a firm structure and pushes against it.

Circulatory System

Although reptiles do not possess a diaphragm, varanids (and *Heloderma* and *Lanthanotus*) have a well-developed septum that separates the thoracic and abdominal cavities.

The varanid heart is not a typical lizard heart. It is located further posterior in the body cavity than in other lizards and is surrounded by a thick pericardium. Oxygen transport by the blood is enhanced due to the arrangement of the chambers and valves, which results in limited ventricular mixing of pulmonary and systemic blood streams (Webb, Heatwole & De Bavay 1971; Heisler, Neumann & Maloiy 1983). Systemic blood pressure also exceeds pulmonary blood pressure because of the contact between a muscular ridge (muskelleiste) in the ventricle and the exterior wall of the heart during systole (Heisler *et al.* 1983) and effectively creates a four-chambered heart at that stage and largely separates the systemic and pulmonary blood streams.

During changes in body temperature, the pH of the blood is closely regulated by buffers, which enables a high level of oxygen transport and aerobic activity to continue (Bennett 1973a).

Varanids also have higher levels of myoglobin in the muscles than other lizards (Bennett 1973a), which facilitates the rapid transport of oxygen from blood to muscles.

Respiration

The intra-pulmonary ducts in the lungs are reinforced with cartilage and connect with a number of small chambers (multi-cameral). The lungs are larger than those of most other reptiles (Perry 1983). They provide an enlarged surface for gas exchange and a starting point for the evolution of high performance lungs which have large surface areas and can be ventilated easily at a low energy cost (Perry 1983). The lungs are attached directly to the body wall under the rib cage, have a strong compliance with body movements, and are efficiently ventilated by costal breathing alone. The gas exchange strategy is convection-dominated and the lungs do not have to be actively deflated like those of most lizards (Perry 1983).

Varanids have a greater aerobic capacity than other reptiles (Bartholomew & Tucker 1964; Bennett 1972) and, except for amphibious forms under water, do not function anaerobically for the long periods shown by other reptiles. Generally they maintain low blood levels of lactic acid through efficient blood buffering and gaseous exchange in the lungs (Hicks, Ishimatsu & Heisler 1987). Varanids can thus repay their oxygen debt quickly after exertion.

Table 30.1 Water turnover rates of free-living varanid lizards in spring (sp) and summer (su).

Species	Season	Weight (g)	Percent body water	Water turnover (ml/kg/day)
V. acanthurus	sp	60	70.3	15.9
V. griseus	su	350	77.9	28.3
V. gouldii	su	493	77.0	23.5
V. rosenbergi	su sp	1086 1089	76.7 76.5	22.0 15.8
V. varius	su sp	4300 –	72.7 –	24.6 15.0
V. giganteus	su	7700	68.4	22.3
V. komodoensis	su	45000	74.9	25.5
Tropical varanids				
V. bengalensis	–	2560	–	60.5 76.9
V. salvator	–	7600	74.9	54.4

The chemical control of ventilation of the lungs is rapid and efficient (Glass, Wood, Hoyt & Johansen 1979) which increases and maintains their high level of performance. The advanced structure and performance of the lungs and circulatory system allow varanids to respire efficiently for long periods without becoming exhausted. These adaptations enable them to adopt an active, wide-ranging foraging strategy.

Excretion

Six species of varanid are closely associated with water, including the Australian species *V. mertensi* and *V. semiremex*. However, most species inhabit environments that are arid or semi-arid for substantial parts of the year. Evaporative water loss in varanids is low compared to that of most other squamates (Green 1969).

Renal studies show that *V. rosenbergi* and *V. gouldii* can regulate glomerular filtration rate, tubular reabsorption and secretion, and ureteral urine flow over a broad range in response to different environmental and experimental conditions (Green 1972; Bradshaw & Rice 1981). The ureteral urine is passed into the coprodaeum of the cloaca, where further water is removed from the excreta by solute-linked sodium transport (Braysher & Green 1970). Renal and cloacal function is regulated mainly by the anti-diuretic hormone arginine vasotocin (AVT) (Braysher & Green 1970; Green 1972; Bradshaw & Rice 1981), circulating levels of which vary in response to the lizard's environmental state (Rice 1982). The water contents of urinary pellets are quite low when they are finally expelled (Seshadri 1959; Green 1969) and the amount of water lost relative to nitrogen excreted is much lower even than in the urine of desert mammals (King & Green 1993).

Excess cations can be excreted via the nasal salt glands that have been identified in several varanid species, such as *V. rosenbergi* and *V. semiremex* (reviewed by Minnich 1979). Sodium is the main cation secreted by the salt glands of varanids, reflecting the predominance of this ion in their prey and habitats. The nasal secretion of hyperosmotic sodium facilitates the sodium-linked reabsorption of water from the kidney tubules, cloaca and rectum.

Field studies have been made of the total water fluxes of a number of varanids (Table 30.1). Clear seasonal patterns of water use are evident in *V. rosenbergi* and *V. varius* (Green 1972; Weavers 1983), and the water fluxes of some tropical species appear to be substantially higher than in species from semi-arid/arid environments.

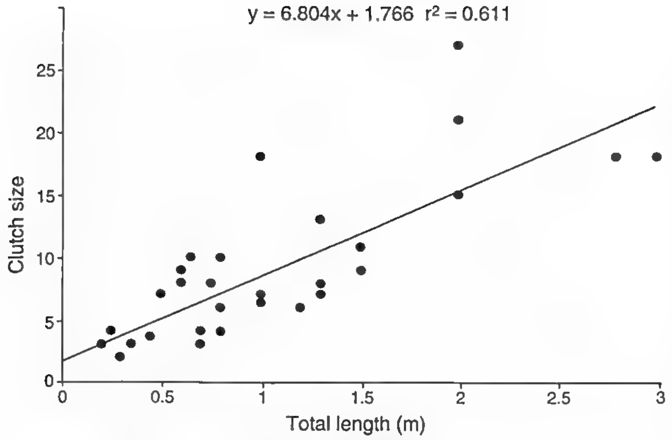

Figure 30.1 The relationship between clutch size and body size in varanid lizards. (After King & Green 1993) [W. Mumford]

There are few reports of metabolic rates in free-living varanids. However, it seems clear that seasonal variations are marked (Green, Dryden & Dryden 1991) and tropical species show higher CO_2 production rates than non-tropical forms (Dryden, Green, King & Losos 1990).

Sense Organs and Nervous System

Varanids rely heavily on the tongue, which collects scent particles and transfers them to the Jacobson's organs, to provide sensory stimuli during hunting and reproductive behaviour (Auffenberg 1981, 1988; Smith 1986). Vision seems less important than smell in food detection (Auffenberg 1988).

Reproduction

Some Australian and African species of varanids have sex chromosomes with female heterogamety (King & King 1975; King, Mengden & King 1982).

All varanids are oviparous. Clutch size is positively correlated with body length (Fig. 30.1) in varanids, (King 1991). In some species, gravid females become so distended with eggs that they are unable to feed for several weeks prior to egg laying (Auffenberg 1988).

Although captive animals are able to produce two clutches a year (Horn & Visser 1989), wild varanids apparently breed only once a year.

Some species (*V. rosenbergi, V. varius, V. giganteus, V. gouldii, V. albigularis, V. niloticus, V. bengalensis*) lay their eggs in termite mounds (Cowles 1930; King & Green 1979; Carter 1990; Branch 1991) which maintain their temperature above 25°C, with high humidity, throughout winter (Green, MacKelvie & Rismiller unpub. data). This provides perfect conditions for the development of reptile eggs. Other species simply bury their clutch deep in the soil, while *V. olivaceus* reportedly lays its eggs in hollow trunks and limbs of trees (Auffenberg 1988). Some species appear to deposit their eggs in communal warrens (King & Green 1993).

The timing of breeding varies substantially between species and there can be marked differences between localities within a species (King, Masini & Robinson unpub. data), or between species at a particular locality, particularly in the tropics (Shine 1986d; James *et al.* 1992).

The age of sexual maturity for most species is not known, but it probably occurs at an older age in large species that in small species. It is estimated that *V. komodoensis* take about five years to mature (Auffenberg 1981) and four to six years in *V. albigularis* (Branch 1991). *Varanus olivaceus* reaches sexual maturity at about three years old (Auffenberg 1988). Captive *V. varius* bred at the age of seven to eight years (Horn & Visser 1991). It has been estimated that wild *V. acanthurus* may reach sexual maturity in one to two years (King & Rhodes 1982).

Embryology and Development

Incubation times in the field for the eggs of different species which do not lay in termitaria are variable, and range from an estimated 90 to 120 days in *V. acanthurus* (King & Rhodes 1982) to 250 or 265 days for eggs of *V. komodoensis* (Auffenberg 1981). Incubation times at similar temperatures in captivity vary from approximately 75 to 250 days (Horn & Visser 1989), and are related to maternal body size (Fig. 30.2; King 1991).

Growth rates of the young of all species are rapid during the first three months after hatching, and adult size is reached within one to two years in the smaller species (King & Rhodes 1982; Horn & Visser 1991), whereas the larger species may take up to five years to reach adult size (Auffenberg 1981; Horn & Visser 1991).

NATURAL HISTORY

Life History

There are few data on the longevity of varanids in the wild, on their age of maturity or age specific fecundity, or on other demographic parameters (Auffenberg 1988). Several species (*V. komodoensis, V. albigularis, V. niloticus*) have been held in captivity for periods of 15 to 20 years, suggesting long life spans are also possible in the wild (Auffenberg 1981; Branch 1991). Auffenberg (1981) agreed with Darevsky's (1963) estimate of a probable lifespan of 50 years for *V. komodoensis* in the wild.

The sex ratios of varanids in museum collections are often strongly biased in favour of males (King & Green 1979) but this is probably a result of differences in activity patterns between the sexes (King & Rhodes 1982).

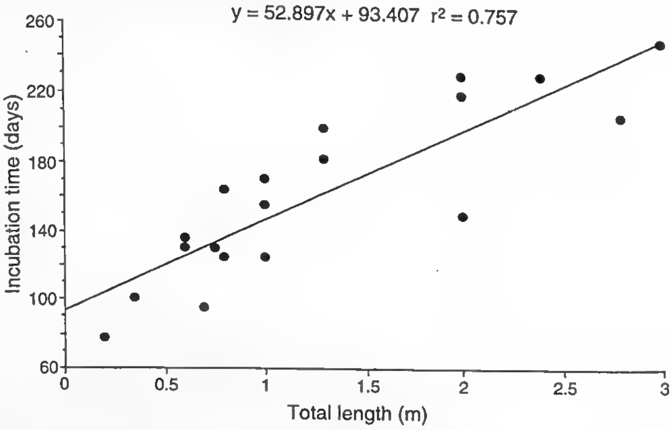

Figure 30.2 The relationship between incubation time and body size in varanid lizards. (After King & Green 1993) [W. Mumford]

Ecology

Varanids utilise a wide variety of habitats, ranging from aquatic to terrestrial and arboreal, and from arid deserts to temperate shrublands with tropical forests (Cogger & Heatwole 1981).

Most varanids forage over large areas (Green, King & Butler 1986; Pianka 1986; Vernet, Lemire & Grenot 1988a). Population densities of varanids are generally low (Stanner & Mendelssohn 1987) although there are some exceptions (Auffenberg 1981). There are no indications that any of the six species of varanids whose movements have been well studied using radiotelemetry (*V. rosenbergi, V. komodoensis, V. olivaceus, V. varius, V. griseus, V. giganteus*) are territorial (Green & King 1978; Auffenberg 1981, 1988; Weavers 1983; Stanner & Mendelssohn 1987; King *et al.* 1989; Vernet, Lemire Grenot & Francaz 1988b). All six species have well-defined home ranges or activity areas. These overlap extensively, within and between sexes (Green & King 1978; Auffenberg 1981, 1988; Weavers 1983; Stanner & Mendelssohn 1987; Vernet et al. 1988b; King *et al.* 1989) and are highly variable in size. The activity areas of *V. olivaceus* are much smaller (Auffenberg 1988) than predicted by the formula of

Turner, Jennrich & Weintraub (1969) on the basis of body mass, perhaps because of the importance of fruit in their diet (Auffenberg 1988). Those of the other species are larger than predicted, and all of those are strictly carnivorous (Stanner & Mendelssohn 1986). There is a positive correlation between the size of individual *V. komodoensis* and the size of their foraging areas (Auffenberg 1981). The home ranges of males are larger than those of females (Stanner & Mendelssohn 1987; Auffenberg 1988), and male varanids are more active than females (Auffenberg 1981; Stanner & Mendelssohn 1987).

The sizes of home ranges/activity areas are strongly influenced by seasonal conditions in *V. rosenbergi*, being larger in summer and smaller in spring and autumn. The animals generally do not move far away from the immediate vicinity of their burrows in winter (King & Green 1993).

Varanids are generally solitary and they are almost exclusively diurnal (Cogger, Cameron & Cogger 1983a), although some rock-dwelling species may occasionally be crepuscular (Wilson & Knowles 1988). They are also strictly carnivorous (Pianka 1986), with one exception (Auffenberg 1988). As far as is known all species are wide-ranging foragers (Pianka 1986). Most varanids eat a variety of invertebrates, including insects, molluscs and crustaceans, and an occasional large vertebrate (Losos & Greene 1988). Even some relatively large varanids (*V. gouldii, V. griseus, V. indicus, V. rosenbergi*) include considerable numbers of invertebrates in their diets (Dryden 1965; Cissé 1972; King & Green 1979; Stanner & Mendelssohn 1986), and they appear to be opportunistic predators. They forage over large areas and investigate fallen logs, burrows, nesting areas of birds or reptiles, leaf litter, crevices and recently disturbed areas, and will apparently eat almost anything they can capture (Losos & Greene 1988). Varanids can chase prey over long distances (Bennett 1973a).

As the size of the species of varanid increases, the range in size of the prey species broadens (Losos & Greene 1988; King unpub. data), and adults of some of the larger species (*V. giganteus, V. glebopalma, V. komodoensis*) specialise in feeding on vertebrates (Auffenberg 1981; King, Green & Butler 1989; James, Losos & King 1992). Large *V. komodoensis* use sit-and-wait tactics and ambush pigs, deer and other large mammals beside game trails (Auffenberg 1981). Adults of the large species, such as *V. komodoensis, V. rosenbergi, V. salvator* and *V. varius* are able to dismember carcasses (Losos & Greene 1988; King & Green 1993) and frequently consume carrion. Smaller varanids consume their prey whole (Losos & Greene 1988).

Cannibalism has been recorded in several species of varanids, including *V. rosenbergi, V. komodoensis* and *V. giganteus*, (King & Green 1979; Auffenberg 1981; King *et al.* 1989).

Intraspecific differences in diet occur and generally reflect prey availability, habitat use or seasonal abundance of prey (Shine 1986d; Losos & Greene 1988; King *et al.* 1989; James *et al.* 1992; Thompson & King in press). Some species, such as *V. dumerili, V. mertensi, V. mitchelli* and *V. semiremex*, do specialise and primarily eat aquatic forms (Krebs 1979; Shine 1986d; Losos & Greene 1988; James *et al.* 1992), while species in Australian deserts such as *V. eremius* and *V. gouldii* (Pl. 5.10) prey heavily on the abundant and diverse lizard fauna (Pianka 1982). Eggs of birds or reptiles are frequently eaten by a number of species, such as *V. rosenbergi, V. tristis* and *V. giganteus* (King & Green 1979; Pianka 1982; King *et al.* 1989).

The diet of the arboreal *V. olivaceus*, from the southern Philippines, contains many invertebrates, however it also includes a large amount of fruit at some times of the year, particularly between May and September (Auffenberg 1988). A few other species of varanids have been reported to eat fruit in captivity but no others include vegetation in their diet in the wild (Auffenberg 1988).

Parasites

Varanids tolerate large numbers of internal and external parasites, seemingly with little or no discomfort or harmful effects. All species of varanids harbour a range of nematodes in their gastrointestinal tract. In Australia, these worms are generally species of *Abbreviata*. Each species usually occurs in several *Varanus* species, but some are specific to one host species (Jones 1985a). Each host species usually has one or two dominant species of nematodes, but may have four or more species

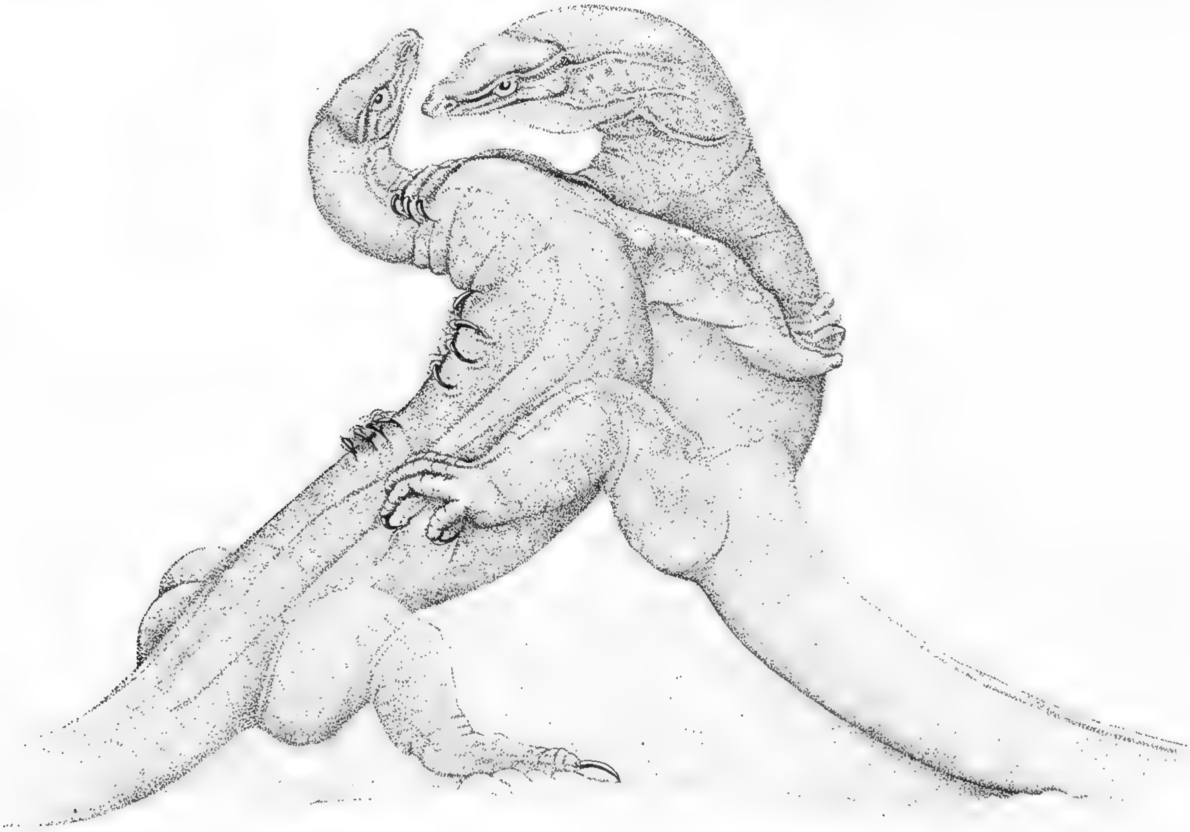

Figure 30.3 Male ritual combat in *Varanus gouldii*. (After photo by D. & T. O'Byrne/ANT) [T. Wright]

parasitising them (Jones 1988). Almost all adult *V. rosenbergi* support numerous *Abbreviata antarctica* in their digestive tracts (Jones 1983). These nematodes can mature in either *V. rosenbergi* or in several species of elapid snakes. Their intermediate hosts are arthropods.

Cestodes occur commonly in the intestines of varanids and their larvae often are found in large numbers under the skin or in the connective tissue of the lizards (Auffenberg 1981).

Pentastomes of the genus *Elenia* parasitise varanids from the Australian region (Bosch 1991). The intermediate host is a vertebrate (amphibian, reptile or mammal) although auto-infections can also occur. Sexually mature parasites occur in the mouth–throat region of varanids.

Protozoans, particularly *Entamoeba* species and *Isospora* species., are also abundant in the gastrointestinal tracts of some species of varanids (Keymer 1981).

Varanids also host blood parasites, such as the protozoans *Trypanosoma* species and *Hepatozoon* species (Keymer 1981) and malarial plasmodia (Auffenberg 1988), but their effect on the lizards is unknown.

Ticks and mites are very common on monitors. Most ticks found on goannas in Australia belong to the genera *Amblyomma* or *Aponomma* (Roberts 1970; Sharrad & King 1981), and *Aponomma fimbriatum* is a common external parasite of *V. rosenbergi* and *V. gouldii* (Sharrad & King 1981). These ticks generally attach themselves to the chest, at the base of the tail behind the cloaca, between the eyes and the nares, in the nares, or in the axillary regions. Up to 30, or occasionally more, of these ticks can be found attached to an individual.

Although various species of mites occur on varanids, they are not usually present in high numbers.

Behaviour

During courtship and mating, licking, stroking and scratching are used by the male to maintain the close attention of the female (Auffenberg 1988; Carter 1990; King & Green 1993).

During the breeding season, males engage in ritual combat behaviour, which involves bipedal clinches and wrestling by the larger species (*V. bengalensis, V. gouldii, V. komodoensis, V. mertensi, V. salvator, V. spenceri, V. olivaceus, V. varius*). They clutch each other with the forelegs only (Fig. 30.3), and try to overpower their opponent, which may result in the animals rolling on the ground. Occasionally, in some species, the victor may bite (*V. gilleni, V. komodoensis, V. niloticus, V. olivaceus, V. varius*), but apparently not in others such as *V. bengalensis* and *V. salvator* (Horn 1985; Auffenberg 1988; Twigg 1988). Severe wounds are sometimes inflicted by teeth or claws. Combat in the smaller species (*V. gilleni, V. semiremex, V. caudolineatus, V. timorensis*) does not include a bipedal phase, but mainly involves clutching with the forelegs and hindlegs and body-arching (Horn 1985). There appears to be a phylogenetic basis to this behavioural difference (Horn 1985).

Male *V. varius* with large wounds are often observed during the mating season, which suggests strong competition for mates (Carter 1990). Interspecific defensive behaviour involves a number of aggressive postures, such as assuming an upright threatening posture (Fig. 30.4), elevating the body on all four legs, inflating the gular pouch and tail-lashing, as well as the display of weaponry, including teeth (Auffenberg 1981; Auffenberg 1988). Hissing is used as a vocal threat (Auffenberg 1981).

Female varanids may mate frequently with one or several males over a period of a few days, and groups of males have been observed trying to mate with one female (Carter 1990). During mating, they communicate via olfactory, visual and tactile stimuli (Auffenberg 1981; Carter 1990). Both hemipenes are used, usually alternately, during copulation (Carter 1990; King & Green 1993).

Figure 30.4 *Varanus panoptes* in bipedal threat display. (After King & Green 1993) [T. Wright]

A pair of *V. rosenbergi* will spend about 10 days engaged in intermittent copulation. Each bout of copulation lasts about 10 minutes. Between these bouts the female often retreats to the shared burrow. The male subsequently enters the burrow and coaxes the female outside by extensive licking, and by rubbing her body with his head. The male uses the base of his tail and his hind limbs to raise the females hindquarters sufficiently to enable penile penetration (King & Green 1993). In *V. bengalensis, V. komodoensis* (Auffenberg 1983), *V. varius* (Carter 1990) and *V. indicus* (McCoid & Hensley 1991) the male scratches the base of the female's tail with his claws, before intromission.

Males of some of the larger species (*V. bengalensis, V. komodoensis*) embrace the female during mating in such a way as to immobilise her by pinning her front legs to her side, preventing her from moving forward and escaping or damaging him (Auffenberg 1983).

The gravid female buries her eggs in a nest, and in some species (*V. rosenbergi, V. gouldii, V. niloticus, V. varius, V. giganteus, V. albigularis, V. bengalensis*) the nest is dug deeply into a termite mound. The female backfills the entrance shaft she has dug and, in *V. rosenbergi*, is sometimes assisted in this by the male (Green *et al.* unpub. data). The termites soon complete the task of sealing off the egg chamber.

The hatchlings of *V. niloticus* escape from termitaria without the assistance of adults (Cowles 1930), as do those of *V. rosenbergi* (Green, MacKelvie & Rismiller, unpub. data). However, parental assistance in hatchling release apparently occurs in *V. varius* and perhaps in other species (Carter 1992; Fig. 30.5). While the young of *V. niloticus* immediately desert the nest in the termitarium, hatchlings of *V. rosenbergi* may continue to use the termitaria as refuge sites for up to four months after hatching (Green *et al.* unpub. data). The young of *V. varius* spend most of their time in trees during the first weeks after emerging from the termitaria (Carter 1992).

Seasonal activity patterns of varanids vary greatly, as these lizards occur in a wide variety of climates and habitat types. Species in tropical regions (*V. komodoensis, V. olivaceus, V. giganteus, V. gouldii, V. panoptes* (Pl. 8.12)) are generally active throughout the year (Auffenberg 1981; 1988; Green *et al.* 1986; Shine 1986d). Some species from desert environments, such as *V. gouldii* and *V. griseus*, show seasonal inactivity during hot or cold periods (King 1980; Stanner & Mendelssohn 1987; Vernet *et al.* 1988b), whereas some of the smaller species, such as *V. eremius*, do not (Pianka 1986). Species in temperate regions of southern Australia are active year round, although activity is restricted in winter and they show different activity patterns

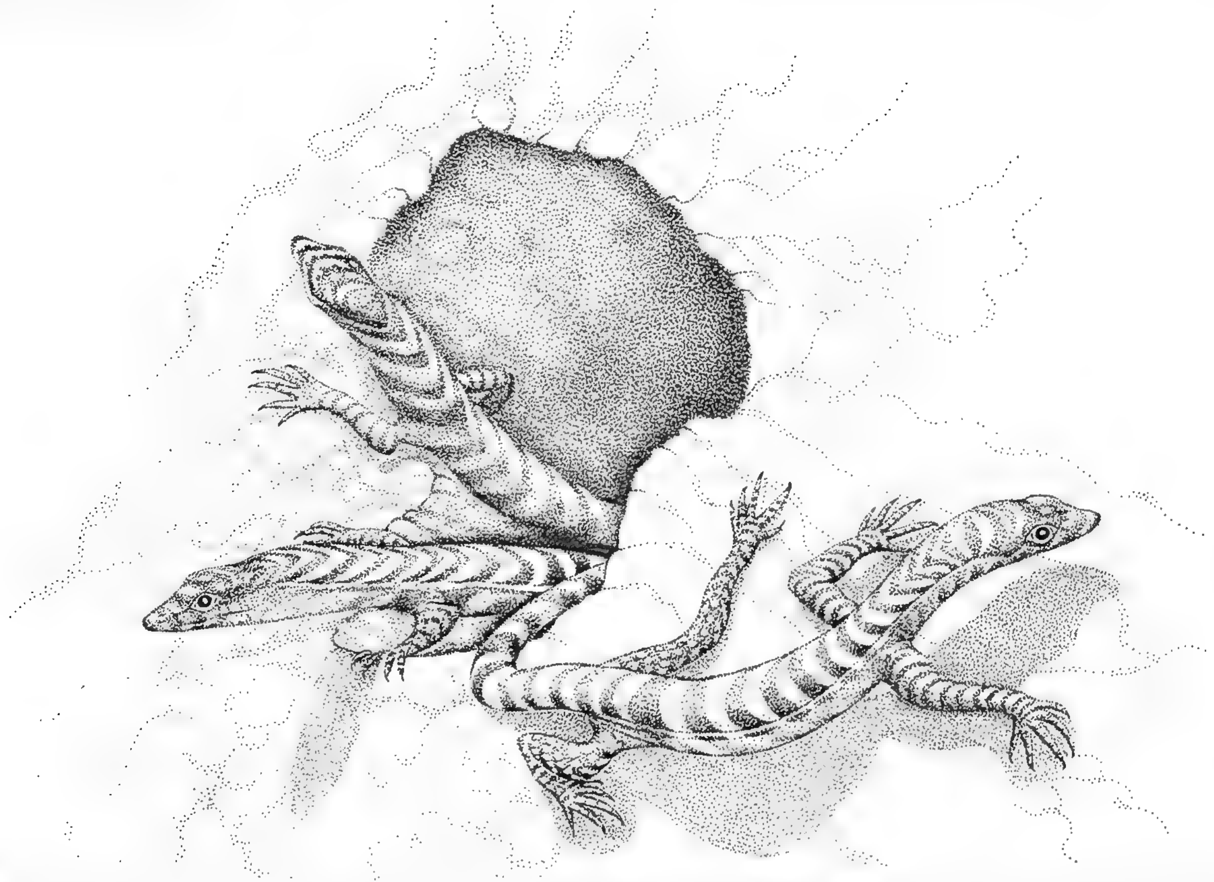

Figure 30.5 After incubation in the protection of a termite mound, newly hatched *Varanus varius* leave through a hole opened by one of the parents. (After BBC 1990) [T. Wright]

during summer and winter (King 1980; Weavers 1983). Seasonal activity varies geographically in species which occupy several climatic regions, such as *V. gouldii* in tropical (Shine 1986d) or arid Australia (King 1980), and *V. niloticus* in South Africa (Cowles 1930) and Sudan (Cloudsley-Thompson 1966). *Varanus griseus* is active throughout the day in winter but shows a bimodal daily activity pattern in summer in Iraq (Corkill 1928); however it is inactive during the cold winters in north Africa (Vernet *et al.* 1988b), Israel (Stanner & Mendelssohn 1987) and Iran (Anderson 1963).

Table 30.2 Activity temperatures of 15 species of varanids. Single values of body temperature were taken by thermometer.

Species	Free-living (°C)	Captive (°C)	Total length (m)
Arboreal or terrestrial			
V. bengalensis	32–37	–	2.0
V. caudolineatus	37.8	–	0.25
V. eremius	37.5	35.9	0.45
V. exanthematicus	36.4	36.5	2.0
V. giganteus	36.1	–	2.4
V. gilleni	37.4	37.1	0.7
V. gouldii	37.0	35.3	1.0
V. griseus	38.5	36.4	1.3
V. komodoensis	36–40	36.3	2.8
V. rosenbergi	35.1	35.2	1.5
V. tristis	34.8	35.4	0.8
V. varius	34.7	33.5	2.0
Amphibious			
V. niloticus	32.7	34.8	2.0
V. mertensi	32.7	32.5	1.3
V. salvator	27–32	35.6	2.5

When active, all terrestrial varanids are able to maintain their body temperatures within two or three degrees of 36°C over a wide range of ambient temperatures (Table 30.2). They do not regulate their body temperatures as precisely as do some other reptiles. However, this allows them greater behavioural latitude during their periods of active foraging. Under extremely hot or cold conditions most species retreat to thermal shelters such as burrows and tree-holes. After several hours in thermal shelters the body temperatures of the lizards approximate those of the shelter, and during winter those of *V. rosenbergi* or *V. varius* in southern Australia may fall below 10°C (King 1980; Weavers 1983). Amphibious species tend to exhibit lower active body temperatures than terrestrial species (Table 30.2), since they lose body heat quickly when foraging in water. Attempting to maintain body temperatures around 36°C would encroach on the time available to them for foraging.

Varanids can maintain temperature differences between the head and body by circulatory adjustments and evaporation from the buccal cavity/gular pouch (King 1977d; Weavers 1983). The brain temperature of *V. varius* can be as much as 6°C higher than the general body temperature before emergence in the morning and during the initial period of basking (Weavers 1983). However, once the animal becomes active, brain and body temperatures are similar (King 1977d; Weavers 1983).

If body temperatures exceed approximately 38°C, some varanids (*V. gouldii*, *V. griseus*, *V. komodoensis* and *V. rosenbergi*) hold their mouth open and start to flutter the gular pouch (King 1977d; King & Green 1993). This increases greatly the rate of evaporation from the buccal cavity (Green 1969) and maintains the temperature of the brain below that of the body (King 1977d). This behaviour is used to only a limited extent before the animal retreats to a thermal refuge such as a burrow or a shaded area.

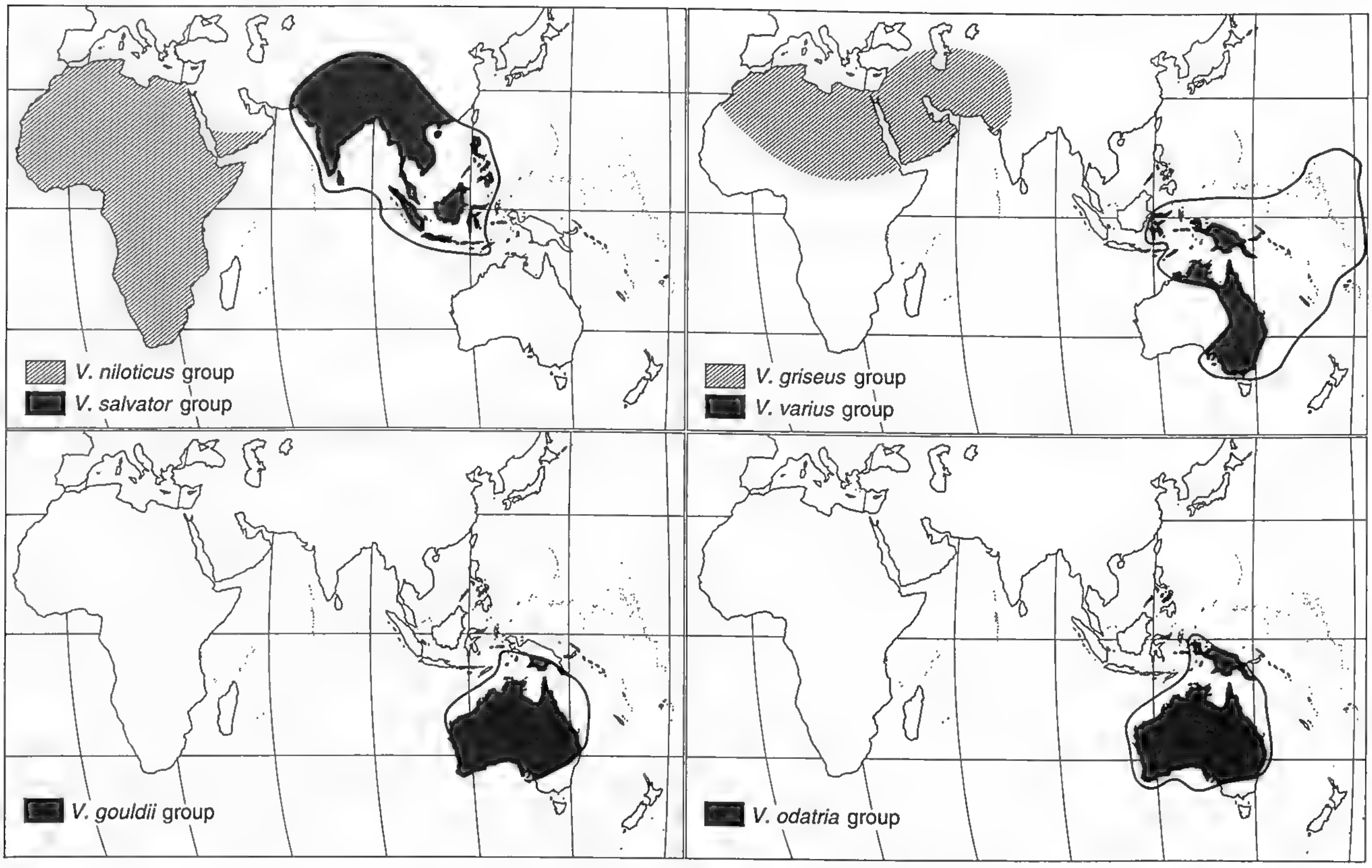

Figure 30.6 The world distribution of varanids. (After King & Green 1993) [W. Mumford]

The anterior nasal tubes of varanids have a large surface area (King 1977d). As inhaled air moves along the tubes it is warmed before reaching the lungs, and air being exhaled is cooled below deep body temperature. Water vapour is thus condensed onto the surface of the tubes, and water loss is also lessened.

Reflectivity of the skin is highly variable between species. Forms which inhabit areas of high insolation generally have a higher skin reflectivity, particularly in the near infra-red portion of the spectrum, than those from cooler or more vegetated areas (King 1977d; King & Green 1993).

Economic Significance

In Australia, all species of varanids are protected by state, federal and international legislation. Although they are hunted to some extent by Aboriginal people, it seems to pose no threat to their survival. There is no commercial harvesting of varanids in Australia.

Huge numbers of skins of several species (*V. salvator*, *V. bengalensis*, *V. indicus*, *V. flavescens*, *V. niloticus*, *V. exanthematicus*) have been exported from some countries in South-East Asia (425 000 to 1 300 000 per year) and Africa (275 000 to 800 000 per year) during the last decade, for use in the leathergoods industry (Luxmoore, Groombridge & Broad 1988). Little or nothing is known of the maximum sustainable levels of harvest for these species. The main exporters were Indonesia, Singapore, Sudan, Nigeria and Mali, and the main importing countries were Belgium, France, Italy, United States of America and Japan (Luxmoore *et al.* 1988). Although international legislation protects all varanid species, not all countries are signatories to the treaties and levels of legislative protection and enforcement are variable between countries in these regions (Luxmoore *et al.* 1988).

No data are available on threats to the survival of varanids through habitat alteration and industrial pollution in many third world countries.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Different karyotypic groups of the Varanidae occur in a broad array of habitats in South-East Asia, the Middle East, Africa and Australia (Fig. 30.6). They are found throughout the continent in Australia, except in Tasmania and parts of southern Victoria (Fig. 30.7). The Kimberley and Arnhem Land have the highest species densities (10 species each); both have extensive areas of sandstone plateau. Areas with the lowest species densities (two species; Fig. 30.7), are near the southern coast (Cogger & Heatwole 1981).

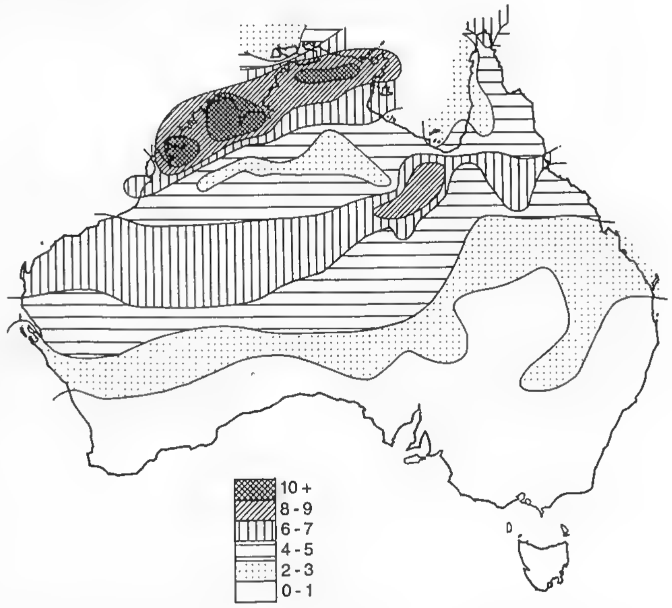

Figure 30.7 The distribution and species density of varanids in Australia. (After Cogger & Heatwole 1984) [W. Mumford]

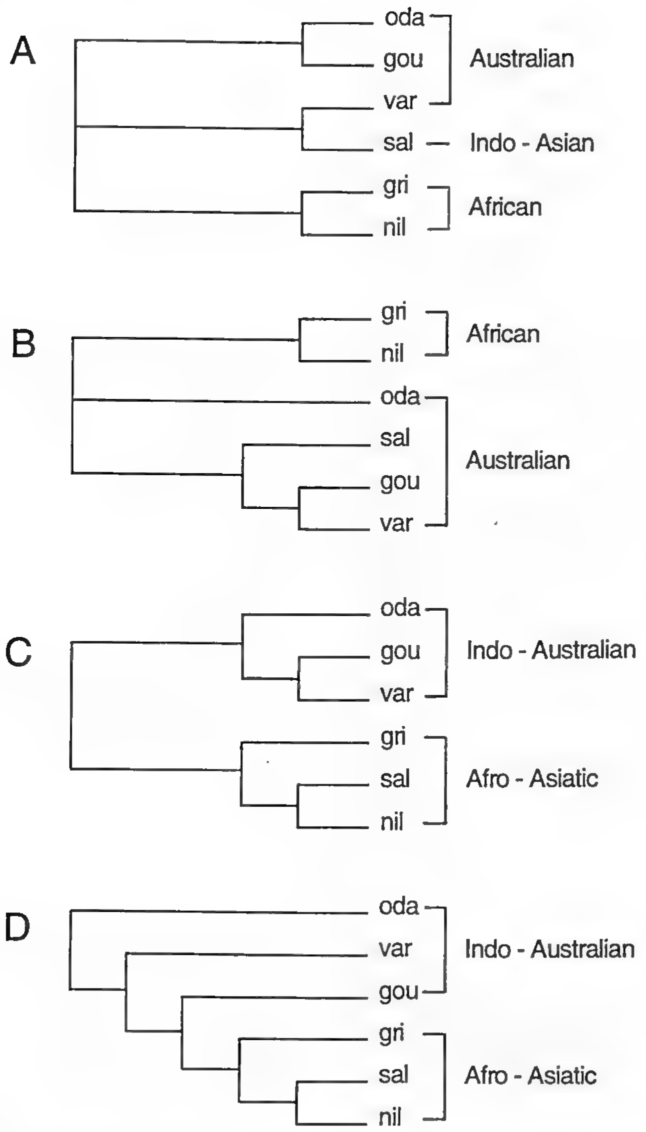

Figure 30.8 Comparison of phylogenies of the Varanidae. Based on A, chromosomal data; B, revised chromosomal and MC'F data; C, hemipenial morphology; D, lung morphology. **gou**, *gouldii* group; **gri**, *griseus* group; **nil**, *niloticus* group; **oda**, *Odatria* group; **sal**, *salvator* group; **var**, *varius* group. (A, after King & King 1975; B, after King 1990; C, after Böhme 1988), D, after Becker *et al.* 1989) [D. Wahl]

Affinities with other Groups

Varanids are anguimorph, platynotan lizards (Rieppel 1980b). The group Varanoidea, including Varanidae, Helodermatidae and Lanthanotidae was formed by McDowell & Bogert (1954) and it was regarded as a monophyletic assemblage within the Platynota by Rieppel (1980b). Each family contains only one extant genus (*Varanus*, *Heloderma* and *Lanthanotus*), and it appears that the lineages they represent are of considerable antiquity (Pregill, Gauthier & Greene 1986).

Affinities within the Taxon

Mertens (1942) was the first to attempt to classify the Varanidae. He based his work on the osteology and morphology of the group, and was hampered by restricted access to specimens. He did not attempt to construct a phylogeny for the Varanidae, and he named 10 subgenera, most of which are not supported by studies using more modern techniques.

A chromosomal analysis of 16 species in the family by King & King (1975) attempted to determine the most likely origin of the Varanidae and to construct a phylogeny for them. They recognised six karyotype groups (Fig. 30.8A) and suggested an Asian origin with two radiations into Australia and development of an endemic group there, and a westward radiation into the Middle East and North Africa, with a subsequent southern radiation into Africa. These and additional data have been reanalysed by King (1990) and the conclusions have been modified. The revised interpretation of these results agrees very closely (Fig. 30.8B) with the phylogeny proposed from a recent study (Fig. 26.8) based on microcomplement fixation (Baverstock, King, King, Birrell & Kreig in press).

Other phylogenies have been proposed recently, based on the results of studies on hemipenal morphology (Branch 1982; Böhme 1988) and lung morphology (Becker, Böhme & Perry 1989). Studies on hemipenes grouped most of the species in clusters similar to those of the chromosomal and immunological studies, whereas the lung morphology study grouped several species in assemblages not supported by other techniques. The phylogenies derived from the morphological studies of hemipenes and lungs do not agree closely with those based on chromosomal or immunological data (Fig. 30.8C, D; King 1990; King et al 1991; Baverstock *et al.* in press). The major differences between them relate to the position of the Asian species-cluster in relation to the African cluster and the two Australian clusters. Further studies using other techniques will be necessary to resolve these differences.

Fossil Record

The oldest fossil varanoids are in the extinct subfamily Saniwanae, from the upper Cretaceous of eastern Asia and North America (McDowell & Bogert 1954). Accurate conclusions on the history of the Varanidae cannot be drawn because of a lack of knowledge of Cretaceous fauna (Pregill *et al.* 1986). The subfamily Saniwanae is known from the Paleocene-Eocene of North America and the Eocene of Europe (McDowell & Bogert 1954) and another varanoid family, the Necrosauridae, occurred in Europe from the Upper Paleocene to the Oligocene (Hoffstetter 1968). The earliest member of the Varanidae is *Telmatosaurus* from the Upper Cretaceous of Mongolia (Hoffstetter 1968). The oldest representative of the genus *Varanus*, subfamily Varaninae, is *V. hofmanni* from Miocene deposits in eastern Europe (Hoffstetter 1968). There is thus a large gap between members of the Saniwanae and the Varaninae in Europe. Hoffstetter (1968) proposed a possible origin of the Varanidae, suggesting that the genus *Varanus* differentiated from the Saniwanae in Asia and migrated from there into Europe, displacing the European descendants of the Saniwanae during the Miocene. The oldest varanid fossils in Australia (Estes 1984) and Africa (Estes 1983a) are also from the Miocene, suggesting a recent radiation (King & King 1975). Other varanid species, including the extinct giant *Megalania prisca* (estimated to have reached a total length of up 7 m and a mass of approximately 600 kg) and smaller *Varanus* species, occur in Australia in Pleistocene and Pliocene deposits in central Australia (Hecht 1975).

31. FAMILY SCINCIDAE

Mark N. Hutchinson

DEFINITION AND GENERAL DESCRIPTION

The family Scincidae is the largest of the sixteen or so families of lizards. Scincids (skinks) belong to the infraorder Scincomorpha, a monophyletic group of families whose members tend to be elongate and have relatively long-snouted and somewhat flattened skulls, in which the upper temporal opening is usually reduced or lost. The head is usually covered with enlarged plates, termed head shields (Fig. 31.1), and osteoderms are frequently present in some or all scales.

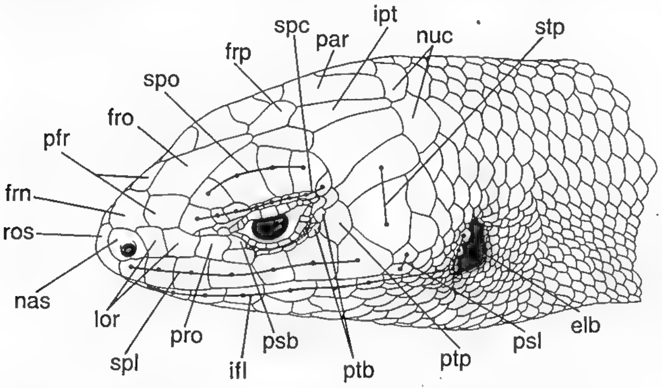

Figure 31.1 Head of a skink, *Egernia whitei*, showing the enlarged shields and their nomenclature. **elb**, ear lobules; **frn**, frontonasal; **fro**, frontal; **frp**, frontoparietal; **ifl**, infralabials; **ipt**, interparietal; **lor**, loreals; **nas**, nasal; **nuc**, nuchals; **par**, parietal; **pfr**, prefrontals; **pro**, preocular; **psb**, presubocular; **psl**, postsupralabials; **ptb**, postsubocular; **ptp**, primary temporal; **ros**, rostral; **spc**, supraciliaries; **spl**, supralabials; **spo**, supraoculars; **stp**, secondary temporals [J. Thurmer]

Typically scincids are slightly to markedly elongate lizards with moderate to short limbs and glossy cycloid scales, reinforced by characteristic compound osteoderms (Fig. 31.2). The partially to well-developed secondary palate is a distinctive feature of the skull. It is formed primarily by development of a novel lamina of the palatine bone on each side, which together essentially floor and prolong the choanal passage. In some species the palatal rami of the pterygoids extend the secondary palate posteriorly to about the level of the back of the tongue. Other osteological characteristics include paired premaxillae, descending processes from the parietals which meet the epipterygoids and an enlarged labial coronoid process of the dentary.

The inner ear has an accessory inertial body, the culmen (Wever 1978), which modulates hair cell sensitivity, and largely replaces the tectorial membrane, which is vestigial in skinks. Preanal and femoral pores are absent. The tail is usually long and tapering and, except for a very few species, can be shed and regenerated. The tongue is broad, has an arrowhead-shaped tip and is covered with serrated scales (Schwenk 1988). Many species have reduced limbs, sometimes accompanied by a loss of digits; nine Australian species are completely limbless.

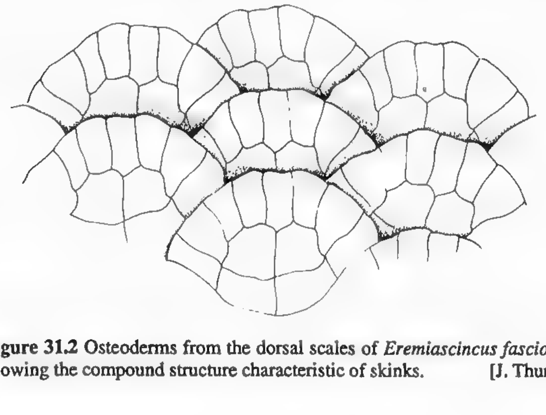

Figure 31.2 Osteoderms from the dorsal scales of *Eremiascincus fasciolatus* showing the compound structure characteristic of skinks. [J. Thurmer]

Skinks are typically diurnal, terrestrial and active on the surface of the ground or low perches; a significant number are secretive to fossorial, carrying out most activities within leaf litter or underground. Some species are climbers, living in trees or on rocks. Skinks are found in all terrestrial ecosystems, from tropical forests to desert sand dunes and alpine habitats. A few are semiaquatic, able to swim and hide under water to escape predators (Daniels 1990), and some species inhabit the intertidal zone, on rocky shores, beaches or mangroves.

Though the family is cosmopolitan, it has centres of diversity in the Australian, Ethiopian and Oriental Regions and is relatively poorly represented in the Neotropic and Holarctic Regions. The family is still expanding, as new species are described. Halliday & Adler (1986) provided an estimate of 1275 species in 85 genera, although recent generic rearrangements have increased the latter figure. In Australia and its external territories there are 325 species in about 32 genera (as of 12 December 1990). The Australian genera form three monophyletic assemblages, informally termed the *Egernia* Group, the *Eugongylus* Group and the *Sphenomorphus* Group (Greer 1979b). The taxa comprising these groups are shown in Table 31.1.

HISTORY OF DISCOVERY

The first Australian skinks to be described scientifically were among the animals treated by White (1790). White gave descriptions of two species that he placed in the Linnaean genus *Lacerta*, the genus which included all fully limbed, non-gliding lizards. These two species are now known as *Tiliqua scincoides*, the eastern bluetongue, and *Ctenotus taeniolatus*, the coppertail skink.

British and French collectors (notably the 1800–1804 Baudin expedition; Bonnemains, Forsyth & Smith 1988), and the European museum taxonomists who described the collections, steadily increased the number of species known from Australia. Twenty-one species of Australian skinks were listed by Duméril & Bibron (1839), representing twelve modern genera. At this time the concept of a family Scincidae began to emerge, although Duméril and Bibron also placed other degenerate-limbed and skink-like taxa (amphisbaenians and diploglossine anguids for example) with their 'Scincoidiens'. In those pre-Darwinian times, much taxonomic weight was placed on easy-to-score external features, such as degree of limb degeneration; thus the three species of *Lerista* known at the time (*L. bougainvillii*, *L. lineata* and *L. praepedita*) were placed in three separate genera and two different subfamilies.

The century's most significant work on reptiles was George Boulenger's British Museum catalogues, published in three volumes between 1885 and 1887. In Volume III (Boulenger 1887), 78 species of Australian skinks were listed. These species, mostly still valid, represent 23 of the genera currently recognised. Boulenger's family and generic definitions were relatively broadly based on combinations of both internal and external anatomical features, and easily accomodated additional species as they

Table 31.1 Distribution of skinks in the Australian zoogeographic subregions. In addition, the genera *Lygosoma* and *Oligosoma* occur on Christmas Island and Lord Howe Island respectively.

Genera	Number of species	Torresian	Eyrean	Bassian
Egernia Group				
Cyclodomorphus	4	2	2	2
Egernia	29	6	12	10
Tiliqua	10	1	4	5
Eugongylus Group				
Bartleia	1	1	–	–
Bassiana	3	–	–	3
Carlia	21	22	2	2
Cautula	1	1	–	–
Cryptoblepharus	7	6	4	2
Emoia	2	2	–	–
Eugongylus	1	1	–	–
Lampropholis	11	9	–	4
Lygisaurus	5	5	–	1
Menetia	6	5	3	1
Morethia	8	3	6	4
Nannoscincus	1	–	–	1
Niveoscincus	8	–	–	8
Proablepharus	3	1	3	–
Pseudemoia	4	–	1	4
Shenomorphus Group				
Anomalopus	7	6	–	4
Calyptotis	5	4	–	1
Coeranoscincus	2	2	–	–
Ctenotus	86	30	55	8
Eremiascincus	2	2	2	–
Eulamprus	10	6	–	5
Glaphyromorpha	11	12	–	1
Gnypetoscincus	1	1	–	–
Hemiergis	5	–	3	5
Lerista	62	12	54	6
Notoscincus	3	1	2	–
Ophioscincus	3	3	–	–
Saiphos	1	1	–	1

became known. As a result, Boulenger's scheme became widely accepted for the next fifty years, and was still in use in modified form long afterwards, for example, in Eric Worrell's (1963) *Reptiles of Australia.*

So successful was Boulenger's taxonomy that systematic studies of Australian skinks slowed post-Boulenger. Research on skinks worldwide tended to shift towards anatomical studies, taking a stable taxonomy for granted. Notable amongst these were several on osteology (Siebenrock 1892, 1895; Kingman 1932; Haas 1936; El Toubi 1938; Brock 1941), embryology (Rice 1920) and palatal anatomy (Busch 1898). During the first half of the twentieth century, the major taxonomic advances centred on attempts to break down Boulenger's unwieldy genus *Lygosoma* into more natural genera (Smith 1937). The subfamilial and generic scheme which resulted (Mittleman 1952) was not widely or fully accepted, since many of the genera appeared to be based on trivial external features, so that in subsequent years various *ad hoc* combinations of Boulenger's, Smith's and Mittleman's taxonomic systems appeared in the literature.

A resurgence of interest in skink systematics in Australia began in the mid 1960s, with publications by Fuhn (1969) and Greer (1967; Greer & Parker 1968), which showed that the skink secondary palate was far more variable in its detailed osteology than had been realised and that these variations were useful in indicating phylogenetic relationships. At the same time, Storr (for example, Storr 1968b, 1969) began to revolutionise alpha taxonomy, showing that the Australian skink fauna is far richer in species than was indicated by the then current taxonomy. Storr (1964b) also provided a benchmark review on the biogeography of Australian skinks, summing up a view that followed from the taxonomy and static continent orthodoxy of the time.

Bewteen 1965 and 1990, the number of skink genera recognised in Australia grew from about 14 to 32 and the number of species from approximately 140 to over 300. The fauna is now regarded as highly endemic, and characteristic not just of the Australian region but of the Australian continent. Few Australian genera extend beyond southern New Guinea, and most of the diversity seems to have developed *in situ*, rather than having derived from multiple invasions. The recent book by Greer (1989) summarised the state of knowledge for many aspects of the natural history and morphology of the Australian skinks, and reviewed the phylogenetic relationships of the fauna as seen by the most influential student of scincid relationships over the last twenty years.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Australian skinks range in size from an adult snout-vent length of 35 mm in *Menetia* to over 350 mm in *Tiliqua* (maximum 371 mm for *T. scincoides intermedia*; Shea, in Greer 1989). Adult mass in these same genera ranges from 0.4 g to over 1000 g (Henle 1989a; Hutchinson pers. obs.).

Most skinks have a small head which is not delineated from the neck, a body square in cross-section with well-developed limbs bearing graduated toes (4>3>2 = 5>1) and a long tapering tail (usually more than 120% of snout-vent length when original). Several major variations occur (Pl. 6). In fossorial, litter or sand-swimming species, the head becomes relatively smaller, narrower and wedge-shaped. Associated with this is elongation of the body and reduction of limb size and often digit number. Examples of this trend include members of the genera *Lerista* (Pl. 6.12; Greer 1987c, 1990a) and *Anomalopus* (Pl. 6.13; Greer & Cogger 1985). Although relatively few skinks are truly arboreal or saxicoline, those that are share a morphology which includes a broad and flattened head and body, and long, strong and sharply clawed limbs and toes used for climbing. Some species of *Egernia*, members of the *E. whitii* and *E. major* species groups, are unusually robust with a deep head, stocky body and muscular appendages. Another group of giant skinks, the genus *Tiliqua*, has a peculiar body form which combines a large, heavily built head and bulky, flattened body with very short, seemingly weak limbs and a tail shorter than the body (Pl. 6.3, 6.4).

Sexual dimorphism in size and proportions is usual in skinks, although often only subtly apparent (Hutchinson & Donnellan 1988, 1992; Hutchinson, Robertson & Rawlinson 1989; Simbotwe 1985; Yeatman 1988). In general, females have longer bodies than males, and proportionately narrower heads and shorter appendages. Often, especially in elongate species, females average higher presacral vertebral counts than males. Examples are *Lerista* (Greer 1987c), *Pseudemoia* (Hutchinson & Donnellan 1992), *Tiliqua* (Shea pers. comm.) and those in Greer (1989, Table 4).

Colour patterns are extremely variable. A trend is for longitudinal patterns in terrestrial species, especially grass-dwellers, while transverse barring is much rarer, usually in secretive shade or litter-dwelling species. A combination of grey-brown dorsum and blackish sides forms a common colour pattern for surface-dwelling woodland species (Greer 1989, Fig. 59). Climbing species, especially rock dwellers, are usually spotted or mottled, with little trace of linear pattern elements (Covacevich 1984). Burrowers or cryptozoic species tend to be weakly patterned but may have contrasting or bright colours on the tail, belly or head. Colour change as a result of melanocyte expansion/contraction as occurs in iguanian and gekkotan lizards is not present, although longer term (measured in days rather than minutes) changes in degree of pigmentation have been suggested to occur in *Lampropholis* (Greer 1989).

Sexual dichromatism is not generally a feature of Australian skinks, but does occur in some *Eugongylus* Group genera. The most striking dichromatism occurs in the genus *Carlia* (Covacevich & Ingram 1975; Ingram & Covacevich 1989) in which males of most species develop bright lateral colouring, usually red, green or blue (sometimes in combination), sometimes with black pigment patches on the neck or chin for further emphasis, while females retain the cryptic pattern of a dark, sometimes light-edged lateral stripe. Other genera exhibit dichromatism. Males of *Lygisaurus* develop a red flush on the tail (Ingram & Covacevich 1988). In *Bassiana, Morethia, Pseudemoia* and *Proablepharus*, males of most species develop red pigmentation on the throat or belly (Pl. 6.10; Donnellan & Hutchinson 1990; Greer 1980b, 1982; Hutchinson 1990a; Hutchinson, Donnellan, Baverstock, Krieg, Simms & Burgin 1990). Males of at least some species of *Menetia*, a genus in which relationships are obscure, develop bright yellow to orange ventral colouring (Greer 1989; pers. obs.). Populations of *Lampropholis delicata* from Queensland (Greer 1989) and Eyre Peninsula, South Australia (Hutchinson pers. obs.) show a pattern dimorphism, in which females have a white midlateral line which is absent in males.

Body Wall

Scale size in skinks is relatively large, with generally fewer than 40 longitudinal rows of body scales. All scales are supported by compound osteoderms (Fig. 31.2), those on the head, especially the frontal, interparietal and parietals often becoming fused to underlying skull bones during postembryonic ontogeny.

The numbers of longitudinal rows of scales along the body are correlated to some extent with mode of life. Reduced-limbed species and litter- or grass-dwelling species tend to have relatively few rows (less than 28) of relatively large scales (Fig. 31.3), while climbing species, especially rock dwellers, have increased numbers (often 34 or more rows) of small scales. This may enhance, respectively, 'armour-plating' of the burrowing/litter dwelling species and softness and flexibility of the skin, facilitating entry into crevices, in the climbers.

Macroscopically, scale surfaces of skinks are usually smooth, often with a matt surface dorsally but polished and highly glossy laterally and ventrally (and dorsally in cryptozoic taxa). Keels or striations are present in some taxa, often variably developed in congeneric species. In a few species, the keels are pronounced, such as in some *Carlia* (Ingram & Covacevich 1989). In the *Egernia cunninghami* species group (Horton 1972) they are extended into backward-facing spines which are longest and strongest on the tail. *Gnypetoscincus queenslandiae* has bizarre, pointed, juxtaposed scales, giving it a coarse, atypical skin texture. A second, somewhat similar, spiny-scaled skink taxon has been discovered recently in south-eastern Queensland (Covacevich pers. comm.). Scalation modified in a similar way is also found in some non-Australian genera (*Tribolonotus* and *Fojia*), both of which inhabit rainforest areas, either beside streams or within saturated rotting logs (Cogger 1972; Greer & Simon 1982; McCoy 1980). The shingleback, *Tiliqua rugosa*, has massive, ridged dorsal scales with thick osteoderms that effectively form an armoured shield (Pl. 6.1). A study of the micro-ornamentation of lizard scales by Renous & Gasc (1989) included a number of skinks and showed that the ornamentation varies according to the degree of contact between a region of the body surface and the substrate. Micro-ornamentation of the skin has been used in some reptiles as a phylogenetically informative character, but has not yet been used in skinks.

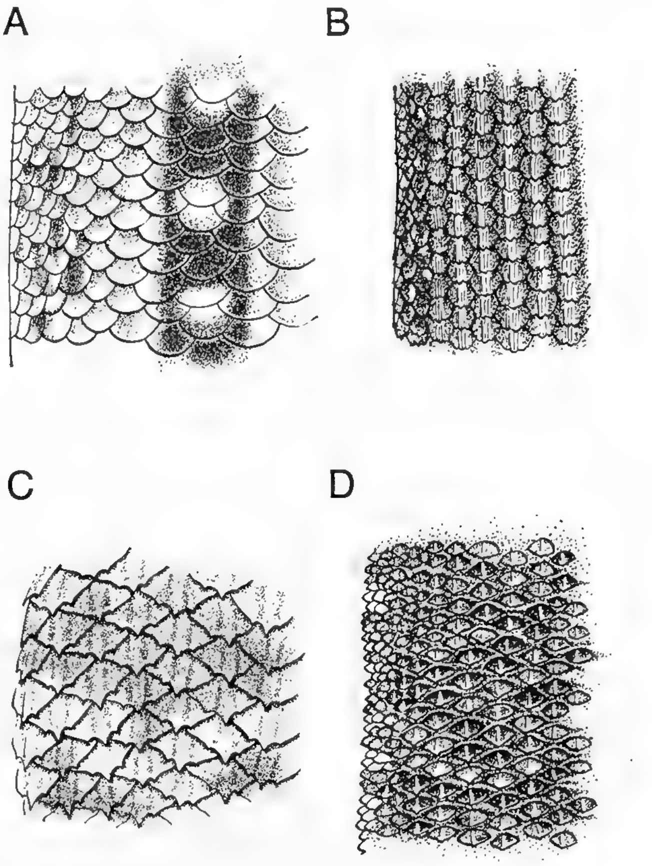

Figure 31.3 Scale variation in skinks. **A**, typical smooth cylcoid scales of *Egernia whitei*; **B**, keeled, or carinate, scales of *Carlia jarnoldae*; **C**, spiny scales of *Egernia depressa*; **D**, juxtaposed, tubercular scales of *Gnypetoscincus queenslandiae*. [K. Bowshall-Hill]

The structure of the dermis in squamates and the control of skin-shedding was reviewed by Maderson (1984). As in other squamates, skinks periodically shed a complete outer epidermal layer. It is shed in several large patches, and does not form a coherent 'ghost' as it does in snakes and gekkotan lizards.

The lining of the body wall is distinctively pigmented in a way which reflects habits and mode of thermoregulation. Diurnal, surface-active skinks have a black lining to the cranial and body cavities, but this is absent in nocturnal or fossorial species (Greer 1989). The black colouring has been explained by Porter (1967) as providing an internal shield blocking high energy ultra-violet radiation which is able to penetrate lizard skin and could cause tissue damage.

Skeletal System

The typically scincomorphan skull is broad and flattened, with a reduced upper temporal opening and a relatively long snout. The family as a whole shows considerable variation, so this discussion will be confined to Australian taxa. King's (1964) study on *Eulamprus quoyii* is the only one which has attempted to describe the entire skeleton of an Australian skink. Partial descriptions, especially of the skull, of numerous species have been published, but no overall review of the trends and major patterns of variation is available for the Australian fauna.

The skull of a relatively unmodified skink, *Ctenotus leae*, is shown in Figure 31.4 and can be taken as typical in many respects of the structure of a terrestrial, surface-dwelling skink. As in all Australian species, the premaxillae are paired and asymmetric, the right premaxilla bearing one more tooth than the left; symmetrical premaxillary counts are seen in a few taxa, for example most *Egernia* (Greer 1979b). Premaxillary tooth counts tend to be stable within related groups but vary between groups, thus providing a useful taxonomic character (Greer 1974, 1979b). In *Ctenotus* the paired nasals are not in contact with the prefrontals, the most common condition in skinks (Estes, De Queiroz & Gauthier 1988), although the complementary arrangement with a nasal-prefrontal suture is often seen (for example, most genera in the *Eugongylus* Group). The frontal forms the dorsal border of the orbit of most skinks, but in some species with reduced limbs, the pre- and postfrontals are closely apposed or in contact along the orbital margin, apparently correlated with reduction of the relative size of the orbit (Greer & Cogger 1985; Shea 1990). The lacrimal and postorbital are both absent in *Ctenotus leae*, and are at best only small in most lygosomines that retain them. Even when well developed, as in *Hemiergis*, the postorbital is excluded from the orbit by contact between the postfrontal and the jugal.

Members of the genus *Ctenotus* generally retain an upper temporal fenestra which is large for a lygosomine; most Australian taxa have a reduced or rudimentary fenestra as a result of closure by the posterior expansion of the postfrontal plus lateral expansion of the parietal. The post-temporal fenestrae are open in larger skinks. However, they are closed in small species, especially burrowers, and the posterior margin of the parietal is contiguous with the anterior margin of the supraoccipital (Rieppel 1984a).

The single parietal is pierced by a parietal foramen. In a minority of species, the foramen closes as the animal ages, such as in some *Egernia* (Hutchinson pers. obs.). The squamosal in skinks is said to contact the jugal, or nearly do so (Estes *et al.* 1988), but often terminates well short of the jugal in many Australian lygosomines. A small, slender supratemporal is wedged between the squamosal, laterally, and the extremities of the processus parietalis and crista prootica, medially (Rao & Ramaswami 1952).

In lateral view, most of the snout is formed by the maxilla, which extends posteriorly to form most of the lower orbital border. The dorsal ramus of the maxilla may contact the frontal (as in *C. leae*) or may be excluded because of contact between the prefrontal and nasal. The paired septomaxillae are mostly hidden within the nasal cavity but are visible as the posterior floor and internal lining of the external nostril.

On the palate, the vomers are fused in *C. leae*, as in most lygosomines; the members of the *Egernia* Group retain paired vomers. The fissure (*fenestra exochoanalis*) which separates the vomer laterally from the maxilla is closed in life by a vomerine epithelial pad and the choanal opening has shifted posteriorly (see below). The postero-ventral ends of the vomers bear short tooth-like processes, which are fused into a triangular wedge in most lygosomines but posteriorly lengthened in *Egernia* (Hutchinson 1981; Greer 1989). In ventral view, only the ventral laminae of the palatines are visible in *Ctenotus* as in most Australian skinks, the exception being species of *Egernia* in which the ventral laminae do not meet medially in most species, leaving a cleft in the palate, through which the dorsal laminae can be seen. In the *Eugongylus* Group the postero-medial corner of the palatine is drawn into a prong which extends into the interpterygoid vacuity (Greer 1974; Hutchinson *et al.* 1990).

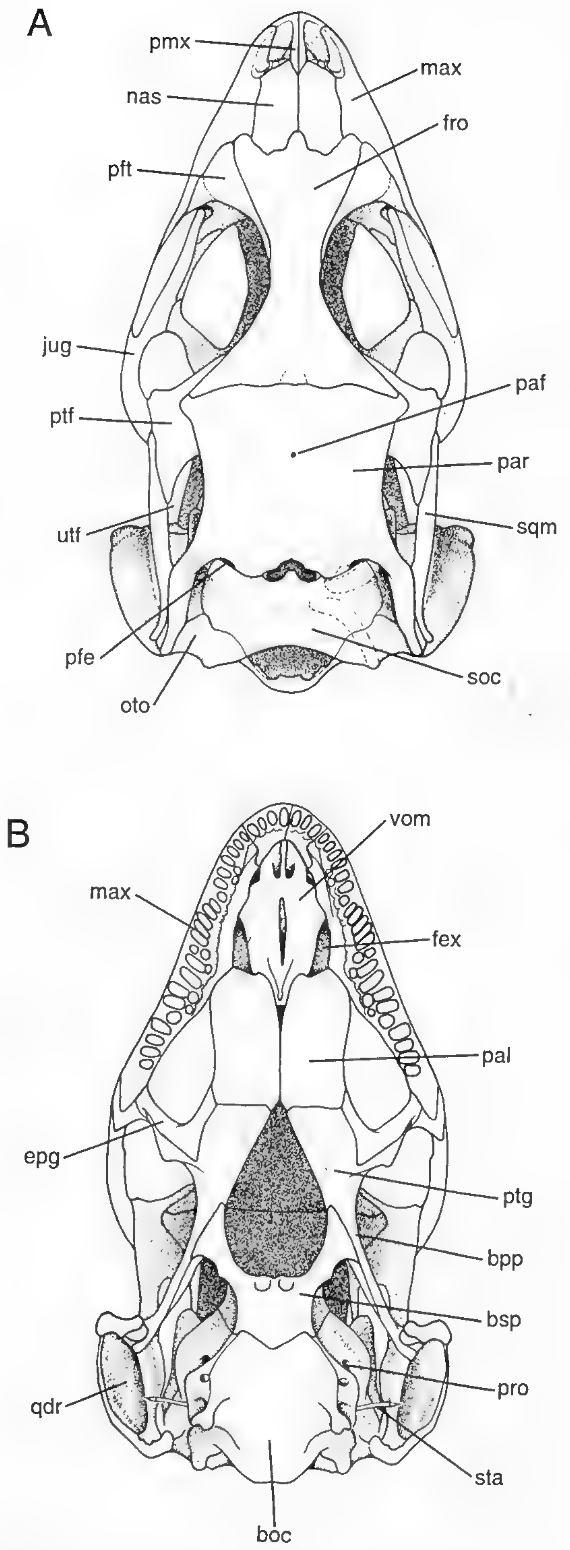

Figure 31.4 Skull of *Ctenotus leae*. **A**, dorsal view; **B**, ventral view. **boc**, basioccipital; **bpp**, basipterygoid processes **bsp**, basisphenoid; **ect**, ectopterygoid; **fex**, *fenestra exochoanalis*; **fro**, frontal; **jug**, jugal; **max**, maxilla; **nas**, nasal; **oto**, otoccipital; **paf**, parietal foramen; **pal**, ventral lamina of palatine; **par**, parietal; **ptf**, post-temporal fenestra; **pft**, prefrontal; **pmx**, premaxilla; **pro**, prootic; **ptf**, postfrontal; **ptg**, pterygoid; **qdr**, quadrate; **soc**, supraoccipital; **sqm**, squamosal; **sta**, stapes; **utf**, upper temporal fenestra; **vom**, vomer. [J. Thurmer]

The palatal ramus of the pterygoid is only slightly expanded in *C. leae*, as in most *Ctenotus*, and makes virtually no contribution to the secondary palate. However, in many skinks of the *Sphenomorphus* Group the palatal rami of the pterygoids are expanded and in medial contact, and prolong the palate to the level of the basipterygoid articulation. In some members of both the *Eugongylus* and *Sphenomorphus* (for example, *Ophioscincus*, Greer & Cogger 1985; *Saiphos*, Greer 1983b) groups, the pterygoids are not in contact on the palate but send postero-medial prongs into the interpterygoid vacuity (forming the so-called beta palate configuration; Greer & Parker 1968; Greer 1974, 1979b). The function of this structure was suggested by Greer & Parker (1968) to be a 'catch' which prevents excessive antero-posterior movement of the pterygoids on the basipterygoid processes. However, in life the area over which the pterygoids could apparently move is filled with cartilage so that little displacement is possible. It appears more likely that the pterygoid prongs serve to extend the secondary palate further to the rear; as the palate expands posteriorly it must grow around the basipterygoid cartilage, creating the hooked shape of the pterygoid extension which supports the palatal mucosa. Pterygoid teeth, which occur in several groups of skinks (Kingman 1932; Greer & Parker 1968), are not found in any Australian species.

The neurocranium consists of the sphenoid, basioccipital. supraoccipital and paired otoccipitals and prootics (Rao & Ramaswami 1952; Skinner 1973). In most Australian species all bones fuse during postembryonic ontogeny, so that the sutures between the bones become difficult to see or are obliterated.

Other modifications of the skull involve the proportions of the skull as an entire unit, as well as alterations to individual bones. A consistent trend in burrowing and other reduced-limbed taxa is for the skull to become smaller, relative to body size, and for the dermal elements to become more closely applied to the neurocranium. The lateral skull bones, especially the jugal and squamosal become narrowed. As a result, the skull is longer and narrower in burrowing taxa than in surface-dwellers. The anatomical changes involved have been reviewed by Rieppel (1984a) for lizards in general, and by Greer & Cogger (1985) for several reduced-limbed Australian genera.

The mandible (Fig. 31.5) primitively retains the full complement of bones found in lepidosaurs, except that the articular is indistinguishably fused with the prearticular during early embryology (Skinner 1973). The surangular and the prearticular fuse progressively during postembryonic ontogeny. The suture on the labial surface of the mandible becomes obliterated first, followed by the suture on the lingual surface, and the anteriormost part of the suture, below the coronoid, usually persists. The angular is greatly reduced in most of the *Eugongylus* Group, and is absent in some taxa (*Cryptoblepharus*, some *Carlia*). The splenial is also reduced to a greater or lesser extent in the *Eugongylus* Group. The groove for Meckel's cartilage is exposed on the lingual face of the dentary in most members of the *Sphenomorphus* Group, but is completely lost by overgrowth of the dentary in the other two Australian lineages, as well as in some *Sphenomorphus* Group taxa (*Notoscincus*, Greer 1979b; some *Lerista* and *Ctenotus*, Hutchinson pers. obs.). The retroarticular process varies greatly in shape, from the primitive (scincine and cordylid) condition showing a prominent inflection (Estes *et al.* 1988), which is largely retained in the *Egernia* and *Eugongylus* Groups, to the parallel-sided, often slender process characteristic of the *Sphenomorphus* Group.

The hyobranchial apparatus is conservative in skinks, with practically no variation from the pattern reported by Rao & Ramaswami (1952) for *Mabuya* or King (1964) for *Eulamprus*. All of the elements present primitively in lizards are present in skinks (Camp 1923; Estes *et al.* 1988), although the epibranchials are reduced (EB I), or unossified and not in contact with the corresponding ceratobranchial (EB II). This terminology follows that of Camp (1923), although Skinner (1973) identifies the free-lying element as the first, rather than the second epibranchial, and does not identify the terminal segment of the first ceratobranchial (although she illustrates it).

The vertebrae are procoelous, with a centrum that tapers posteriorly (Siebenrock 1895; Hoffstetter & Gasc 1969). Primitively there are 26 presacral vertebrae in skinks (Hoffstetter & Gasc 1969), and this count is retained in the normally proportioned members of the *Egernia* and *Sphenomorphus* Groups.

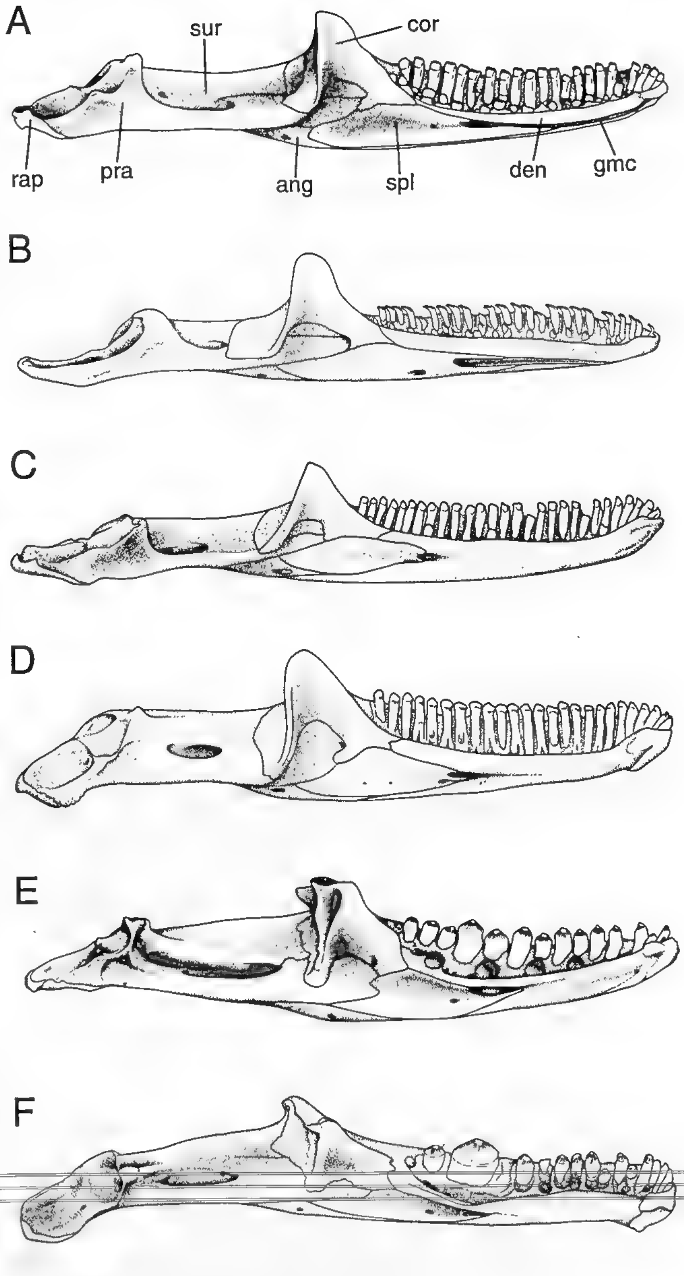

Figure 31.5 Mandibular variation in skinks. A, *Eulamprus murrayi*; B, *Coeranoscincus reticulatus*; C, *Eugongylus rufescens*; D, *Egernia cunninghami*; E, *Tiliqua scincoides*; F, *Cyclodomorphus gerradii*. **ang**, angular; **cor**, coronoid; **den**, dentary; **gmc**, groove for Meckel's cartilage; **pra**, prearticular; **rap**, retroarticular process; **sur**, surangular; **spl**, splenial.

[J. Thurmer]

The atlas-axis complex of *Eulamprus quoyii*, described by King (1964), is typical in that the atlantal neural arches are separated dorsally and not fused to the centrum ventrally (Greer 1989). In some members of the *Eugongylus* Group, the neural arches fuse to the centrum (Greer 1989) and sometimes dorsally as well (Sadlier 1990). The axis bears two hypapophyses, as the intercentra from both the second and third vertebrae are fused to the second centrum (Hoffstetter & Gasc 1969).

In the more elongate members of the *Egernia* and *Sphenomorphus* Groups, and in all members of the *Eugongylus* Group, presacral counts exceed 26. Normally-proportioned members of the *Eugongylus* Group usually have 27 to 29 presacrals. In elongate, reduced limbed species of all groups, the number of presacrals exceeds 30, and the highest counts are recorded in the limbless *Coeranoscincus frontalis*, which has 72 to 76 presacral vertebrae (Greer & Cogger 1985; Greer 1989, Table 3, for a summary of presacral counts).

All but the first five (less often four) caudal vertebrae have fracture planes, the line of weakness separating the anterior third of the vertebra and passing through the anterior part of the base of the transverse process (Etheridge 1967; Hoffstetter & Gasc 1969). In *Egernia stokesii* and *E. depressa* and in *Tiliqua rugosa*, fracture planes are absent, and they disappear ontogenetically in some other species of *Tiliqua* (Arnold 1988). Caudal chevrons start on the third (less commonly the second or fourth) caudal. They are usually placed slightly forward of the primitive intervertebral position, attached to the posterior end of the preceding vertebral centrum. Caudal vertebrae usually number between 40 and 50 in Australian species, and range from 14 in *E. stokesii* to 70 in *Emoia atrocostata* (Greer 1989).

The ribs of Australian skinks are simple and lack any processes for muscle attachment (but such a process, the pseudotuberculum, is seen in African acontines; Hoffstetter & Gasc 1969). In skinks, ribs are present on all but the first three cervical vertebrae. The nature of the rib contact divides the vertebral column into a cervical region, defined as ending with the last vertebra (the eighth) with an associated rib not attached to the sternum (Greer 1989; Siebenrock 1895), and the dorso-lumbar vertebrae which can be further subdivided on the rib attachments, as only the first five (vertebrae 9 to 13) have ribs contacting the sternum.

The sternal skeletal elements are fairly constant in morphology and in their relationships with the ribs in most normally proportioned skinks (Lécuru 1968b; Hutchinson pers. obs.). The presternum is a squat, kite-shaped element, occasionally with a small to large fontanelle, and in contact with three ribs (on vertebrae 9 to 11). The mesosternum is a rhomboid structure with a large fontanelle, in contact with the ribs of vertebra 12 laterally and vertebra 13 at its posterior vertex. Generally a complete inscriptional rib (vertebra 14) lies posterior to the mesosternal ribs. In some species (for example *Eulamprus quoyii*, see Fig. 10 in King 1964) there are additional chevrons lying free posterior to the complete inscriptional rib, associated with the fifteenth and sixteenth vertebrae. This is especially true of species with reduced limbs. In *Lerista*, species with more reduced limbs have sternal elements that are diminished in size, concomitant with shoulder girdle reduction, but this is compensated for by an increased number of complete inscriptional ribs which partly form a visceral basket under the anterior body organs (stomach, lungs and liver).

The shoulder girdle of *Eulamprus quoyii* was described by King (1964), and Lécuru (1968a; 1968b) reviewed this region generally in lizards, including species from the Australian genera *Cryptoblepharus*, *Egernia* and *Tiliqua*. The clavicles are generally perforated in Australian lygosomines, except in species of *Tiliqua*. In most small skinks, only the leading edge of the clavicle is well ossified, and the trailing edge that overlies the coracoid is a thin, often ragged-edged sheet. The interclavicle is well ossified and cruciform. The scapulocoracoid appears to be constant in shape, with no reported variation from the condition with three fontanelles described by Lécuru (1968a). Though the whole shoulder girdle becomes reduced in size in species with reduced limbs, all elements retain normal appearance and proportions until the limbs have completely disappeared (Howie 1963).

The pelvic girdle, as described by King (1964) for *Eulamprus quoyii*, varies little in skinks. Arnold (1984a) noted that unlike many lizards, skinks lack a well-developed hypoischium, a cartilaginous rod which projects posteriorly from the ischial symphysis. Again, the pelvic girdle remains unmodified except in relative size in reduced-limbed species. In limbless species (*Coeranoscincus frontalis* and *Ophioscincus ophioscincus*), the pelvic bones are present, but the two halves no longer make contact medially (Howie 1963).

The manus and pes are primitively pentadactyl, with phalangeal formulae of 2.3.4.5.3 and 2.3.4.5.4 respectively. In reduced-limbed species, phalangeal loss commonly occurs (Chocquenot & Greer 1989; Greer 1990a), sometimes accompanied by brachyphalangy (for example, in *Anomalopus*, Howie 1963) (Fig. 31.6).

Locomotion

Most skinks have well-developed limbs and are adept at running. Russell (1988) reviewed the limb muscles of lizards, including the skink genera *Ctenotus*, *Egernia* and *Tiliqua*. Speed depends to a large extent on limb length in normally proportioned species, but the tail and sinuosity of the body become significant in reduced limbed species (Gans 1975; John-Alder, Garland & Bennett 1986). Loss of the tail can enable normally limbed species to run even faster, but is likely to impede locomotion in reduced-limbed species and is known to greatly decrease swimming speed (Daniels 1985a).

There is some variation in detailed foot structure, which suggests mechanical adaptations that improve traction on certain surfaces. Several small skinks, such as members of the *Ctenotus schomburgkii* and *C. colletti* species groups, *Morethia adelaidensis* and *Cryptoblepharus carnabyi*, characteristically have spinose (mucronate) subdigital lamellae (Greer 1980b; Storr, Smith & Johnstone 1981). This list, however, demonstrates the difficulty of finding a functional explanation for such structures. The *Ctenotus* species are mostly sand-runners, *M. adelaidensis* lives in clayey and salt-pan areas, and *C. carnabyi* is a climber.

When running, the alternating gait used by skinks leads to some sinusoidal movement of the vertebral column, and this suggests that transition to a more snake-like locomotion is a relatively straight-forward process. Skinks show the morphological stages in this transformation better than any other lizard group. Reduction in the size of the limbs is usually accompanied by reduction of the size gradient between the toes, often with phalangeal loss, and is generally followed by digital loss, beginning with the smallest and outermost toes and progressing medially (Gans 1975; Lande 1978). Limb loss pattern in *Lerista* is unusual in that the toes tend to retain the proportions of a normal pentadactyl skink, even when greatly reduced in absolute size, and phalangeal reduction seems to be 'held off' until the digit is on the point of being lost (Greer 1990a).

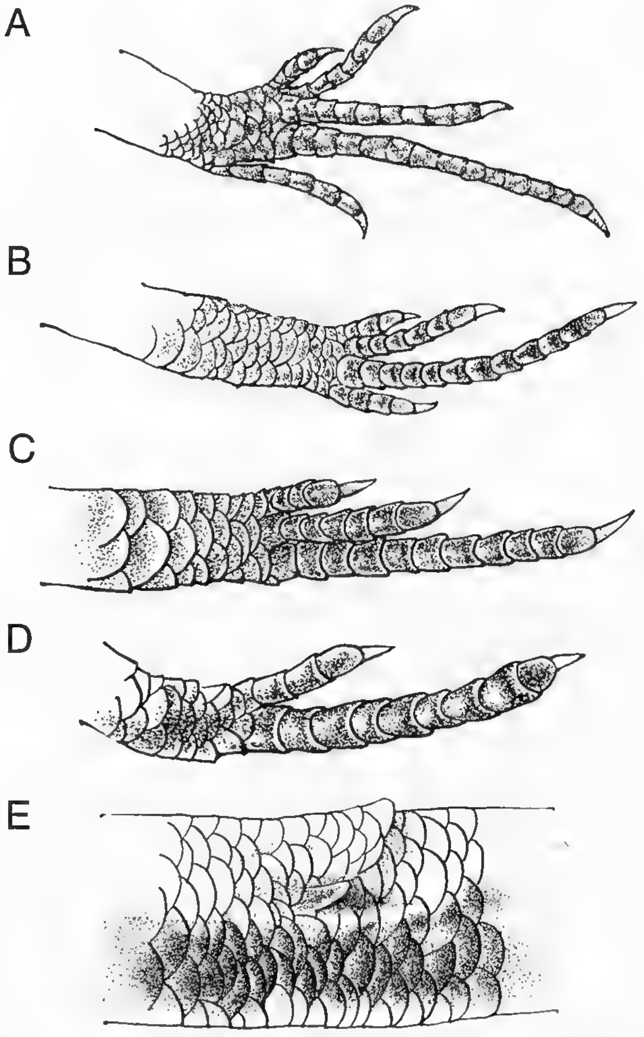

Figure 31.6 Variation in the structure of the foot in skinks. **A**, *L. microtis*; **B**, *L. dorsalis*; *C*, *L. terdigitata*; **D**, *L. edwardsae*; **E**, *L. stylis*.
[K. Bowshall-Hill]

Reduced-limbed species, even those with extremely small and seemingly almost useless limbs, use their legs to help obtain purchase, especially on smooth surfaces. In litter or soil these species progress primarily by undulation of the body and tail, the multiplication of presacral vertebrae seen in these forms increasing spinal flexibility and increasing the number of waves that can be developed along the body. A body muscle element, the *m. rectus abdominis lateralis*, is characteristic of skinks (and other taxa not included in the Iguania) (Moody 1983) and is thought to assist in undulatory movements of the lizard's trunk (Camp 1923). During undulatory locomotion the limbs stay folded against the sides of the body, often lying in shallow grooves behind the limb bases. In these species, the tail tends not to taper, staying the same length as the body until close to the tip. Presumably this prolongs the propulsive surface available, since the caudal musculature is effective for further along the tail than would be the case in a slender, tapering tail (Gans 1975). In spite of its apparent usefulness in locomotion, the tail of all of the reduced-limbed skinks is readily autotomised.

Feeding and Digestive System

Skinks are usually regarded as relying heavily on the olfactory rather than visual senses for detecting prey, but most surface-dwelling species also depend heavily on sight, being quick to detect moving prey (Nicoletto 1985). Studies of actively foraging species of *Ctenotus* (James 1991; Pianka 1969c; Taylor 1986) and the American *Eumeces* (Vitt & Cooper 1986) reveal that they frequently appear to investigate potential hiding places of prey, presumably using olfaction to confirm presence or absence. Analysis of diet reveals the presence of cryptic prey items more likely to have been found by scent than sight. In litter and sand-swimming species, vision may well be much less important than olfaction in locating food, but the appropriate studies have not been done.

The skull of skinks is typically amphikinetic (Iordansky 1990), with flexible fronto-parietal, basipterygoid, pterygo-quadrate and squamosal-quadrate joints and a pivoting epipterygoid. Most species also appear to have some movement between the pterygoid and ectopterygoid (flexipalatility). The heavily armoured skull of *Tiliqua rugosa* has secondarily lost most of its kinetic capability, although the cartilaginous joints and appropriate muscles remain (De Vree & Gans 1987).

The tongue is used in conjunction with Jacobson's organ to locate and recognise food. Unlike agamids, skinks do not use the tongue to catch prey, although it is used in drinking. *Tiliqua* species use the tongue to remove broken pieces of shell when eating snails.

Dentition varies among skinks (Fig. 31.5A–F), although diets of too few species are known well enough to permit a functional interpretation of much of the variation. Most skinks have cylindrical teeth with obtusely pointed or chisel-shaped crowns, generally with an apical crest which may be emphasised by an apical groove. The small insectivores may have teeth which are more slender and more sharply pointed, while larger species tend to have blunter, more robust teeth.

The durophagous dentition of *Tiliqua* and *Cyclodomorphus* has been noted and described by several authors, starting as early as Wagler (1830), and more recently Edmund (1969) and Estes & Williams (1984). *Cyclodomorphus gerrardii* is the most specialised of this group, having an enormously enlarged molariform tooth towards the back of each tooth row (Fig. 31.5F). The enlarged teeth do not occlude, but instead the upper tooth closes in front of the lower, and produces a shearing action rather than a direct crushing effect on any object being chewed.

The species of *Coeranoscincus*, *C. reticulatus* and *C. frontalis*, have characteristic recurved teeth which are believed to be specialisations used in preying on earthworms (Ehmann 1987; Greer & Cogger 1985; McDonald 1977). No dietary information is available for the burrowing skinks of the genus *Ophioscincus*, which also have recurved teeth with flattened, slightly flared and bicuspid crowns. The primarily vegetarian species of the *Egernia cunninghami* species group (for example, *E. cunninghami* and *E. stokesii*) have many, small, close-packed teeth, with linguo-labially compressed crowns which collectively form a crude cutting edge along the tooth row (Fig. 31.5D).

The arrangement and innervation of the jaw musculature of lizards was described by Haas (1973) and Gomes (1974), although the only Australian skink species for which detailed descriptions exist are *Tiliqua rugosa* (see also De Vree & Gans 1987) and *T. scincoides*. Available data suggest that the layout of scincid jaw muscles is typical of lizards generally.

The gastrointestinal tract is simple in most species. The stomach is muscular, and the relatively simple, tubular small and large intestine terminate at a cloaca. Significant modifications occur in some of the larger omnivorous and herbivorous species, which have broadened, but not lengthened, hindguts (Mackenzie & Owen 1923; Pollock 1989; Yeatman 1988), apparently associated with an enhanced ability to digest vegetation (unpub. studies cited by Pollock 1989).

Circulatory System

The structure of the heart in lizards was reviewed by Webb *et al.* (1974), and the innervation and layout of the major arteries in *Tiliqua* have been illustrated by Berger, Evans & Smith (1980), Burnstock & Wood (1967) and Rogers (1967). White (1976) reviewed the functional aspects of the circulatory system in lizards and other reptiles.

Skinks, like other lizards, probably use the circulatory system to assist in thermoregulatory control (White 1976). Head-body thermal differentials (Webb, Johnson & Firth 1972) and asymmetric heating and cooling curves have both been recorded in skinks, although the mechanisms behind these phenomena are not yet well documented. Studies of the large skinks, *Egernia cunninghami* and *Tiliqua scincoides*, show that they heat more rapidly than they cool (Bartholomew, Tucker & Lee 1965; Fraser 1985). In *T. scincoides*, differential heating is partly the result of variations in heart rate, and heating animals have an accelerated rate compared with cooling animals at the same body temperature. However, several studies (Daniels, Heatwole & Oakes 1987a; Fraser & Grigg 1984; Spellerberg 1972c) have shown that such physiological control of temperature is not significant in small to medium-sized skinks, such as species of *Ctenotus*, *Eulamprus* and *Lampropholis*. Some inconsistency is evident in the results obtaind by the three studies just cited. Spellerberg found that species of the *Eulamprus quoyii* complex, like the larger skinks, heated twenty to thirty percent faster than they cooled, while the other two studies (involving some of the same species) found that these skinks actually cool faster than they heat. Fraser & Grigg (1984) speculated that the disadvantage suffered by small lizards, in their lack of physiological control, is compensated for by the potential for rapid heat exchange, and allows opportunistic responses to brief periods of heat.

The nature of the heat shunting mechanisms suggested by these studies is not known in skinks. Hammel, Caldwell & Abrams (1967) showed that the head temperature in *Tiliqua scincoides* was more finely controlled than the body (colonic) temperature, and inferred the presence of hypothalamic sensory control systems. Analogy with other lizards suggests that such control systems would act to reroute blood circulation between peripheral and deep vascular circuits (White 1976) or to set up arterio-venous countercurrent heat exchanges. The peripheral vascular system can be elaborate to the tips of scales, and has been explained as facilitating heat uptake (though not retarding heat loss) in *Tiliqua scincoides* (Drane & Webb 1980). One technique denied skinks is cooling of blood in the suborbital sinus by panting. Apart from *Tiliqua*, in which the behaviour is probably secondarily derived, skinks do not pant (Heatwole, Firth & Webb 1973; Greer 1980a; Webb *et al.* 1972).

Red blood cells in skinks are elongate-oval in shape and nucleated, and range in size from 14 to 17 µm in length and 9 to 10 µm in diameter in *Ctenotus*, *Egernia* and *Tiliqua* (M.-C. Saint Girons 1970). Packed cell volume (haematocrit) in Australian skinks is typically about 30% (Hutchinson unpub. data), which appears to be typical of the concentration found in other lizards (Dessauer 1970).

Research based largely on *Tiliqua* and the non-Australian scincine *Chalcides* shows that skinks have a well-developed immune system (Cooper, Klempau & Zapata 1985; Wetherall & Turner 1972). Humoral (immunoglobulin-based) antibody responses can be obtained to a variety of foreign antigens, including a vigorous secondary response following an initial immunisation. Two classes of antibodies have been recorded: a heavy 19S antibody and a light 7S antibody (single unit). These would be analogous, if not homologous, with eutherian IgM and IgG respectively, but unlike the situation in mammals, the heavy antibody persists in high concentration after the light antibody is being produced (Wetherall & Turner 1972).

Wetherall & Turner (1972) and Cooper *et al.* (1985) reported lymphoid tissue in a number of organs, including the marrow, spleen, thymus and kidney. Presumably the thymus (Sidky 1967, Fig. 2) is a vital part of the immune system, but reptilian thymic function has yet to be studied (Bockman 1970). The white blood cells of *Tiliqua scincoides* resemble those of mammals in producing a variety of chemicals, such as the prostaglandin PGI_2, involved in inflammatory responses such as vasodilation and the inhibition of platelet aggregation (McColl & Daniels 1988).

The topology of the lymphatic system in lizards was extensively reviewed by Ottaviani & Tazzi (1977), but few data applied specifically to skinks; the European scincine *Chalcides ocellatus* was the only species discussed.

Respiration

Tenney & Tenney (1970) described the lungs in a number of reptiles and amphibians, but included no skinks. In general they found that reptilian lung surface area is proportional to metabolic rate, and that reptile lungs are not simple sacs but show pronounced compartmentalisation.

Ventilation of the lungs is mainly achieved by contractions of the intercostal muscles (Wood & Lenfant 1976). Typical skink ventilation occurs in three phases — rapid expiration followed by rapid inspiration, then a pause with the lungs inflated. Greer (1989) reviewed variation in ventilation patterns in skinks, in which displacement of the rib cage laterally in the area behind the forelimbs represents the primitive condition. In sand-swimmers, a respiratory mode is used in which the ventral part of the ribcage moves, and causes a vertical rather than a lateral displacement. This mode was first described in skinks by Pough (1969) for the African sand-swimmer *Lygosoma sundevalli*, and he suggested it is also used by the Saharan *Scincus* and *Sphenops*. To these, Greer added *Eremiascincus* and *Lerista*. Limbless skinks (except *Lerista* as noted above) expand and contract the chest cavity symmetrically, termed circumferential breathing by Greer (1989). Besides chest movements, the smooth muscle of the lung itself is involved in assisting inspiration and expiration, under the control of vago-sympathetic nerve trunks (Burnstock & Wood 1967).

Aerobic respiration is dependent on both the rate of breathing (ventilation frequency) and the amount of air exchanged with each breath (tidal volume). Bennett (1973b) reviewed these phenomena in lizards, including data on the skink *Egernia cunninghami*. In *E. cunninghami*, ventilation frequency is temperature sensitive, and rises from 22/min at 30°C to 38/min at 37°C, but is little affected by activity level. Increased oxygen demands made by high activity levels are met not by adjusting ventilation frequency, which increases by only about half again, but by three to six-fold increases in tidal volume during activity.

Exercise capability of skinks depends on both aerobic and anaerobic respiration, and like other lizards, they are less able to sustain high levels of activity than are mammals and birds. Standard metabolic rate, measured as oxygen consumption, is generally rather low in skinks, relative to other lizards (Andrews & Pough 1985). Skinks with normally developed limbs are capable of short bursts of speed of up to 2 m/sec or more (Huey & Bennett 1987; John-Alder *et al.* 1986), but short-limbed species are capable of much less (0.5 to 0.7 m/sec in *Hemiergis*). Stamina is also limited. *Egernia cunninghami* can reach nearly 3 m/sec in short bursts, but on average can maintain 0.27 m/sec (1 km/hr) for only seven minutes (John-Alder *et al.* 1986). Anaerobic respiration has been studied little in skinks, but Bennett (1982) reported that during strenuous activity about half (49%) of the energy produced by the scincine *Eumeces obsoletus* is contributed by anaerobic metabolism.

Excretion

The kidneys lie posteriorly against the dorsal wall of the body cavity, and usually extend into the pelvic region. A bladder is known to be present in at least some skinks (Bentley 1976). Nitrogenous waste is excreted mainly in the form of uric acid, but some urea production also occurs (Dantzler 1976; Hunt 1972). The kidneys and bladder are both involved in ion exchange and water reabsorption (Bentley 1976; Schmidt-Nielsen & Davis 1968).

Osmoregulation has been studied intensively in *Tiliqua rugosa* (Bentley 1976 and included references). Like most lizards, and in contrast to mammals, *T. rugosa* is able to tolerate wide fluctuations in plasma sodium concentration, from 152 to 240 mEquiv/l, which facilitates retention of body fluids during periods of desiccation. During such times these lizards seem able to shut down kidney function altogether.

A nasal salt gland was first identified in *T. rugosa* by Braysher (1971), and subsequent studies on its structure and function have been summarised by Bradshaw (1986). The salt gland only becomes active when the lizard's body temperature climbs above 30°C. It is capable of responding to both sodium and potassium loading by selectively secreting the ion in excess (Braysher 1971) and is a 'true' salt gland in that it produces a hyperosmotic secretion (Bradshaw 1986). It is not yet known whether the nasal glands of any other Australian skinks have a salt-excreting capacity.

Sense Organs

The brain of skinks is similar in topology to that of other lizards (see Fig. 1 in Senn 1979); Snyder, Gannon & Baudinette (1990) show the outline of the major regions of the brain of *Tiliqua rugosa* and its vascular system.

Relative brain size in skinks and other squamates was reviewed by Platel (1979), whose data indicated that skinks are unusually small-brained (low indices of encephalisation) compared to lizards in general. It is worth noting that most skinks examined by Platel were reduced-limbed, fossorial species in which the head is miniaturised (Rieppel 1984a), so that small indices of encephalisation could be expected. The one surface-dwelling, normally proportioned species examined (*Eumeces schneiderii*) had the largest relative brain size, and was close to the lizard average (index of encephalisation 90). The autonomic nervous system of lizards was reviewed by Berger & Burnstock (1979).

The eye is large and fully developed in most skinks, and usually has a round pupil, a distinct iris, a movable lower lid and a nictitating membrane (Fig. 31.7). The eyeball is lubricated by the posterior lacrimal and Harderian glands, sometimes supplemented by an anterior lacrimal gland (Saint Girons 1982). The eyeball is supported by a circumferential series of bony plates, the scleral

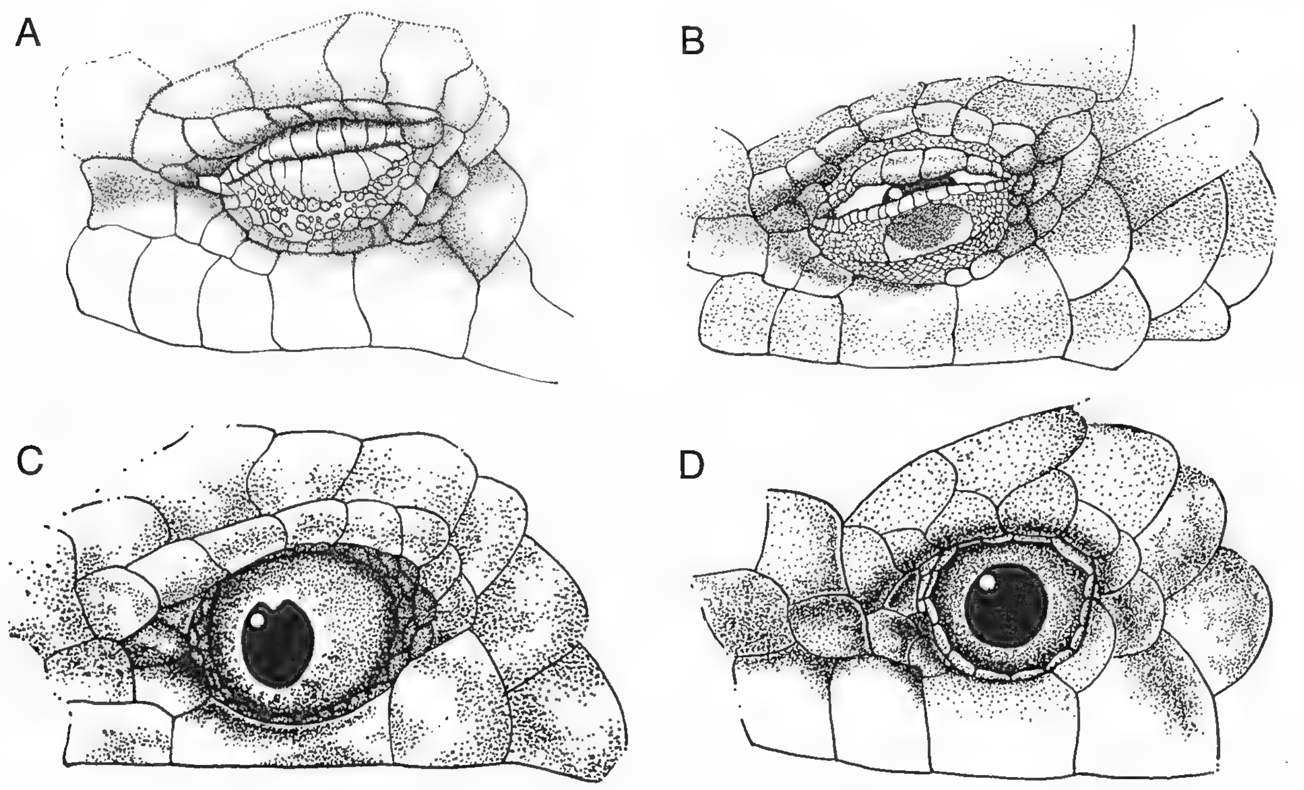

Figure 31.7 Variation in the lower eyelid in skinks. A, scaly and movable, *Egernia whitii*; movable, with a transparent 'window', *Carlia longipes*; C, transparent and immovable but distinct from the upper eyelid, *Lygisaurus foliorum*; D, transparent and completely fused to the upper eyelid, *Lerista xanthura*. [K. Bowshall-Hill]

ossicles (Underwood 1984), which usually number 14 (13 in some *Tiliqua*, Underwood 1970).

Little is known of the retinal structure of skinks (Peterson 1992) and no direct demonstration of colour vision has been made. Lizards have an all cone retina (Goldsmith 1990), with multiple visual pigments, and 'all species tested in discrimination studies have colour vision' (Cooper & Greenberg 1992), so that colour vision is probably normal for this group.

In the nocturnal species, *Egernia striata*, the pupil is vertically elliptical (Bustard 1970b), but this is not true of other nocturnal *Egernia*, or of nocturnal members of other genera, such as *Eremiascincus*. One lineage of skinks, the *Sphenomorphus* Group, is characterised by a very dark iris, from which the pupil can only be distinguished in good light. Some other species, for example *Tiliqua rugosa* and the alpine Tasmanian species of *Niveoscincus*, also have such a solidly black iris colour. Many skinks have a transparent disc (spectacle, window or brille), in the lower eyelid (Fig. 31.7B), and some have an immovable, transparent lower eyelid (the ablepharine condition, Greer 1974; Fig. 31.7C). The most likely adaptive explanation for the ablepharine spectacle is avoidance of corneal water loss in small species inhabiting habitats which are relatively drier than those of their relatives with movable eyelids (Greer 1983a).

All Australian skinks have a third light receptor, the parietal eye, which lies below a foramen in the parietal bone and is visible externally in most species as a circular spot in the rear half of the interparietal shield. The parietal eye in skinks is probably both a light and heat detector, probably acting as in other lizards as a radiation dosimeter (Firth & Kennaway 1989; Ralph, Firth & Turner 1979a).

Most skinks have a well-developed tympanic membrane sunk in a moderately deep auditory meatus. The stapes in such species is golf-tee shaped, with a long, imperforate shaft and a moderate circular footplate. The quadrate has a well-developed conch which supports the leading edge of the tympanum on its outer rim. Some skinks, all litter dwellers or burrowers, have lost the eardrum, including all species of *Anomalopus*, *Hemiergis*, *Ophioscincus* and *Saiphos*. In these taxa, the quadrate has lost the conch and the stapedial shaft is short and stout with a ligamentous attachment to the skin. The attachment puckers the skin inwards at this point producing an externally visible depression.

The principle structure which acts as a sound transducer in the inner ear of reptiles is the basilar or auditory papilla, a structure which is elaborated into the organ of Corti in mammals (Romer 1970). The auditory papilla lies in the cochlear duct (Baird 1970), an antero-ventral extension of the membranous labyrinth of the inner ear which otherwise functions in the maintenance of balance. In skinks some hair cells of the papilla are free but those in a demarcated ventral lobe of the papilla are capped by a large cupula-like structure termed a culmen (Wever 1978). The tectorial membrane, which is the usual structure providing inertial control of the sensory hair cells of the auditory papilla in most lizards, is rudimentary in skinks.

Wever (1978), surveying auditory sensitivities in lizards, found that his small but representative sample of skink genera (including the Australian genus *Tiliqua*) have hearing which could be described as 'of better than ordinary quality' by comparison with other lizards. The scincid ear is well adapted for the reception of faint sounds but poorly able to discriminate between frequencies. The single species studied which lacks a tympanum, the African *Acontias plumbeus*, retains an ability to detect airborne sounds, although with greatly reduced sensitivity.

Chemoreception in skinks, as in other lizards, is mediated by two structures, the sensory epithelium of the nose and Jacobson's organ (= vomeronasal organ) (Parsons 1970; Halpern 1992). The anatomy of the nose was reviewed by Parsons (1970). In skinks, the nasolaryngeal duct, which conducts air from the nasal cavity to the mouth cavity, is elongated, in accord with the more or less complete bony secondary palate, but in other respects appears to be similar to other scincomorphan lizards. In this group, non-sensory respiratory epithelium lines the choanal tube and the ventral surface of the nasal cavity, while sensory epithelium lies dorsally, especially over the surface of an internal fold, the concha, which projects into the medial wall of the nasal cavity of lizards.

In skinks, Jacobson's organ lies at the front of the roof of the mouth, supported below by the antero-lateral extremity of each vomer and protected above by the septomaxillae (Skinner 1973). A duct connects the sensory epithelium of this pouch-like structure with the mouth cavity. The precise manner in which scent particles are transferred to the sensory epithelium of Jacobson's organ is not certain. Pratt (1948), who included the Australian species *Tiliqua rugosa* in his study, suggested that ciliary action along the duct of Jacobson's organ would be sufficient to transfer chemical particles wiped off the tongue tip to the sensory region of the organ.

Jacobson's organ may provide fine discrimination at close range, while the nose is used to detect more distant chemical stimuli with less resolution (Cowles & Phelan 1958; Bellairs 1984). This accords with data which indicates that Jacobson's organ preferentially responds to non-volatile chemicals (Graves & Halpern 1989). Several studies have investigated use of chemical senses by skinks, based on North American species of the genera *Eumeces* and *Scincella* (Cooper & Vitt 1987; Nicoletto 1985; Simon 1983). However, comparable studies of Australian species are few (Graves & Halpern 1991).

Endocrine and Exocrine Systems

The pituitary gland of reptiles was reviewed by Saint Girons (1970), who described the scincid pituitary (including those of the Australian genera *Egernia* and *Tiliqua*) as having a unique morphology compared with several morphological trends seen in other families. Different aspects of cellular structure are similar to either anguoid or lacertoid lizards. The pituitary hormones of lizards have been reviewed by Licht & Rosenberg (1969).

The pineal complex (pineal organ plus parietal eye) is well-developed in skinks. Ralph *et al.* (1979a) and Ralph, Firth, Gern & Owens (1979b) have reviewed the function of this complex, and suggested that it has a major role in the control of thermoregulatory behaviour, including voluntary maximum and preferred body temperatures. Firth and coworkers (Firth, Kennaway & Belan 1991 and included references) have shown that in *Tiliqua rugosa* the pineal complex monitors both thermal and day-night cycles, reflected by cycles of melatonin production. The 24 hour melatonin cycles in turn are likely to be important in the timing of annual physiological cycles.

Lynn (1970) reviewed the general structure, function and variation of the thyroid in lizards and other reptiles. Lynn & Zmich (1967) reported on thyroid morphology in 56 species of skinks, including Australian species now placed in the genera *Anomalopus*, *Calyptotis*, *Cyclodomorphus*, *Egernia*, *Hemiergis*, *Lerista* and *Tiliqua*. In all of these the thyroid was single, usually strap-like in shape and located just anterior to the heart and ventral to the trachea. The thyroid is similar in function to that of other vertebrates, and it secretes iodotyrosine hormones which are controlled by the pituitary and have stimulatory effects on several aspects of a lizard's metabolism (Hulbert & Williams 1988). Wilhoft (1964), studying *Carlia rubrigularis* (*fide* Ingram & Covacevich 1989), found that thyroid activity increased, especially in females, during peak reproductive metabolic activity (mating in males, yolk deposition in females). In at least some lizards (Maderson 1984), thyroid activity is correlated positively with rates of skin sloughing, although no data are yet available for skinks.

The parathyroid is located in the neck at the bases of the carotid arteries (Clark 1970), and is paired in the four species of skinks (including the Australian species *Tiliqua occipitalis* and *T. rugosa*) which have been investigated (Rogers 1963; Clark 1970). As in mammals, parathyroid hormones control phosphate and calcium levels. The effect of altered calcium levels was noted by Sidky (1966) in the Mediterranean skink *Chalcides ocellatus* when parathyroidectomised skinks became hyperexcitable and developed muscle spasms.

The pancreas in lizards (Miller & Lagios 1970) is a three-limbed structure, with projections towards the gall bladder, small intestine and spleen. It has not been studied in Australian skinks. The American *Eumeces fasciatus* had both alpha and beta islet cells, indicating the production of both glucagon and insulin and a glucose control system comparable to that of mammals. Studies of glucose control in skinks have not been done (Burton & Vensel 1966).

The adrenals are relatively slender and are attached to the mesentery of the gonad, lying medial to the latter. Two Australian species, *Tiliqua scincoides* (Gabe & Martoja 1961) and *Carlia rubrigularis* (Wilhoft 1964) have been the subjects of adrenal gland structural and functional studies. The general anatomy, embryology and function of the adrenal in reptiles was reviewed by Gabe (1970). The adrenal has been implicated as a major secretor of progesterone in *Tiliqua rugosa* (Bourne 1981; Bourne, Stewart & Watson 1986a).

Cephalic exocrine glands in skinks include a single lower labial, up to two palatines, two anterior sublinguals, sometimes a lingual, two to three nasals, and in the orbital region a Harderian and one or two (rarely none) lacrimals (Saint Girons 1988). The anterior sublingual glands are the main salivary glands, and, at least in *Tiliqua rugosa*, one of the nasal glands is a salt gland (Braysher 1971), while most of the others serve to lubricate exposed or sensory epithelial surfaces (Saint Girons 1989). The three orbital glands are usually present in species with a movable eyelid and nictitating membrane, but in ablepharine species the nictitating membrane is lost, and with it the anterior lacrimal gland (Saint Girons 1982, 1989). The Harderian gland may have functions other than that of orbital lubrication (reviewed by Saint Girons 1989) in some other reptile groups. Suggested functions include the enhancment of olfaction by improving the collection of dissolved particles by Harderian secretions or to improve lubrication during swallowing in snakes, but no such suggestion has been made for skinks.

Exocrine glands have been identified in the cloacal region of *Eumeces* (Trauth, Cooper, Vitt & Perrill 1987). These have been suggested as sources of both species-identifying chemical cues and female sex pheromones. Unlike many other lizards, skinks lack both femoral and preanal pores.

Reproduction

The structure and position of gonads and reproductive tract were described and figured by Egan (1984) for *Tiliqua rugosa* and described briefly by Taylor (1985) for *Ctenotus taeniolatus*. The anatomy appears to be as conservative in skinks as it is for lizards in general (Fox 1977). An unusual feature seen in one Australian skink, the limbless *Anomalopus pluto*, is loss of the right oviduct (Greer & Cogger 1985).

The male reproductive system includes the sex segment of the kidney. This androgen-sensitive region of uncertain function may possibly act in a fashion analogous to the mammalian prostate, and provide nutrient support for the sperm (Cuellar, Roth, Fawcett & Jones 1972). In the two Australian genera for which data are available, *Carlia* and *Tiliqua*, the sex segment involves the collecting ducts and the proximal portion of the ureter, in which the epithelium hypertrophies at the same time as testicular activity reaches its maximum (Egan 1984; Wilhoft & Reiter 1965).

Chromosomes of skinks are relatively conservative in number and morphology, and heteromorphic sex chromosomes are the exception rather than the rule (Donnellan 1985). Each lineage has a unique karyotype, which shows little major within-group variation, most of which involves pericentric rearrangements in a few chromosomes (Donnellan 1985; King 1973). The major group trends are: *Egernia* Group, $2n = 32$, (nine pairs of macrochromosomes, pair 6 smaller than pair 5); *Eugongylus* Group $2n = 30$ (nine pairs of macrochromosomes, pair 6 smaller than pair 5); *Sphenomorphus* Group $2n = 30$ (eight pairs of macrochromosomes, pair six same length as pair 5). When present, sex chromosome heteromorphism in Australian species almost always involves pair seven, and for males and females is XY and XX respectively. Pair seven XY chromosomes characterise one lineage in the *Eugongylus* Group, namely *Bassiana*, *Morethia* and *Pseudemoia* (Hutchinson *et al.* 1990), and are present also in *Menetia greyii*, *Carlia* (*C. longipes* and *C. rhomboidalis*) and *Saproscincus czechurai.* Donnellan's (1991b) report of possible sex chromosomes involving a microchromosome pair (14 or 15) in *Lampropholis coggeri* (*L.* sp. D of Mather 1990) provides a unique exception to the general trend. Pair seven XY heteromorphism also occurs in the *Sphenomorphus* Group in some *Ctenotus* and two species of *Glaphyromorphus* (*G. fuscicaudis* and *G. nigricaudis*).

The timing of mating and gonadal cycles have been best studied in temperate southeastern Australian species (for example, Smyth & Smith 1968, 1974; Pengilley 1972; Taylor 1985), but several studies have also been carried out on tropical Australian and New Guinean species in the genus *Carlia* (Wilhoft 1963; Wilhoft & Reiter 1965; Zug, Barber & Dudley 1982). James & Shine (1985) summarised data on a variety of tropical taxa, and hormonal control of gonad activity was reviewed by Licht (1979).

Reproductive cycles of skinks vary in the timing of events and in the degree of synchrony of the cycles of the male and female reproductive organs. Taylor (1985) and Heatwole & Taylor (1988) have described eleven cycle types, but these tabulations contain several errors, and divide the variation rather artificially. In the most common cycle in temperate skinks, male and female gonads reach their maximum size in spring, and mating and fertilisation occur during late spring. Testicular and sometimes ovarian activity may begin before spring, as in *Eulamprus quoyii* (Veron 1969), *Nannoscincus maccoyi* (Robertson 1981) and *Tiliqua rugosa* (Bourne, Taylor & Watson 1986b), or may be entirely confined to spring, as in *Ctenotus taeniolatus* (Taylor 1985).

Some temperate viviparous species are characterised by desynchronised gonadal cycles, in which the males undergo spermatogenesis in autumn, when mating occurs, while females overwinter with stored sperm and ovulate in spring, when fertilisation occurs. Such a pattern is known in *Hemiergis* (Smyth & Smith 1968) and *Pseudemoia* (Hutchinson & Donnellan 1992; Pengilley 1972; Rawlinson 1974b), and has been stated to occur in *Niveoscincus* (Rawlinson 1974a; 1975), although some field observations suggest spring mating in *N. microlepidotus* (Hudson & Shine pers. comm.). Greer (1982), Hutchinson, Schwaner & Medlock (1988) and Hutchibson *et al.* (1989) reported that only about half of the females of *N. greeni*, *N. microlepidotus* and *N. orocryptus* are gravid in any one year. The extended cycle is not yet fully explained, but based on personal observations at Mt Wellington, females of *N. microlepidotus* give birth in November, while non-breeding females are ovulating. This implies that gestation is not complete before the onset of the alpine winter, and is only finished after the embryos have overwintered, leaving the female with insufficient time to provide ova with yolk during that spring. In contrast to the biennial female cycles, the testes of all males of *Niveoscincus* reach maximum size during autumn but the time of mating is not known.

Joss & Minard (1985) reported a double peak in the testicular cycles of *Lampropholis guichenoti* and *L. delicata* in early spring (September-October) and late summer (January-March). Peaks in testis mass are accompanied by maximum sperm production. In *L. guichenoti* these peaks coincide with, or follow shortly after, two episodes of ovulation in the female population. However, ovulation in *L. delicata* occurs in October-November, between the testicular peaks.

Cycles in tropical species have been less well studied, but were investigated in detail in *Carlia* by Wilhoft (1963; Wilhoft & Reiter 1965) and reviewed by James & Shine (1985). Tropical species may show almost continuous gonadal activity (*Carlia rubrigularis* and *Cryptoblepharus plagiocephalus*), or may show strong seasonality, with breeding during the wet season (*Carlia* spp., *Glaphyromorphus* spp.) or the dry season (*Morethia taeniopleura* species group). Both wet season and dry season breeders are known in tropical *Ctenotus* (James & Shine 1985). Arid zone species have not been much studied, but available data indicate late spring-early summer breeding in *Ctenotus*, *Egernia*, *Eremiascincus*, *Lerista* and *Morethia* (Henle 1989a, 1989b; Pianka & Giles 1982).

Ovulation is preceded by yolking (vitellogenesis) of the ovarian follicles. This occurs with great rapidity and seemingly relies largely on fat stores (Robertson 1981). The importance of caudal fat bodies is thus critical, especially in the *Sphenomorphus* Group, most members of which lack abdominal fat bodies (Greer 1986b). For this reason, use of caudal autotomy as an escape strategy can entail a considerable reproductive cost (Robertson 1981; Smyth 1974).

Androgens are known to reach a peak at the time of mating in at least some skinks, such as in a well-studied example, *Tiliqua rugosa* (Bourne & Seamark 1975, 1978; Bourne *et al.* 1986b). In other species, there is indirect evidence of a link between observed mating activity and testicular maximum, for example, in *Pseudemoia* (Hutchinson & Donnellan 1992), and by inference high androgen levels, but it is possible that mating activity in some species may be independent of androgen levels (*Hemiergis decresiensis*, Leigh pers. comm.), with copulation occurring at a time of testicular regression.

Steep increases (approximately eight-fold) in plasma oestradiol and progesterone levels occur during vitellogenesis in female *Lampropholis* (Joss 1985). Ovulation is preceded by a sharp drop in oestradiol levels and a peak in progesterone levels. In females of the viviparous Mediterranean genus *Chalcides*, oestradiol level peaks at ovulation, and progesterone levels are elevated through gestation until just before parturition, which is preceded by a minor peak in oestradiol (Ghiara, Angelini, Zerani, Gobbetti, Cafiero & Caputo 1987). Bourne *et al.* (1986a) reported that progesterone levels were elevated in gravid *Tiliqua rugosa*, and reached a maximum during the middle third of the 140 to 170 day gestation period. In this species, a significant proportion of the progesterone is adrenal rather than ovarian in origin (Bourne 1981).

Sperm storage by females over winter was reported by Smyth & Smith (1968) for *Hemiergis peronii.* Mating occurs in autumn, and females retain sperm until ovulation and fertilisation in spring. The oviduct is the site of sperm storage in those species of *Pseudemoia* with similar, desynchronised gonadal cycling (Pengilley 1972). The question of which sex stores the sperm relates to the issue of when mating occurs. In *Hemiergis decresiensis* from the Adelaide area (Leigh pers. comm.). The male stores the sperm, in the vasa deferentia, until mating in spring. This is in contrast to Pengilley's (1972) report of autumn mating in the south-eastern highlands population of *H. decresiensis*, and suggests an unexpected degree of lability in a physiologically and behaviourally complex characteristic.

Skinks may be either oviparous or viviparous and there is almost a continuum of modes linking the two extremes, in which oviposition occurs soon after fertilisation, through varying degrees of egg retention to placental viviparity (Shine 1983b). In two Australian species, *Lerista bougainvillii* and *Saiphos equalis*, the degree of egg retention varies geographically (Greer 1989; Robertson pers. comm.), whereby populations from cooler parts of the species ranges are essentially viviparous (Bustard 1964; Rawlinson 1974a), while those from warmer areas produce nearly full-term young in poorly calcified eggs (*S. equalis* and some *L. bougainvillii*), or early embryos in well-calcified, normal eggs (most populations of *L. bougainvillii*).

Several oviparous *Eugongylus* Group skinks oviposit communally (Greer 1989), and large egg aggregations (over 50) have been reported for *Bassiana* (Rounsevell 1978), *Lampropholis* (Fig. 31.8) (Clarke 1965; Mitchell 1959; Wells 1981) and *Nannoscincus* (Robertson pers. comm.). Maternal care, in the form of nest attendance, in species of the non-Australian genus *Eumeces*, has been well documented (Shine 1988c), but until recently there was no indication that any Australian species showed such behaviour. Ehmann (1988) reported briefly on observations of captive female *Calyptotis*, *Cautula* and *Saproscincus* and their newly laid eggs; females moved eggs by mouth from one site to another, reburied exposed eggs and seemingly attempted to prevent eggs from becoming too wet or too dry. The degree to which these behaviours persist beyond the post-laying period is not known, nor is the possible contribution to the observations from continued enforced proximity to the eggs as a result of the small size of the containers in which the lizards were kept.

Placentation in Australian skinks was first reviewed in detail by Weekes (1935), but has not been followed up by many subsequent workers. Most viviparous skinks studied have a simple, chorio-allantoic placenta with a large yolk sac, comparable to similar-sized oviparous species (Weekes 1934). Maternal and foetal circulations link simply through thinning and close contact with the epithelium of the maternal oviduct and embryonic chorio-allantoic membranes over the surface of the egg; this placental type is known in *Egernia*, *Eulamprus*, *Hemiergis* and *Tiliqua* (Weekes 1927, 1930). A more specialised placenta is known in *Pseudemoia* where yolk supply is much smaller than for comparable oviparous species (Weekes 1930; Stewart & Thompson 1993) and a specialised, elliptical, allantoplacental region develops in which maternal and foetal tissue interdigitate and fold together deeply (Harrison & Weekes 1925; Weekes 1930). Yaron (1985) reviewed reptile placentation generally, and Ghiara *et al.* (1987) and Blackburn, Vitt & Beuchat (1984) have reviewed the ultrastructural anatomy of the placenta in *Chalcides* and *Mabuya* respectively and its possible role in nutrient supply to the embryo.

Böhme (1988) reviewed hemipenial structure in lizards, although few skinks were considered. Two basic hemipenial types occur in the Australian fauna. One is relatively short and single (Greer 1979b). The second type is bifurcate, with elongate apical extensions, and is regarded as a synapomorphy of the *Sphenomorphus* Group. Arnold (1984a) reviewed cloacal and hemipenial musculature of lizards, suggesting that lygosomines may have a derived muscle complex.

Reproductive effort, as relative clutch mass, was summarised by Greer (1989), and Henle (1989a, 1989b, 1989c) has provided further data on this topic. Skinks generally produce clutches which weigh 30 to 40% of the female's body mass.

Embryology and Development

The early embryological development of *Mabuya* was described by Pasteels (1970), and Dufaure & Hubert (1961) provided a standard set of embryological stages for lizards. Bellairs & Kamal (1981) reviewed lizard embryology in general and Weekes (1927, 1930) illustrated several early embryonic stages of Australian skinks and discussed aspects of development concerned with placental formation. Skinner (1973), also using *Mabuya*, described development of the cranium, hyoid and mandible. Incubation times for eggs are generally between 30 and 60 days (Greer 1989) and gestation in viviparous species is longer, between 50 and 100 days.

Growth of juveniles may be rapid, whereby sexual maturity is reached in less than a year (Henle 1989c; Joss & Minard 1985), or may be more prolonged (Bull 1987). Tilley (1984) found that juvenile *Eulamprus tympanum* grew at similar rates until reaching sexual maturity, after which continued growth occurred at quite uneven rates. Hudson (1989), however, found that uneven growth rates were evident from hatching and birth in *Bassiana duperreyi* and *Pseudemoia pagenstecheri*, so much so that some individuals took a year longer than others to breed for the first time. Like other lizards, skinks should have determinant growth (Estes *et al.* 1988), although the few available studies (for example, Hudson 1989; Tilley 1984) show that the oldest individuals in a population tend to be the largest. Possibly most skinks do not survive long enough to reach an age where growth has ceased completely.

Postembryonic ontogenetic changes include allometry and fusion of some bones of the skull, such as those of the braincase, anterior portion of the frontals in *Tiliqua* (Rawlinson 1974a; Hutchinson 1981) and fusion of surangular to prearticular (Hutchinson pers. obs.). Colour pattern changes during growth are most marked in *Coeranoscincus* (Greer & Cogger 1985; McDonald 1977), in which complex lined or banded juvenile patterns are reduced or lost in adults. In *Cyclodomorphus*, juveniles are usually more brightly patterned with stripes (*C. gerrardii*; Field 1980), spots (*C. melanops* and *C. maximus*, Hutchinson pers. obs.; Shea pers. comm.) or head patches (*C. casuarinae*; Hutchinson pers. obs.) which fade ontogenetically. A red tail forms part of a juvenile colour pattern in many *Morethia* and *Lerista*.

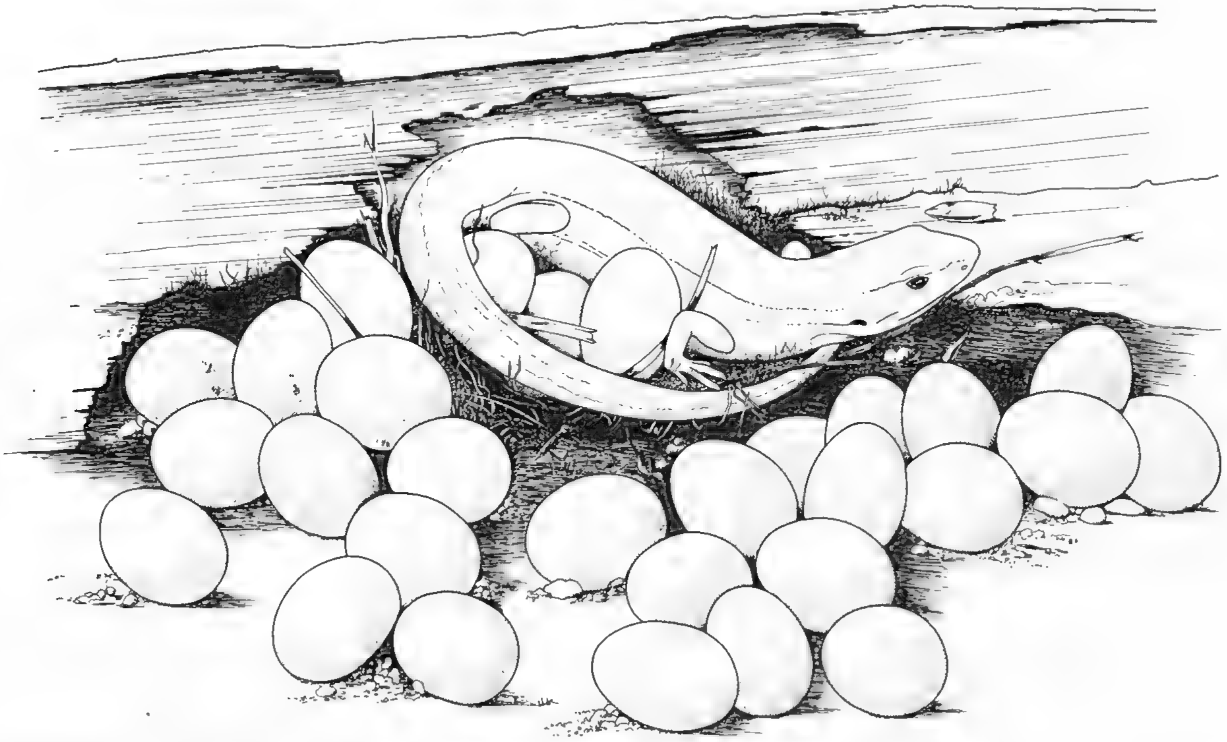

Figure 31.8 Communal nesting, as shown by *Lampropholis guichenoti*, is a feature of several skink genera. [J. Thurmer]

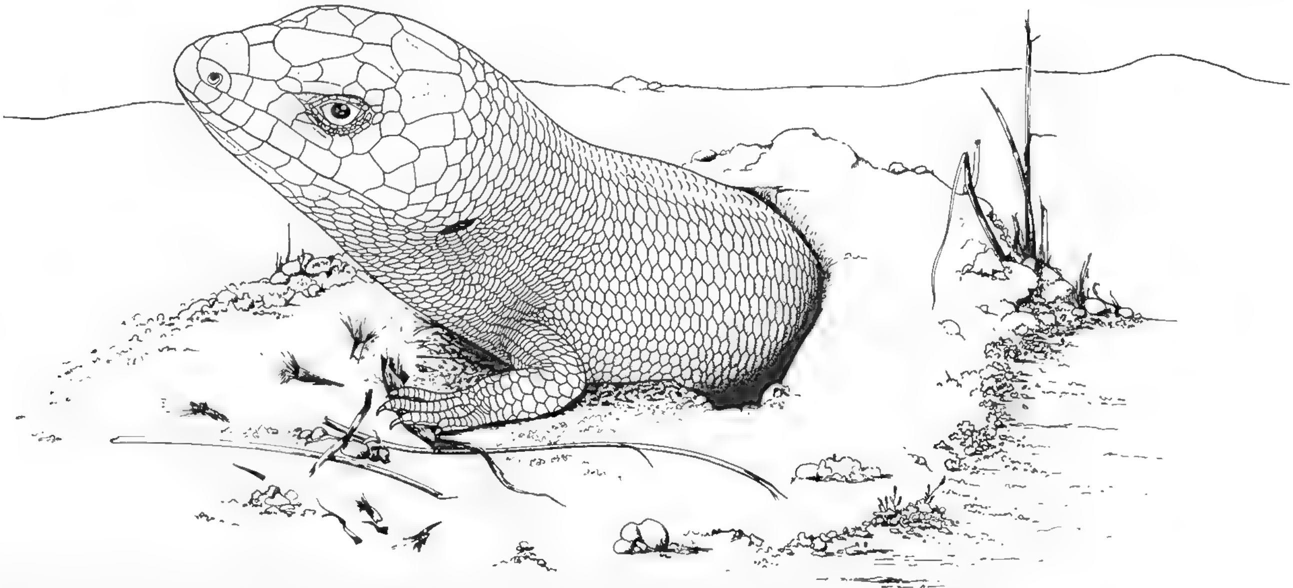

Figure 31.9 The recently rediscovered pigmy bluetongue, *Tiliqua adelaidensis*, at the mouth of its burrow, a spider's tunnel. (After photo by P. Robertson) [J. Thurmer]

NATURAL HISTORY

Life History

Few Australian skinks have been subjected to detailed life history studies. Most skinks are small, weighing less than 10 g, so that by analogy with the better known birds and mammals they might be expected to have high rates of maturation and population turnover. One of the most complete demographic studies of a small Australian species shows precisely this type of life history. Henle (1989c) reported on the life history and ecology of *Morethia boulengeri* in western New South Wales. This small species (adult mass about 1.5 g) shows a high population turnover, in which mortality plus emigration total 84 to 89% of the population per year. Associated with this is a high reproductive effort. Females produce three clutches per year, with a mean clutch size of 2.8 eggs, and both sexes reproduce in their first year. At some of the sites in this study, rates of mortality depended upon both size and body condition.

The breeding biology of the small, abundant, eastern Australian skinks *Lampropholis delicata* and *L. guichenoti* has been studied by several workers (Pengilley 1972; Simbotwe 1985; Joss & Minard 1985). These studies report a similar rapid-maturing, high turnover demographic pattern, confirmed to some extent by direct aging of individuals by skeletochronology (Hudson 1989), which detected no animals as old as two years. In cooler areas (Pengilley 1972), *L. guichenoti* grows more slowly and lives longer, probably reflecting the shorter activity period. In the Sydney area, *L. guichenoti* can produce two broods per year (Joss & Minard 1985).

Not all small skinks follow this rapid-growth, high-turnover strategy. Hudson's (1989) study of *Bassiana duperreyi* and *Pseudemoia pagenstecheri* shows that they mature relatively slowly and are long-lived species. Some individuals of *P. pagenstecheri* breed in their first year, but others take two years to mature, while *B. duperreyi* takes two or three years. Rarity of juveniles between six months and two years of age implies a heavy juvenile mortality, but adults have a relatively long life expectancy of up to seven years.

Some larger species may mature rapidly. Henle (1989a) found that *Ctenotus regius* reached sexual maturity in less than a year, and estimated a mortality rate during spring (September–November) of 67%. Age-specific mortality was not assessed, so that the degree to which this mortality occurs among the juveniles is not known. Taylor (1985) found that *C. taeniolatus*, a temperate relative of *C. regius* and similar in size, took two years to reach sexual maturity. Other species in this medium size range (about 8 to 20 g body mass) are definitely longer-lived. Tilley (1984), using skeletochronology, found that *Eulamprus tympanum* may survive for up to fifteen years, and took two years to mature. Juvenile mortality is apparently severe, but once these skinks mature, their life expectancy is high. Females had a better survival rate than males, living on average two years longer once sexually mature.

Larger skinks studied so far have proven to be relatively slow-growing species with low fecundity and long life expectancy. Barwick (1965) reported that individuals in his high altitude population of *Egernia cunninghami* took five years to mature, and Bull (1987) estimated that *Tiliqua rugosa* reaches maturity in three years and may survive for twenty or more.

Ecology

Australian skinks make use of the full range of habitats occupied by terrestrial vertebrates, with the possible exception of the outer tree canopy, though *Emoia longicauda* may come close in this respect (Ingram 1979). Most species are diurnally active on the ground surface, but there are rock specialists, for example the *Egernia cunninghami* species group, various species of *Carlia* (Ingram & Covacevich 1989) and *Niveoscincus* (Hutchinson *et al.* 1989). Members of some genera are primarily arboreal, usually on the trunks and lower branches, notably *Cryptoblepharus* species, *Pseudemoia spenceri* (Rawlinson 1974b; Webb 1985) and *Niveoscincus pretiosus* (Hutchinson *et al.* 1989). These species, as well as others such as *Egernia striolata*, are flexibly arboreal or saxicoline, depending upon the local availability of suitable hiding places, but truly saxicoline species include the alpine species of *Niveoscincus* (Hutchinson *et al.* 1989), several *Carlia* (Ingram & Covacevich 1980, 1989) and the robust, spiny-scaled species of the *Egernia cunninghami* species group.

The water skinks of the *Eulamprus quoyii* species-group are semi-aquatic (Daniels 1987; Daniels, Oakes & Heatwole 1987b) and exploit freshwater stream and lake margins. Other species may include the shoreline as one of several habitats exploited, of which examples are *Niveoscincus pretiosus* (Hutchinson *et al.* 1989), *N. metallicus* (Hutchinson pers. obs.), *Egernia coventryi* (Schulz 1985) and *Lerista arenicola* (Storr *et al.* 1981). *Cryptoblepharus litoralis* (Covacevich & Ingram 1978) and *Emoia atrocostata* (Ingram 1979; McCoy 1980) are confined to this habitat, the former species on rocky shores and the latter in mangroves.

Microhabitats chosen also vary widely. Many species with normal or long limbs are active on the surface of the ground, venturing into open areas to forage. Other species are more cryptic and stay within the shelter of loose leaf litter or inside grass tussocks. Species often show considerable fidelity to particular soil types or landforms. Thus *Ctenotus brooksi*, *C. schombugkii*, *C. leonhardii* and *C. pantherinus* are restricted to sandridges, to sandplains, to *Acacia*-dominated sites, or to where *Triodia* is present, respectively (Pianka 1969c). The spiny desert grasses of the genus *Triodia* are particularly important. Many skinks spend much or all of their lives in and around *Triodia* tussocks (Pianka 1981; Coventry 1976), and much of the high diversity of Australian desert lizards has been attributed by Pianka to the presence of this grass (see also Morton & James 1988; Pianka 1989).

Saxicoline species may be confined to massive rock outcrops, where deep cracks provide shelter (the rock-dwelling *Egernia* species fit this description), or inhabit boulder screes, where shelter is obtained in the interstices between the loose rocks (Ingram & Covacevich 1980). *Tiliqua adelaidensis* maintains its cryptic lifestyle in the burrows of ground dwelling spiders (Fig. 31.9). Arboreal species tend to live on dead trees or the dead portions of living trees, and use splits in the wood or the space beneath the bark as refuges (Bustard 1970b).

Reduced-limbed species vary greatly in microhabitat exploited. Although often loosely characterised as fossorial, many such skinks do not truly burrow. Instead members of genera such as *Calyptotis*, *Hemiergis* and *Nannoscincus* (Robertson 1981) move through dense grass or debris, or infiltrate soil cracks or the galleries of rotting logs. True sand or soil swimming fossorial types are generally recognisable by their wedge-shaped snouts, and often a countersunk lower jaw; the best examples are members of the genera *Lerista* and *Anomalopus*.

Skinks can be very numerous in some localities. Henle (1989c) estimated that *Morethia boulengeri* reached densities of 421 to 1823 individuals/ha in, and adjacent to, arid riverine woodland in western New South Wales, which represents a biomass of 0.6 to 2.4 kg/ha for this small skink. Henle's (1990a) estimate for density of another skink sympatric with *Morethia*, the comparatively gigantic *Tiliqua rugosa*, was one individual per hectare, or a biomass of about 0.8 kg/ha, based on an average adult mass for the area. Bull's (1987) more detailed study of a South Australian population of the same species yielded an estimate of 2.7 individuals/ha, and as the mean adult mass of *T. rugosa* was smaller in the South Australian population (about 575 g), the biomass estimate is again similar, at 1.6 kg/ha. These species are apparently uniformly distributed in their habitat. Other species may be highly clumped because of dependence on a particular microhabitat. Examples of this are found in species of *Egernia*, which may achieve high densities in optimal habitat but be virtually absent from intervening areas, for example *E. cunninghami* (Barwick 1965) and *E. striolata* (Bustard 1970b).

Skinks are usually solitary, but some are colonial, the best examples being species of *Egernia*, such as *E. multiscutata* (Coventry & Robertson 1980), *E. whitii* (Hickman 1960), *E. cunninghami* and *E. saxatilis* (Hutchinson pers. obs.), and some of the arboreal species in the *Eugongylus* Group, for eaxmple, *Pseudemoia spenceri* (Rawlinson 1974b), *Niveoscincus pretiosus* and *Cryptoblepharus virgatus* (Hutchinson pers. obs.). In these species, individuals may be very tolerant of one another and show little aggression, for example, *E. cunninghami* (Greer 1989), or, paradoxically, aggression may be quite intense, as shown by members of the *E. whitii* complex (Hutchinson pers. obs.). In all of the species mentioned above, juveniles and subadults may share home sites with adults, presumably their parents (Hickman 1960).

Territoriality and home range have not been studied extensively in Australian skinks. The few available studies suggest a variety of strategies. Some species show very strong attachments to particular sites and move very little. Examples are the species of *Egernia* which construct their own burrows (Hickman 1960; Pianka & Giles 1982) or those species for which natural refugia are essential for survival, such as the crevices in logs or rocks used by *Egernia striolata* (Bustard 1970b) and *Eulamprus tympanum* (Tilley 1984). These species tend to defend their home sites strongly and to move only short distance from them. An intermediate strategy is for a species to move regularly through a home range, in which there may be one or more refuges which provide shelter. Such home ranges may overlap considerably and levels of overt aggression are relatively low, as in species of *Tiliqua* (Satrawaha & Bull 1981; Yeatman 1988). Some species, especially smaller skinks for which an abundance of refuges are available, show little evidence of even a home range (Milton 1980).

Skinks are generally regarded as 'widely foraging' predators (Huey & Pianka 1981), although Henle (1989a) and Pianka & Giles (1982) suggest that some species of *Egernia* (*E. inornata, E. striata and E. striolata*) are best described as sit-and-wait predators. *Ctenotus taeniolatus* uses both foraging modes (Taylor 1986), and adults actually spend much more time sitting-and-waiting than foraging widely. As predicted by Huey & Pianka (1981), periods of wide foraging are much more productive in terms of prey capture frequency (three-fold).

Scincid diets consist mostly of arthropods (Brown 1986, 1988; Bustard 1970b; Henle 1989a, 1989b; Pianka 1986; Taylor 1986; Wilhoft 1963), and skinks are predominantly opportunistic feeders (Brown 1991). Few reports indicate either dietary specialisation or predation on vertebrate prey. Large species of *Tiliqua* and *Egernia* are omnivores (Brown 1991), although the enlarged cheek teeth of both *Cyclodomorphus* and *Tiliqua* suggest that their diets would include hard-shelled prey, such as beetles and snails, as has been observed in field studies (Dubas & Bull 1991; Shea 1988; Yeatman 1988). *Cyclodomorphus gerrardii* is probably a specialised mollusc-eater (Field 1980).

The fossorial *Coeranoscincus reticulatus* is a specialist earthworm feeder (Ehmann 1987; McDonald 1977), and the same may be true of *C. frontalis*, which has similar (although not identical) dentition (Greer & Cogger 1985). Termites form the predominant prey of several of the species of *Ctenotus* studied by Pianka (1969c) in the Great Victoria Desert, but it is not yet clear whether this represents opportunism, in taking advantage of an abundant resource, or a genetically programmed adaptation. Monitoring of populations over more than one season has shown that one species, *Ctenotus pantherinus*, acts as a termite specialist year-round, but other sympatric *Ctenotus* may prey heavily on termites at some times, while taking very few at others (James 1991). *Eulamprus quoyii* takes up to a quarter of its prey from the aquatic environment (Daniels 1987), including anuran tadpoles, which it catches as they rise to the water surface. Small skinks are a minor dietary component for larger skinks; specimens of the genera *Lerista*, *Morethia*, *Menetia* and *Pseudemoia* have been found in the guts of species of *Ctenotus* (Brown 1991; Henle 1989a).

Alpine skinks of the genus *Niveoscincus* include nectar and berries (possibly *Podocarpus*) in their diet (Kirkpatrick, Hutchinson, McQuillan & Nielsson 1991), and larger skinks take variable amounts of leafy or floral vegetation (Brown 1991). Only a few skinks are predominantly vegetarian, for example, large species such as *Tiliqua rugosa* (Dubas & Bull 1991; Henle 1990a) and the members of the *Egernia cunninghami* species group (Barwick 1965). Pollock's (1989) demonstration that *E. cunninghami* is able to survive and grow on a vegetarian diet right from birth, indicates considerable digestive efficiency, and is contrary to the generalised prediction of Pough (1973) that herbivory is only likely to be efficient in large lizards (greater than 100 g). However, no Australian species is known to be an obligate vegetarian, and even species such as *E. cunninghami*, in which plant material forms over 92% of the diet (Brown 1991), will gorge on insect prey, such as swarming field crickets, *Teleogryllus*, when they are abundant (Hutchinson pers. obs.), and will grow faster if reared on an animal rather than a plant diet (Pollock 1989).

Taxa recorded as predators of skinks include mammals, birds, other reptiles and some invertebrates (Daniels & Heatwole 1984). Among the most important predators are several genera of elapid snakes, notably *Cacophis*, *Demansia*, *Drysdalia*, *Rhinoplocephalus* (= *Cryptophis*), and *Suta* (including *Unechis*), which feed predominantly or entirely on lizards, most of which are skinks (Shine 1980a, 1980b, 1981b, 1984a, 1988a). Most skinks are diurnal and surface-dwelling and it could be expected that their snake predators would have similar habits, as is true for *Demansia* and *Drysdalia*. However, an interesting strategy has been adopted by the other genera, which are nocturnal and locate and prey upon diurnal skinks in their night-time refuges.

The pygopodid lizard *Lialis* is an ambush predator of lizards and captures skinks almost exclusively (Murray, Bradshaw & Edward 1991; Patchell & Shine 1986b). *Lialis* has numerous, peculiar, recurved teeth which are attached ligamentously ('hinged'), and are similar to those seen in snake genera, such as the Asian *Sibynophis* and South American *Scaphiodontophis*, which also prey mainly on skinks (Patchell & Shine 1986c; Savitzky 1981). These predators are thought to have developed the dentition in response to the presence of the skin-toughening osteoderms of skinks (Savitzky 1981), whereby the numerous teeth catch on, rather than pierce, the scale edges. On this basis, *Lialis* appears to have adapted more completely to eating skinks than any other Australian predator.

Other reptile predators recorded as preying on skinks include varanids (King & Green 1979; Pianka 1968, 1970b; Shine 1986d) and the colubrid snake *Dendrelaphis punctulatus* (Webb & Rose 1984; Shine 1991c). Avian predators include accipitrids, falconids and alcedinids (Barker & Vestjens 1989), cracticids (Lea & Gray 1936) and corvids (Rowley & Vestjens 1973). Foxes (Coman 1973; Croft & Hone 1978) and domestic cats (Jones & Coman 1981), regularly include reptiles as a minor dietary component.

Several invertebrate taxa are known to prey on small vertebrates and have been recorded eating skinks. Examples are the spider *Latrodectus*, noted feeding on *Anomalopus* and *Cryptoblepharus* (Raven 1990) and *Lampropholis* (McKeown 1952), the scorpion *Urodacus* observed feeding on on *Morethia* (Hutchinson pers. obs.) and *Lerista* (Henle 1989b), and the centipede *Scolopendra* feeding on *Bassiana* (Robertson pers. comm.).

Parasites of skinks include ectoparasitic mites and ticks (Bull, Burzacott & Sharrad 1989; Domrow 1987; Domrow & Lester 1985; Roberts 1970) and a variety of internal helminths (Adamson 1984; Ali, Riley & Self 1984; Angel & Mawson 1968; Daniels 1990; Daniels & Simbotwe 1984; Johnston & Mawson 1947; Jones 1985b) and protozoans (Ayala 1978; Johnston; 1932; Mackerras 1961; Paperna & Landau 1990).

Behaviour

Much of skink behaviour is associated with thermoregulation. Most skinks are diurnal and heliothermic, and most studies of thermoregulation have been carried out on temperate species (Bennett & John-Alder 1986; Brattstrom 1971a; Spellerberg 1972a, 1972b). Preferred body temperatures range from a low of 20.1°C in *Nannoscincus maccoyi* (Robertson 1981) to 38.1°C in *Ctenotus leonhardii* (Pianka 1986). Mean values for critical thermal maxima range from 45°C down to 32.9°C (Greer 1980a) and some rainforest species, such as *Calyptotis thorntonensis* (Greer 1983b) and *Saproscincus graciloides* (Hutchinson pers. obs.) are so heat sensitive that they may die after being held in the hand for a relatively brief period of time. At the other extreme, several cold temperate species can survive supercooling, for example, to –1.2°C in *Eulamprus kosciuskoi* (Spellerberg 1976). Garland *et al.* (1991) concluded that preferred temperature and critical thermal maximum are significantly positively correlated in Australian skinks but the suggestion by Huey & Bennet (1987) that there is also a positive correlation between optimum exercise temperature and either preferred or critical temperatures could not be confirmed.

Spellerberg (1972a) and Rawlinson (1974a) have distinguished two strategies among temperate heliothermic species: the shuttling heliotherms (members of the *Eugongylus* and *Sphenomorphus* Groups) and the posturing heliotherms (members of the *Egernia* Group). Shuttling heliotherms control the body temperature almost entirely by relocation, constantly moving from sun to shade when active, whereas posturing heliotherms tend to stay in a preferred area, but reduce or increase heat uptake by altering the angle of the body to the sun or adopting heat-absorbing or retarding postures (Fig. 31.10). This option may be open to the *Egernia* group purely because of the large size of most species, which enables significant physiological control of temperature flux (Fraser & Grigg 1984). As a consequence, or perhaps it is a cause, shuttling heliotherms show wide normal activity ranges, low voluntary maxima and weakly evident preferred body temperature, while posturing heliotherms have a relatively narrow normal activity range, higher voluntary minima and body temperatures grouped tightly around the preferred temperature.

Thigmothermic skinks include all of the fossorial and degenerate-limbed forms and nocturnal species such as *Eremiascincus*. Some rainforest genera, such as *Gnypetoscincus*, are probably also thigmotherms (Greer 1989), although they have not studied in detail. Thigmotherms have generally lower thermal preferenda than do heliotherms, and narrower thermal tolerances (Rawlinson 1974a). Bennett & John-Alder (1986) found that

Figure 31.10 Thermoregulatory posture of the water skink, *Eulamprus tympanum*, in which the limbs are raised and held along the sides of the body. (After photo by M. Hutchinson) [J. Thurmer]

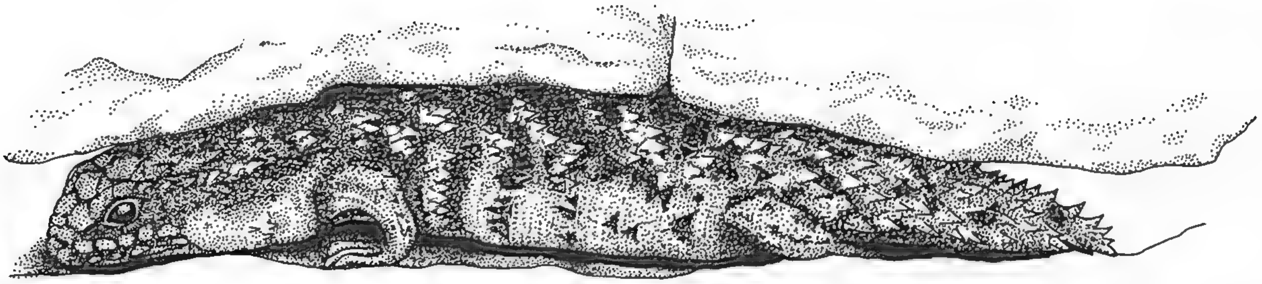

Figure 31.11 Skinks of the *Egernia cunninghami* species group, such as *E. depressa* shown here, wedge themselves into crevices for defence. The spiny scales discourage attack by predators and catch on the surroundings, preventing dislodgement. (After photo by G. Shea) [M. Cilento]

Eremiascincus and *Hemiergis* species selected warmer body temperatures at dusk and early evening than they did during the day. This is explicable as a strategy which minimises energy loss during inactivity while the warmer temperatures selected during the time of peak activity permit greatest metabolic scope.

Many physiological processes only function well or even at all when the lizard's body temperature is at or close to the preferred body temperature. As an example, Hulbert & Williams (1988) demonstrated that the thyroid, a prime controller of metabolic rate, is inactive at 20° to 22°C in *Tiliqua rugosa*, and this species is also insensitive to injected thyroxin at this body temperature; at 30° to 32°C thyroid activity and thyroxin sensitivity are fully functional.

Defensive behaviour includes crypsis, twisting, biting, tail-waving and threat displays. Large species of *Tiliqua* have an elaborate threat display, which includes body inflation, spreading the ribs and tilting the body towards the stimulus, hissing, gaping and tongue protrusion. The elongate *Cyclodomorphus casuarinae* rears the forebody while keeping the front legs pressed tight against the flanks, flickers the tongue and snaps the jaws, and produces a very snake-like overall effect. Most other species flee to cover when detected and will twist and bite if held. Longitudinal twisting of the body is particularly apparent in species of *Lerista* which are amazingly strong for their size. Spiny *Egernia* species hold the limbs against the body and arch the back to more firmly lodge themselves into the crevices in which they shelter (Fig. 31.11).

Caudal autotomy (Arnold 1984b, 1988; Bellairs & Bryant 1985; Dial & Fitzpatrick 1984; Greene 1988; Vitt & Cooper 1986) is an important method of predator avoidance in all skinks except *Tiliqua* and the short-tailed *Egernia depressa* and *E. stokesii* (both *Egernia* species use the short, flat and extremely spiny tail to block the entrances to their crevice retreats (Fig. 31.11)). The riparian *Eulamprus quoyii* alters its behaviour after autotomy, and seeks shelter on land or relies on crypsis, rather than swimming, which is inefficient in tailless lizards (Daniels 1985a; Daniels & Heatwole 1990). Juveniles of most species of *Morethia* and many *Lerista* have red tails, or blue in *L. chalybura*, which may serve to draw the attention of a predator towards this disposable structure. In *Eumeces*, blue juvenile tail colouring may be more important in acting as a social signal to inhibit attacks by adult males (Clark & Hall 1970). The bright red tail in the *Morethia taeniopleura* species group, and the blue tail of *Ctenotus calurus* are retained into adulthood. The costs and benefits of having a tail which draws attention have not been determined. Clearly, it is of advantage to lizards for predators to be encouraged to seize them by the tail rather than by the body, but the bright colour seems likely to compromise crypsis. A possible explanation is that the species concerned are particularly 'busy', widely foraging, surface active species (Greer 1989; Pianka 1969c). When inactive they are under litter, so that crypsis would count for little, and when active, they are likely to betray themselves by their movement. In such a case, detection being inevitable, it is easier to see the value of an eye-catching target to misdirect the attack of a visual predator.

In view of their strong development of chemical sense organs, skinks could be expected to use chemical cues to mediate social interactions. Studies of American species in the genera *Eumeces* and *Scincella* show that this is indeed the case, with skinks able to identify conspecifics and sex of individuals by scent (Cooper & Vitt 1987; Duvall, Herskovitz & Trupiano-Duvall 1980; Trauth *et al.* 1987). The capacity for individual recognition shown by *Tiliqua rugosa* (Bull 1988) and for recognition of 'self' versus 'stranger' scent by *Tiliqua scincoides* (Graves & Halpern 1991) suggests social behaviour that is more subtle than the simple extremes of aggressive combat or indifference previously invoked (Done & Heatwole 1977).

Agonistic behaviour involving neck arching, nose to tail side-on posturing and biting is known to vary considerably in intensity between related species (Done & Heatwole 1977, *Eulamprus*). Done & Heatwole (1977) reported that periods of fighting in captive groups of *Eulamprus kosciuskoi*, mainly among males, were followed by emergence of a single despot which dominated all other lizards and also defended an exclusive core area, although it was active throughout the enclosure. The degree to which these observations are artifacts of captivity has not been assessed by field studies. Little of the expected level of male-male aggression has been recorded in species showing strong dichromatism, for example, *Carlia*, *Pseudemoia* (Maryan 1989, reported combat in *Bassiana trilineata*), and there seems to be no record of male-female displays which emphasise male colouration. Work by Whittier (1992) on *Carlia rostralis* shows that males do use throat colour (black in males, white in females) to make an initial identification of a conspecific's sex, but chemosensory cues are also important.

Mating behaviour in skinks is not well recorded, and there are no records of any preamble apart from approach and pursuit by the male (Wilhoft 1963; Done & Heatwole 1977). Before copulation, the male grasps the female in his jaws, usually seizing the skin over the shoulders or with the upper jaw on the dorsal surface and the lower jaw on the ventral surface. This grasp can be forceful enough to draw blood (Hutchinson pers. obs.) and can leave characteristic V-shaped lines, termed 'mating marks' by Pengilley 1972. A receptive female becomes relaxed in this grasp and raises her tail; the male wraps the rear of his body under the base of the female's tail and a hemipenis is erected into the female's cloaca.

Bull (1988, 1990) discovered a unique behavioural phenomenon in the well-studied *Tiliqua rugosa*: monogamy with mate fidelity. During the spring mating season, the same male-female pair remains together for up to eight weeks, and in successive years 74% of the females and 67% of the males recaptured were with the same partner. Monogamy within a breeding season was predicted by Stamps (1983) for large, non-territorial lizards, but breeding season fidelity is unexpected in a species which is solitary for the rest of the year. Bull suggested that fidelity may ensure that males mate with known mature females, rather than risking mating with an immature, or that the familiarity of the partner might facilitate quicker recognition, mating and thus earlier breeding.

Members of the *Egernia whitii* species group are able to construct quite complex burrow systems. At their simplest (Hickman 1960; Pianka & Giles 1982), burrows have a main entrance and a blind tunnel ending just short of the surface, through which the skink can escape if threatened. More elaborate systems can occur (Coventry & Robertson 1980; Pianka & Giles 1982; Hutchinson pers. obs.) in which there are multiple entrances, branching underground tunnels and even an underground 'latrine' (Hutchinson pers. obs. for *Egernia inornata* in the Simpson Desert).

Economic Significance

Skinks have virtually no direct economic impact. Waite (1929) reported that *Tiliqua rugosa* was a minor pest of soft fruit, such as strawberries and tomatoes, and that it had been 'charged with eating fowls' eggs'. The popularity of the large, omnivorous species of *Egernia* and *Tiliqua* as pets leads to a small-scale trade in these animals in those states where commercial sale is legal.

Skinks are otherwise only likely to impinge on the economy as victims of human activities, leading to the diversion of resources to ensure the preservation of species or populations. No species of skink is known to have become extinct in Australia since white settlement, but several, mainly those with localised geographic distributions, are threatened or vulnerable to varying degrees. Examples are *Tiliqua adelaidensis* (Armstrong *et al.* 1993), *Eulamprus leuraensis* (Shea & Petersen 1985), *Ctenotus lancelini* and *Lerista lineata* (Ehmann & Cogger 1985) and *Niveoscincus palfreymani* (Rounsevell, Brothers & Holdsworth 1985). Resources are also directed to stemming the overseas smuggling trade (of unknown scope, Ehmann & Cogger 1985) in Australian reptiles. Many of the larger skinks are highly prized by European and North American reptile fanciers.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Lygosomine skinks are worldwide in distribution and are the only skinks to occur in the Australian zoogeographic region (Greer 1970a). Geographically, the nearest non-lygosomines are the scincine genera *Brachymeles*, in the Philippines and Borneo (Hikida 1982), and *Davewakeum* in Thailand (Heyer 1972).

Skinks occur in all habitats and throughout Australia, from its southernmost land point (*Niveoscincus palfreymani*, Rounsevell *et al.* 1985) to the islands of Torres Strait, and from sea level to the summit of Mt Kosciusko. In fact, the altitudinal range is encompassed by a single species, *Pseudemoia entrecasteauxii* (Hutchinson & Donnellan 1992). South-eastward from Wallacea, skinks are diverse through Melanesia to New Caledonia and New Zealand, and the genus *Emoia* has radiated through Polynesia.

Other centres of diversity are in sub-Saharan Africa and Madagascar. Outside these areas, skinks are much less diverse, although still widespread, being found through western Asia, North Africa and Mediterranean Europe and throughout temperate North America south to northern South America. In these latter areas, most species belong to a few widespread genera, notably *Eumeces* and *Mabuya*.

Cogger & Heatwole (1981) provided overall summaries of skink species density throughout Australia. In some areas, for example, western and arid Australia, the proliferation of species in two genera, *Ctenotus* and *Lerista*, leads to high species abundance though there is actually only moderate diversity at the generic level. The richest area is south-eastern Queensland which supports over 40 skink species in 15 genera. The distribution of skink genera within the major biogeographic subregions of Australia is shown in Table 26.2.

Lampropholis delicata has become established in two other countries, New Zealand and Hawaii (McKeown 1978; Robb 1980), presumably following accidental introduction. In Hawaii, this species has been accused (McKeown 1978) of supplanting the resident species, *Lipinia noctua*, itself probably a colonist which reached the islands with the Polynesian people. In New Zealand this species may occupy a previously empty niche, as it is considerably smaller than any of the native New Zealand skink species.

Affinities with other Squamates

The Scincidae are well-established as members of the lacertilian infraorder Scincomorpha (Camp 1923), which also includes the Cordylidae, Gerrhosauridae, Gymnophthalmidae, Lacertidae, Teiidae and Xantusiidae (Estes *et al.* 1988; Lang 1991; Presch 1988). None of these other families occurs in Australia, the nearest being the lacertid genus *Takydromus* which reaches Java (De Rooij 1915).

Relationships within the Scincomorpha are still uncertain. Greer (1979b) suggested that the gerrhosaurs are the closest relatives of skinks, although this may mean only that the two taxa share several features which are primitive for a scincid + gerrhosaurid + cordylid clade. Estes *et al.* (1988) indicated that a number of synapomorphies favour such a clade, which they identified as the superfamily Scincoidea. However, the study by Presch (1988), which employed a data set partly overlapping that used by Estes *et al.* (1988), placed the gerrhosaurs and cordylids closer to the Xantusiidae than to the skinks. Lang (1991) redefined the Cordylidae and reinstated the Gerrhosauridae as a separate family. He supported Estes *et al.*'s (1988) concept of a superfamily Scincoidea and found that the evidence favouring gerrhosaurs as the sister group of skinks was significant, although he preferred the arrangement: ((Cordylidae, Gerrhosauridae) Scincidae). Estes *et al.* (1988) and Lang (1991) noted convergence in almost all of the morphological characters used to establish relationships between the scincomorphan families, leading to uncertainties in phylogenetic interpretation.

The possibility that the Scincidae might be paraphyletic potentially confounds the situation. Studies by Rieppel (1984a) and Greer (1985), as well as the review of Estes *et al.* (1988), showed that the enigmatic limbless lizards of the family Dibamidae share many characteristics with acontine and feylinine skinks. The latter two studies equivocated on the taxonomic position of the dibamids, because of the many autapomorphic and lost characters of these extremely specialised burrowers, but it seems possible that future definitions of the Scincidae might have to include dibamids.

Affinities within the Scincidae

The phylogenetic relationships within the family are being unravelled slowly, and most progress has occurred since Greer began his studies of phylogeny. The current subfamilial scheme (Greer 1970a) defines three derived taxa (Lygosominae, Acontinae and Feylininae) and one grade group, the stem group Scincinae (see Fig. 26.7).

The possible paraphyly of the scincines is an obstruction to understanding the relationships of the Lygosominae. Most scincines are actually highly derived in being attenuate litter swimmers and fossorial types, but retain the primitive states of the three characters which define the Lygosominae (the Mascarene-Seychelles genera are partial exceptions, Greer 1970b). Relatively few scincine taxa retain well-developed pentadactyl limbs, 26 presacral vertebrae and relatively unmodified head shields, all characters retained in the 'ancestral lygosomine'. The genus *Eumeces* comes close to being a model for the sister taxon of the Lygosominae, but only because it retains the plesiomorphic character states noted above. Because of its primitiveness, *Eumeces* also qualifies as the sister group of all other skinks.

In Australia and its external territories, all skinks belong to the subfamily Lygosominae. Although some authors have singled out the distinctive genera *Egernia* and *Tiliqua* as having separate affinities, for example, Mittleman (1952), as Scincinae, and Fuhn (1972), as Tiliquinae, they possess the three lygosomine synapomorphies (Greer 1970a; 1986a): fused frontal bones, well-developed palatal laminae (which make contact medially in almost all lygosomines) and the antero-ventral extremity of the frontal is separated from the antero-dorsal extremities of the palatines by the expanded prefrontals.

Greer (1979b) identified three monophyletic lineages within the Australian lygosominae, termed the *Sphenomorphus*, *Egernia* and *Eugongylus* Groups. Later, Greer (1989) expanded his *Egernia* Group to combine it with several other genera, previously informally assembled as the *Mabuya* Group (Hutchinson 1981). However, as there is no strong evidence for the monophyly of the *Mabuya* Group, this review continues to use the earlier (Greer 1979b) concept of the *Egernia* Group, which is monophyletic based on biochemical and chromosomal evidence (Hutchinson 1981; Baverstock & Donnellan 1990; Donnellan 1991a). The current composition of these groups is shown in Table 31.1. Phylogenetic relationships between these three were set out by Greer (1979b), who showed that the *Sphenomorphus* Group is the sister lineage of the other two. Relationships within each lineage and between them and other lygosomines are not yet well understood.

The *Sphenomorphus* Group is the most morphologically diverse and most speciose skink lineage in Australia. However, it is the least well understood in terms of intergeneric relationships. Greer & Parker (1967) tried to unravel relationships within the group by concentrating on the huge and obviously artificial stem genus for the group, *Sphenomorphus*. They suggested the existence of two major radiations, termed the *variegatus* and *fasciatus* groups. This has not yielded much phylogenetic information, especially in Australia where the unmodified members of the *Sphenomorphus* Group tend to show intermediacy in the characters used to diagnose the *variegatus* and *fasciatus* assemblages, and also because much of the Australian fauna consists of highly derived taxa. Relationships within the group must be summarised on a genus by genus basis, but for many genera, including the largest, *Ctenotus*, there are no hypotheses on such relationships.

The genus *Sphenomorphus* in Australia has consisted of those members of the *Sphenomorphus* Group too generalised to be placed in other genera; it is a grade taxon. The morphology of the type species of *Sphenomorphus* indicates that this name applies strictly to a primarily Melanesian group of species not present in Australia. Recently, Cogger (1986) and Greer (1989) have adopted the use of *Eulamprus* for the larger, viviparous species and *Glaphyromorphus* for the more elongate, short-limbed forms. Some data (Greer 1989, 1992) indicate that the former taxon may be monophyletic, but the remaining Australian '*Sphenomorphus*' form only an irreducible cluster of species allocated to a genus (*Glaphyromorphus*) by default.

Within the polyphyletic *Glaphyromorphus*, possible sister species have been identified for *Lerista* (*G. crassicaudus* species group, Greer 1979c), *Eremiascincus* (the *G. douglasi* species group, Greer 1979a) and *Hemiergis* (*G. gracilipes*, Choquenot & Greer 1989; Hutchinson 1983). A sister-group relationship has also been proposed between the genera *Calyptotis* and *Saiphos* (Greer 1983b).

Recent attempts to elucidate intergeneric relationships within the *Sphenomorphus* Group using microcomplement fixation comparisons of serum albumin have not been very informative. The principal finding of these studies (Donnellan pers. comm.) is that all Australian genera are closer to each other than to any exotic taxon, in spite of the wide variety of morphologies. However, relationships within Australia have not been clarified. Some lineages, for example *Ctenotus*, seem to have originated earlier than others, but the overall amount of albumin sequence divergence within the Australian *Sphenomorphus* Group is too small and too evenly spread to enable the generation of well-resolved phylogenies.

The *Egernia* Group has relatively low generic diversity, and only four genera are currently recognised: *Cyclodomorphus* (Shea 1990), confined to Australia, *Egernia* and *Tiliqua* which are primarily Australian, with one species in each occurring in New Guinea, and *Corucia*, a Solomon Islands endemic. *Cyclodomorphus* and *Tiliqua* are sister genera (Shea 1990). Their close relationships have long been recognised, generally by combining the two as *Tiliqua* (Hutchinson 1981; Mitchell 1950; Smith 1937). The problem genus is *Egernia*, which is a grade group of relatively unspecialised species. Several more or less distinct species groups are recognisable in *Egernia* (Horton 1972; Storr 1978b), but relationships among them are poorly understood, and the relationships between *Egernia* and the other Group members are also not yet clear. One derived character state present in *Egernia* is the closure of the secondary palate by extensions of the vomers (Hutchinson 1981; Greer 1989). However, *Corucia* has the same structure (Hutchinson 1989), so that the feature may be primitive for the Group as a whole, or may define only a *Corucia* + *Egernia* lineage within the Group.

The *Eugongylus* Group has been subjected to the greatest scrutiny of the three, and is better understood in terms of its internal relationships. The core of the group has been the genus *Leiolopisma*, which in Boulenger's scheme was the largest of several sections within his unwieldy genus *Lygosoma*. Greer (1974) greatly reduced the size of this genus by describing several new genera and modifying or validating other generic groupings suggested by earlier workers, notably Mittleman (1952). Hardy (1977), Sadlier (1987) and Hutchinson *et al.* (1990) have divided the genus further, and, to varying degrees, the four studies have also shed light on the relationships between the genera of this group.

Comparisons of the molecule serum albumin using micro-complement fixation suggest that within Australia several lineages arose early in the history of the *Eugongylus* Group (Hutchinson *et al.* 1990). One of these is represented by the genera *Bassiana*, *Morethia* and *Pseudemoia* and probably also *Proablepharus*; the latter genus was not included in the biochemical study of Hutchinson *et al.* (1990), but its affinities have been discussed by Greer (1980b). The grouping based on biochemistry is supported by chromosomal data (presence of an XX/XY chromosome heteromorphism in males; Donnellan 1985), morphology (combined elevated presacral vertebral counts of 28 to 30 or more) and red breeding colouration in males. Another lineage which is biochemically cohesive but less easy to define morphologically consists of *Lampropholis*, *Saproscincus*, *Niveoscincus*, *Cautula*, *Bartleia*, *Carlia*, *Lygisaurus* and *Nannoscincus*. Within this group, four genera (*Carlia*, *Lampropholis*, *Saproscincus* and *Lygisaurus*) cluster biochemically, share two derived morphological character states (the beta palate and a mitten-like hemipenis, Greer 1989) and probably form a sub-lineage. The pattern of relationships among the other genera in this second lineage is not yet clear. Genera which are not obviously part of either of the radiations identified by MC'F include *Menetia*, *Cryptoblepharus*, *Emoia* and *Eugongylus*. Greer (1989) tentatively suggested a relationship between *Cryptoblepharus* and *Menetia*. Cogger (1992) placed the Lord Howe/Norfolk Island endemic *lichenigerum* in the Australian genus *Pseudemoia*. However, it is immunologically remote from the Australian mainland species and probably close to the New Zealand genera *Cyclodina* and *Oligosoma* (Hutchinson *et al.* 1990).

Greer (1989) reported that the fusion of the atlantal neural arches to the centrum could be used to define a monophyletic lineage within the *Eugongylus* Group. Such a division does not completely accord with the biochemical and some other morphological data, but does support the association of the beta palate genera with *Nannoscincus*, *Cautula* and *Bartleia*, and also links *Cryptoblepharus* and *Menetia* with this group. Points of difference between the relationships indicated by neural arch condition and primarily biochemically-derived phylogenetic schemes include the relationships of *Pseudemoia* and *Nannoscincus*. Based on MC'F data, *Pseudemoia* is most closely related to *Bassiana* and *Morethia*, taxa with the atlantal neural arches not fused to the centrum. If this is the true state of relationships, then neural arch fusion has occurred in parallel in *Pseudemoia* and the other Australian species, or *Bassiana* and *Morethia* have undergone a reversal, and other features common to the three genera (heteromorphic XY chromosomes; elevated presacral count; males with red ventral colouration) are convergent or primitive. Parallel evolution of the fused condition has probably occurred within *Niveoscincus*. Serum albumin (Hutchinson *et al.* 1990) and electrophoretic comparisons (Hutchinson & Schwaner 1991) provide very strong evidence that *N. palfreymani* (neural arches fused to centrum) is more closely related to other *Niveoscincus* (neural arches not fused to centrum) than to other taxa with the fused condition.

Nannoscincus as presently recognised comprises one Australian species and five in New Caledonia (Sadlier 1990). '*Nannoscincus*' *graciloides* (Czechura 1981) is morphologically very distinct from the other species in the genus, and was not included by Sadlier (1987) when he revised the genus. In colour pattern and proportions, *graciloides* is much closer to *Saproscincus*, especially *S. tetradactylus* (Greer & Kluge 1980). For this review it is included in *Saproscincus*, although *graciloides* lacks (Greer 1974) the beta palate shared by all other *Saproscincus*. If *N. maccoyi* is congeneric with the New Caledonian species, then a member of this genus must have crossed the ocean gap between Australia and New Caledonia relatively recently, probably post-Miocene, given the low level of albumin divergence between *N. maccoyi* and genera such as *Lampropholis* and *Cautula* (Hutchinson *et al.* 1990). MC'F data are not available for New Caledonian species of *Nannoscincus*, but data on other New Caledonian skinks, as well as skinks from other land masses outside Australia consistently suggest no recent interchange between the two faunas. Sadlier (1990) has placed *N. maccoyi* in a separate subgenus, *Nannoseps*; perhaps this subgenus will prove to warrant full generic status.

A clearer understanding of relationships within genera is beginning to emerge. Early definitions of subgroups within genera were mainly attempts to assist taxonomic descriptions, and the species groups of Storr *et al.* (1981) in *Ctenotus* and *Lerista* are good examples. However, other workers were interested in evolutionary relationships, and tried to define lineages reflecting phylogeny (*Egernia*, Horton 1972; Australian *Leiolopisma*, Rawlinson 1975). Recent studies are based on more explicit analyses of morphology (*Lerista*, Greer 1986c; 1990b; *Morethia*, Greer 1980b) or on biochemistry (*Niveoscincus*, Hutchinson & Schwaner 1991).

Fossil Record

The fossil record of skinks worldwide is poor, and until recently was practically non-existent in Australia. Estes (1984) described the only pre-Pleistocene skink from Australia, a species of *Egernia* which was left unnamed as to species. He also reported the presence of *Tiliqua* in this deposit but no description was provided. These finds are from the Etadunna formation of northeastern South Australia, dated at the time of Estes' writing as Middle Miocene (*ca.* 15 million years ago), but now thought to be Late Oligocene to Early Miocene (21 million years ago, or earlier, Flannery 1988; Archer, Godthelp, Hand & Megirian 1989). Pledge (1992) reported *Tiliqua* from cave deposits of probable Pliocene age from the Yorke Peninsula, South Australia.

The extensive Tertiary limestone deposits near Riversleigh, Queensland, have yielded abundant vertebrate remains, including evidence of a diverse skink fauna. Preliminary study of this material has already identified a new and dwarfish species of *Tiliqua* (Shea and Hutchinson 1992) and many other taxa remain to be described (Hutchinson 1992). Most of the Riversleigh skinks are from the System B sites of Archer *et al.* (1989), and probably date from the Early Miocene. All three of the major lineages of lygosomines in Australia were present in Australia at this time; the *Sphenomorphus* Group is the most abundant and the *Eugongylus* Group the rarest. Among the remains (mostly dentaries, maxillae and partial lower mandibles) are forms virtually indistinguishable from living taxa, such as some species groups of *Eulamprus* and *Egernia*, while there are also some distinctive *Sphenomorphus* Group fossils which do not closely resemble any of the living species examined so far.

The Riversleigh finds indicate that the Australian skink radiation predates the Oligo-Miocene boundary, implying that the origins of the three Australian lineages date back to the early Tertiary at least. The fossil data are in broad accord with the MC'F data (Baverstock & Donnellan 1990) which suggested that the Australian skink lineages have been separate from the earliest Tertiary. These fossils also indicate that considerably older finds, possibly Mesozoic, will be required to clarify the ultimate time of arrival of the skinks in Australia, and the extent to which the present diversity was generated within Australia or resulted from immigration.

32. FAMILY TYPHLOPIDAE

Harald Ehmann & Michael J. Bamford

DEFINITION AND GENERAL DESCRIPTION

Typhlopids are small, so-called 'blind' snakes which are highly specialised for a subterranean life. The rigid, cylindrical body bears uniform cycloid scales dorsally and ventrally, and each eye is covered with at least one large head scale which extends well beyond the eye's posterior rim. The mouth is small, crescent-shaped and ventrally located, and the dentition is reduced to a few short, recurved teeth on the maxilla of the upper jaw. The very short tail usually terminates in an obtuse spine. All 31 species of typhlopids in Australia and its territories are placed in the genus *Ramphotyphlops*.

HISTORY OF DISCOVERY

The first typhlopids described from Australia were *Ramphotyphlops australis*, as *Anilios australis* (the type series was composite) and *R. nigrescens*, as *A. nigrescens* (Gray 1845). The two specimens of the former type series (one *R. australis* and one *R. endoterus*) are from the type locality 'Australia', whereas the type locality of *R. nigrescens* is Parramatta (Cogger, Cameron & Cogger 1983a). Between 1839 and 1898, 11 typhlopid species, including the Christmas Island endemic *R. exocoeti*, were described by European taxonomists. This type material is held in European museums (see Cogger *et al.* 1983a for complete citations of all species descriptions). Until the mid-1860s, the known Australian species were placed in up to eight different genera. Jan & Sordelli (1864) placed all species in the genus *Typhlops*.

Krefft (1869) provided the first insight into their natural history, and noted that 'blind snakes burrow in search of their food, which consists chiefly of ants and their eggs and larvae'. This record was probably based on his personal observations of *R. nigrescens*, a species abundant around Sydney where Krefft worked.

Waite (1894) described five additional species of Australian typhlopids; the types of four of these are lodged in Australian museums. His natural history observations of Australian blind snakes (Waite 1918) have been widely accepted, restated and condensed, and subsequent authors have added little that is new until 1990 (Shine & Webb 1990; Webb 1990; Ehmann 1992).

The Australian typhlopids were removed from *Typhlops* by Robb (1966b) on the basis of hemipenial morphology. Since the issue of Opinion 1207 by the ICZN, which suppressed use of *Typhlina*, her resurrected name *Ramphotyphlops* has applied to these snakes.

McDowell (1972) discussed the relationships of 14 Australian species in his systematic study of the Typhlopidae of New Guinea and surrounding islands. This included a thorough analysis of the hemipenes, supralabial condition and distribution of cutaneous glands on the head in three of the Australian species.

The most recent phase in the taxonomy of Australian typhlopids was completed by Storr (1981) when he described six new species in a review of the genus in Western Australia. Two further species were described subsequently by Storr in 1984. All of Storr's type material is held in the Western Australian Museum.

MORPHOLOGY AND PHYSIOLOGY

External characteristics

Adult typhlopids range in length from 150 to 750 mm. The body is nearly cylindrical and is remarkably rigid in cross section; both

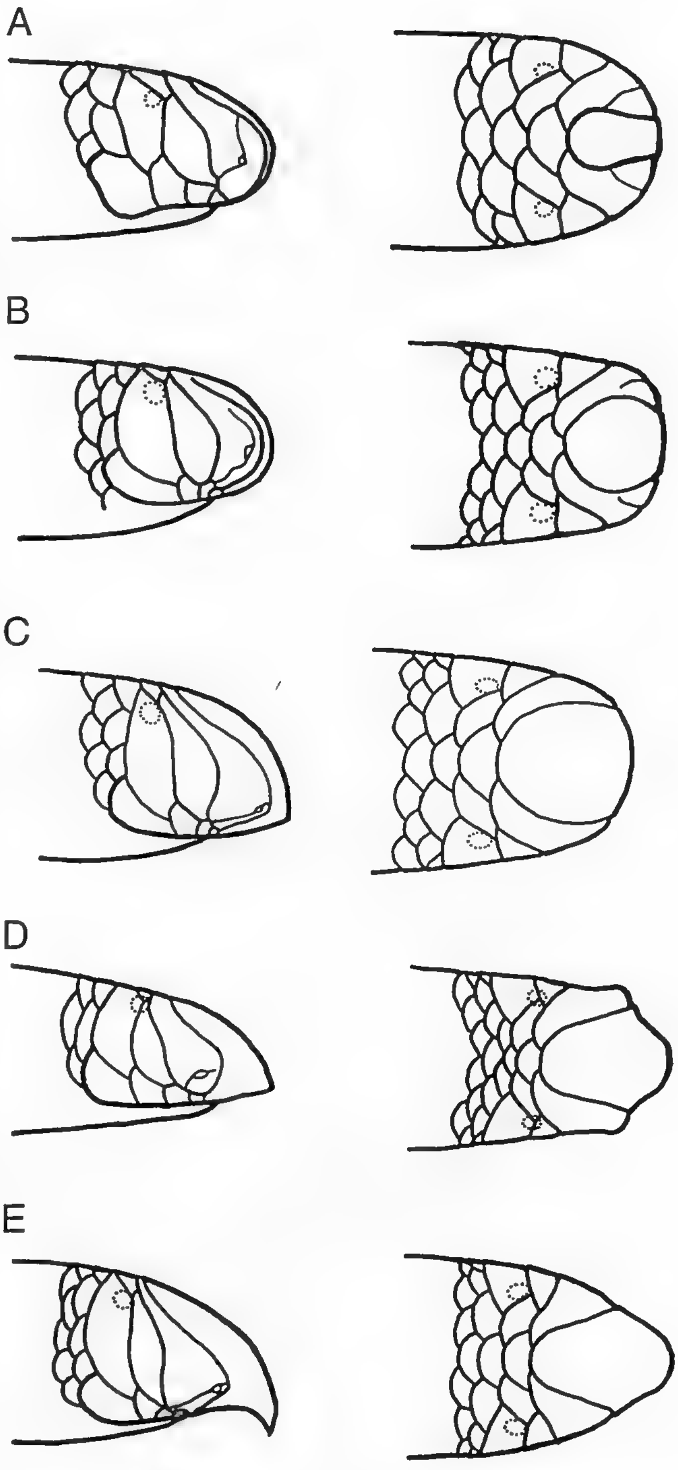

Figure 32.1 Lateral and dorsal views of the head of Australian *Ramphotyphlops*, arranged in order of increasing snout specialisation. The snout shapes of some blind snakes may be adaptations to soil characteristics such as particle size, moisture content and penetrability. **A**, *R. braminus*, sandy or loamy soils with regular hydration; **B**, *R. wiedii*, sandy, clay-loam or loamy soils with fairly predictable year-round hydration; **C**, *R. affinis*, self-mulching loamy or clay soils with unpredictable soil hydration all year; **D**, *R. bituberculatus*, sandy soils, often with calcareous inclusions or clay with unreliable winter hydration; **E**, *R. grypus*, sandy or sandy loam soils with unreliable summer soil hydration. [H. Ehmann]

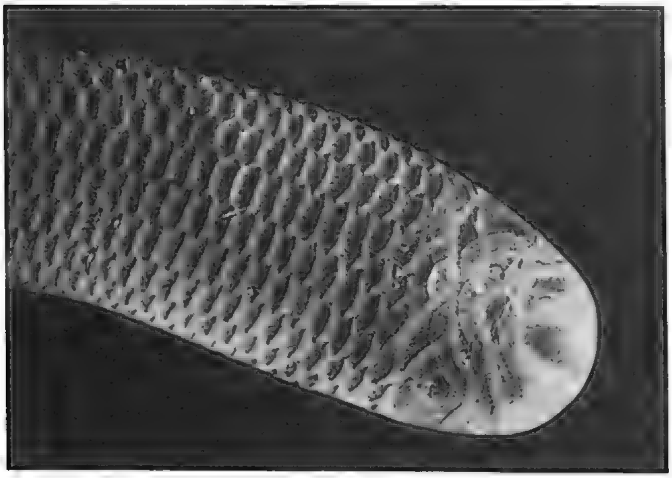

Figure 32.2 Dorsal view of head of *Ramphotyphlops nigrescens* showing overlapping scale margins, cutaneous glands, semitransparent scales. [Photo by D. Frith & H. Ehmann]

characteristics are mechanical adaptations for a subterranean life (Pl. 7.2). Adults, especially of larger species, are slightly thinner anteriorly than posteriorly. The overall appearance of the body of a typhlopid can be expressed as the length divided by the diameter (l/d). Expressed in this form, the greatest range in shape within a single species is 60 to 135. Young (or small) individuals have stouter bodies than old (or large) individuals of the same species (see Gillam 1979a).

In the process of burrowing, typhlopids clear or expand spaces in the soil with movements of the head and neck. This has led to the evolution of unusual head shapes and scale arrangements in many species. The snout may be rounded and blunt, slightly wedged and blunt, wedged with a transverse edge, or noticeably hooked (Fig. 32.1). These features are subject to some individual and geographic variation, presumably in response to particular local substrates. The snout and head shape of each species becomes more characteristic with an increase in size, small individuals often having more rounded head outlines. The shape of the snout of preserved specimens is also variable. The snout, in particular the upper labial area, is somewhat flexible and changes its shape when the mouth is distended (for example, during feeding). This generally unnoticed mobility may affect the profile and probably also the relative position of some of the scale margins, especially the so-called nasal cleft (Ehmann pers. obs.).

The tail of all Australian species is very short (less than 5% of the total length), rounded at the end and with a short, obtuse conical spine directed backward and downward. This spine 'caps' the terminal caudal vertebra (Ehmann pers. obs.).

Between species, colour varies from black, brown, buff and grey to salmon pink, but there is much less variation within a species. The body is darker above and on the sides. The transition to the paler belly is usually consistent within each species, and can be ragged and abrupt, irregular and abrupt, straight and abrupt, graded over a short distance or graduated through the entire lower side. The colour of the head and snout shields is consistent within each species. The tail may be characteristically pigmented in some species and in some species the anterior body is slightly paler.

Body Wall

The scales of blind snakes are glossy, smooth and rigid. Each headshield and body scale has a long, free margin so that consecutive and adjoining scales overlap significantly (Fig. 32.2) and provide a tubular structure that strongly 'encases' the body. The length of the scales also provides considerable leeway for frequent rather deep scratches that can 'fray' the outer edge of a scale without causing damage to its more delicate inner structure (Fig. 32.3). All of these features reduce friction and are adaptive for burrowing.

Cutaneous glands are present under the proximal margins of the head and neck scales (Haas 1932; McDowell 1974), and their evidence or obscurity are characteristic at the species level. These glands secrete a sebaceous substance which probably acts as an interscale lubricant and probably also promotes the resilience of the scales to cracking and abrasion. These cutaneous glands are very pale in some dark species and can easily be mistaken for scale margins. The surface of each head scale (especially the rostral scale) has numerous microscopic pustulate glands which probably also exude a sebum-like substance (Fig. 32.4).

The midbody scale rows can be difficult to count because they are translucent and overlap extensively (see Fig. 32.3). The number of rows, which varies from 16 to 24, is generally thought to be constant within a species although Storr (1981) reported variation in *R. leptosoma*.

Australian blind snakes shed their epidermis within the substratum by crawling forward through a tight-fitting soil hole. The consecutive, rigid rings of scale epidermis may telescope together to form a fairly tight ball or short tube (Ehmann pers. obs.).

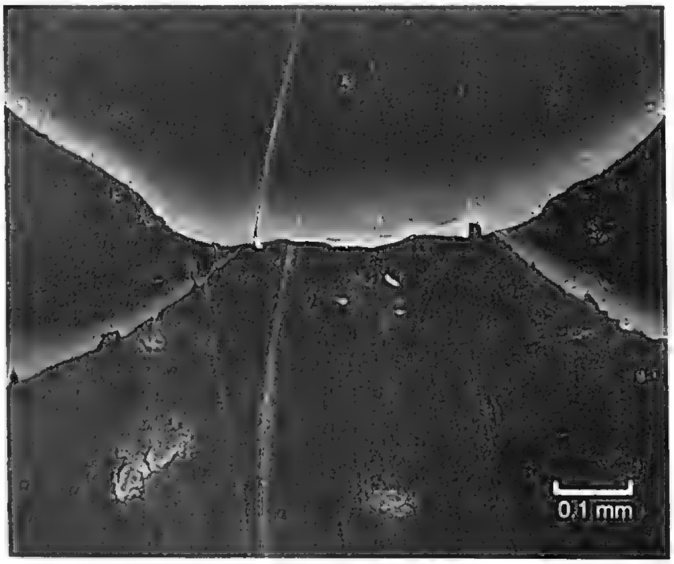

Figure 32.3 Scanning electron micrograph of scales of *Ramphotyphlops nigrescens*, showing frayed edges and deep scratches. [Photo by D. Frith & H. Ehmann]

Skeletal System

The skeletal structure of typhlopids differs from that of other snakes in several aspects. The skull is simple with few distinct bones, and the snout bones and prefrontals are firmly sutured to the brain case (List 1966). Only about three short, weakly recurved and sharp primary teeth are located distally on the maxilla and no teeth occur on the dentary of the lower jaw. The pelvis is represented by a single bone on each side (Waite 1918). The caudal vertebrae curve downward distally and the tip of the terminal vertebra fits into the back of the terminal spine (Ehmann pers. obs.). The vertebrae have strong accessory processes (metapophyses or mamillary processes) which project laterally to the articular facets of the prezygapophyses and the ribs have strong tubera costae projecting backward from the head (McDowell 1974).

The osteology of Australian blind snakes is poorly studied. In *R. australis*, a small ectopterygoid-like bone is present (Waite 1918), though this element is generally considered to be lacking in typhlopids (McDowell 1974).

Locomotion

Blind snakes use lateral undulation to move quickly on the surface and rectilinear, lateral undulation and concertina motion to crawl more slowly on the surface or through insect tunnels and galleries (Ehmann pers. obs.). Gans (1974) discussed these locomotory methods in detail.

Feeding

Ingestion has been studied in detail for *R. nigrescens* by Webb (1990) and a photograph by John Weigel of ingestion of ant pupae in the same species was published by Wilson & Knowles (1988). The pupae and larvae appear to be rapidly 'sucked' into the widely-gaping mouth. During ingestion, the two maxillae probably move rapidly in unison, rather than alternating as in other snakes. The transverse alignment (rather than longitudinal as in other snakes) of the maxillary teeth, the closeness of the left and right maxillae, and the large channelling coronoid processes on the lower jaw's dentary all support this conclusion. At least one typhlopid, *R. nigrescens*, is able to follow scent trails of worker ants of four species (Webb & Shine 1992), and *R. diversus* may be able to forage under water (Ehmann 1992).

Temperature Regulation

Typhlopids are not known to be surface active during the day or to bask in the sun but, since soil temperatures tend to be moderate or relatively high (particularly in warmer months), they can obtain heat from their surroundings and are thigmothermic (see Rawlinson 1974a). The desert species, *R. bituberculatus*, which is active at night on the cool ground surface, burrows down into warmer sub-surface layers and then re-emerges to continue surface activity (Ehmann 1992). When *R. wiedii* is heat-stressed (35°C) on a warm, impenetrable surface, it gapes its mouth, salivates and elevates the head vertically while continuing to crawl along in search of a softer penetrable substrate or other shelter (Ehmann pers. obs.). Head elevation in this situation may serve to keep the head from over-heating.

There are no data on temperature preferences among typhlopids.

Respiration

The external nares of blind snakes are located at the junction of snout scales in the nasal cleft. The cleft is the distal margin of a scale, which forms a partial baffle-like cover over the front of the naris in all species (Fig. 32.4). This provides a narrow slot through which inhaled air must pass before entering the naris, and thus the slot can hold back some soil particles. Furthermore, the external nares are directed ventrally and backward under the snout so that soil particles cannot be forced into them. Air is therefore drawn from below the burrowing head and the snake can form a small, ventral air cavity in soil by raising the snout. *Ramphotyphlops* possesses an anterior tracheal lung and a posterior right lung; there is no left lung (Robb 1960).

Excretion

Blind snakes excrete nitrogenous wastes as a blob of white uric acid paste with a rather wet suspension of faecal material. Their subterranean habitation with relatively high humidity, the high moisture content of their food and restriction of nocturnal surface activity to periods of moist weather conditions combine to minimise the risk of dehydration for typhlopids. The strong smelling cloacal contents are evacuated as a smear when a blind snake is held firmly or roughly handled. The cloacal pouches (Robb 1966a) may also be involved in the storage of some fluids for defence (see Exocrine glands).

Sense Organs

The eyes of typhlopids are small and deeply set in the head (Fig. 32.2). The ocular scale and its dermis overlying the eye are transparent. The eye of *R. ligatus* has an iris, lens and pigmented retina (Ehmann pers. obs.). Typhlopids are probably able to determine light levels and form some visual images (see also Embryology and Development). Like all snakes, typhlopids lack external ear apertures, but a well-developed inner ear is present (McDowell 1974). They respond to vibrations when on or in the ground or in water (Ehmann pers. obs.). John Mitchell (in Schwaner, Miller & Tyler 1985) noted that *R. australis* emits an audible squeak when handled roughly. The olfactory sense of blind snakes is well developed and both surface and subsurface activity is characterised by an almost constant flicking of the small, pale, bifid tongue (Ehmann pers. obs.).

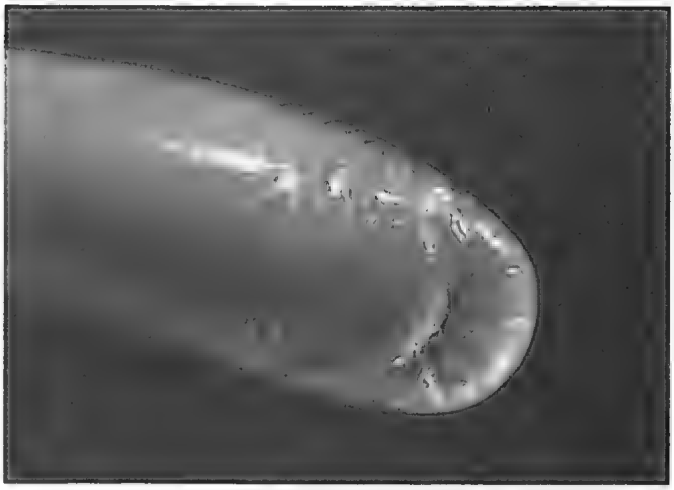

Figure 32.4 Ventral view of head of *Ramphotyphlops nigrescens* showing pustulate glands on the rostral scale, the underslung mouth, and the baffle-like margin of the nasal cleft over anterior half of the external, ventrally directed naris [Photo by D. Frith & H. Ehmann]

Exocrine Glands

The head shields of many Australian blind snakes have prominent cutaneous glands (see Body Wall). Robb (1960, 1966a) found a median cloacal gland and paired scent or anal glands. Maryan (1988) reported 'the foul smelling odour ... from the anal glands was quite strong' in 26 day old *R. australis*, supporting the view that these odours may be used for defence.

Reproduction

The left oviduct is generally considered to be lost in typhlopids (McDowell 1974), but Cogger, Sadlier & Cameron (1983b) reported a female *R. exocoeti* with a well developed left ovary and oviduct. The solid, distal portion of the hemipenis of *Ramphotyphlops* is permanently everted, and is sheathed by the proximal portion when the hemipenis is retracted (McDowell 1974). This contrasts with the eversion of the entire hemipenis, as in all other snakes. The hemipenes may be supplied with sperm stored in the male's cloacal pouches (Robb 1960, 1966a). The sexes are similar in most respects, but on average females are larger and relatively shorter-tailed than males (Shine & Webb 1990) and some become noticeably distended when gravid. Mating has not been observed and probably occurs below the surface. *Ramphotyphlops braminus* is known only from females and is the only snake known that is presumed to be parthenogenetic (McDowell 1974; Nussbaum 1980). All Australian species are believed to produce soft-shelled eggs. Shine & Webb (1990) found 'that most species have highly seasonal reproductive cycles, with vitellogenesis in spring (September to November) and oviposition in summer (December to February)'. In a comparison of nine species, and within *R. nigrescens*, mean clutch size was highly correlated with mean adult female body size. Clutch sizes vary from one to 34 in 11 species with species means from three to 13 (Shine & Webb 1990). There are two accounts of captive females 'lying on' or 'coiled around' their recently laid eggs (Fleay 1981; Maryan 1988) which may indicate at least early parental care.

Embryology and Development

The elongate, white, thick parchment-shelled eggs of *R. nigrescens* absorb moisture from the surroundings throughout the incubation period. As a result, they increase in diameter and slightly in length, and undergo a 2.2 fold increase in weight

(Ehmann pers. obs.). *Ramphotyphlops nigrescens* lays eggs in an advanced stage containing well-developed embryos with large, fully pigmented eyes. Incubation times range from 47 to 51 days at 25°C and 30 to 35 days at 30°C, with a reasonable indication that temperature dependent sex-determination does not occur (Shine & Webb 1990). Hatchlings of *R. australis* remain within the egg cases for about one day after pipping. The earthworm-pink dorsum of the emergent hatchling darkens to a purplish-pink in 26 days; the venter is white (Maryan 1988).

NATURAL HISTORY

Life History

Males reach maturity at a significantly smaller size than females in 11 species, a dimorphism that is more pronounced in larger species (Shine & Webb 1990). Age at sexual maturity and longevity are not known. The elapid, *Vermicella annulata*, preys exclusively on typhlopids (Shine 1980e). Few other data on predators are available, although feral cats are known predators of typhlopids.

Ecology

John Mitchell noted the abundance of *R. bituberculatus* in casuarina country (in Schwaner *et al.* 1985) and Swanson (1981) reported on the preference of *R. braminus* for gardens. *Ramphotyphlops braminus* has also been found in arboreal locations, such as the compressed leaf-bases in the trunks of banana plants (Bamford pers. obs.). Typhlopids are usually not encountered on agricultural land subject to ploughing or intense grazing (Ehmann pers. obs.), but they do survive in remnant ungrazed bushland in agricultural regions in the wheatbelt of Western Australia. For example, *R. australis* may be present in patches of bushland as small as one hectare (Bamford pers. obs.).

Soil characteristics, in particular penetrability, longer-term moisture content, particle sizes, the nature and extent of cracking, and presence of invertebrate prey and burrowing invertebrates are probably essential features of the habitat for typhlopids. Many species probably selectively use ant and termite galleries, cavities and holes in decaying stumps, invertebrate burrows and deep soil cracks. When regularly used by adults, such sites usually have a lesser network of locally enlarged galleries, suggesting active enlargement and maintenance by the snake (Ehmann pers. obs).

Large individual typhlopids enter nests of bull-dog ants, *Myrmecia*, and feed on their pupae and larvae (MacColloch 1909, Shine & Webb 1990); small ones probably do likewise in the nests of smaller ants. This suggests that one snake in its lifetime may utilise a range of ant species' nests. Thus, similarly sized individuals of sympatric typhlopid species could compete. Typhlopids inhabiting and feeding in ant nests appear to be tolerated (Ehmann pers. obs.). Perhaps they provide some benefit or produce a pacifying pheromone.

Mitchell (1961) found earthworms, grubs, weevils, woodlice, ants and termites in stomachs of two South Australian species, and Ehmann (1992) found worms and leeches in a species from New South Wales rainforests.

Aggregations of *R. nigrescens* have been reported. Hoser (1980) found seven and 35 individuals together in January, one female occurred with one to three adult males from September to January inclusive (Shine & Webb 1990), and two females with five males were found together in September (Ehmann pers. obs.). Seven juveniles of *R. wiedii* were noted in August (Hoser 1980) and one female with one to three males in October (Shine & Webb 1990). Springtime aggregations are probably related to mating activity. The well-developed olfactory system of typhlopids, coupled with their likely capacity to produce attractant pheromones, probably assists aggregation.

Behaviour

Typhlopids are most often seen on the surface at night during or after rain or floods or in warm, humid weather. During very wet weather many species take temporary shelter near the surface under rocks, fallen timber, loose soil and leaf litter (Ehmann 1992). Bamford (pers. obs.), however, has recorded *R. australis* and *R. hamatus* active on the surface at night in very dry weather.

Economic Significance

Typhlopids are not known to have economic significance, but forestry, agricultural and grazing practices and predation by feral cats and foxes may affect them significantly. *Ramphotyphlops braminus* is believed to be a recent (1968) arrival in Australia, at Darwin, as a stowaway in pot plants or soil (Storr 1968a). It was discovered in gardens at Katherine by 1978 (Boyd pers. comm.) and it is uncertain whether it could compete with or displace native species. The endemic, rare and similarly sized Christmas Island blind snake, *R. exocoeti* may be affected by *R. braminus*. The status, biology and conservation needs for the 16 species known from about 20 or less specimens should be determined quickly. Amongst this group, *R. affinis*, *R. broomi*, *R. exocoeti*, *R. guentheri*, *R. leptosoma*, *R. pinguis*, *R. tovelli* and *R. unguirostris* are most important because each occurs in areas with the risk of major habitat loss or change.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

There are approximately 40 species in the genus *Ramphotyphlops*, which occurs from India through South-East Asia — Malaysia, the Philippines and Indonesia — and New Guinea to Australia and the western Pacific islands. Thirty species occur within Australia and one on Christmas Island. One species, *R. braminus*, has been spread by human transportation and now occurs in India, Australia, South Africa, Madagascar, much of South-East Asia and western Mexico. There are no typhlopids in Tasmania or in Australian alpine areas.

Distribution maps and ranges for some Australian species are based on very few, often old, collecting records.

Affinities with other Groups

The Typhlopidae is one of three small families of snakes in the infraorder Scolecophidia. All are referred to as blind snakes. The typhlopids are distinguished by the absence of teeth on the lower jaw. This infraorder is the most ancient living snake group and it occurs on all continents and many temperate and tropical islands. Relationships between the Typhlopidae, Leptotyphlopidae and Anomalepididae are unclear, but some aspects of anatomy and morphology show that the typhlopids retain more ancient characteristics than the other two families (McDowell 1987). Because of their small size and fine, brittle bones, these snakes are poorly represented as fossils, and the earliest scolecophidian fossil is known from the early Eocene of Europe. The fossil *Typhlops grivensis* was described from the French mid-Miocene, and *T. cariei* was described from the sub-Recent of Mauritius Island (Rage 1987). Archer, Hand & Godthelp (1991) reported Australian fossil typhlopid material from the Riversleigh deposits.

Affinities within the Taxon

The two genera that comprise this family can be distinguished reliably only by dissection of the paired cloacal pouches in the male (Robb 1966b). McDowell (1974) and Storr (1981) placed some of the Australian species in species groups on the basis of morphology. Cytogenetic and molecular data may provide more accurate determination of intrageneric relationships.

33. FAMILY BOIDAE

Harald Ehmann

DEFINITION AND GENERAL DESCRIPTION

Worldwide the boids include terrestrial, arboreal, burrowing, semi-aquatic and saxicoline species. They are non-venomous, medium-sized or very large snakes. Many of the Australian species are nocturnal and many feed on mammals or birds as adults. Most boids immobilise their prey in tight coilings of the body, and use sustained constriction to kill prey by suffocation (Fig. 33.1).

The Boidae are distinguished from other snakes by the presence of vestiges of the pelvis and, usually, hindlimbs which appear as cloacal spurs in live snakes. The supratemporal and quadrate bones are long, resulting in a relatively large mouth. Uniform, large, recurved sharp teeth are present on the dentary, maxilla, palatine, pterygoid. Teeth are present also on the premaxilla of most pythonines. The rigid lower jaw has a coronoid element, and the anterior skull elements are moderately flexible and mobile on the brain case. The pupils of all boids are vertically elliptical (Underwood 1976; Kluge 1993). Most boids have a functional left lung that is up to 75% the size of the right one (Parker & Grandison 1977). Most pythonines and some boinines possess heat sensitive pits in the labial region of the head.

The family comprises about 85 species, in two subfamilies, distributed through most of the tropical and temperate regions. In Australia, the subfamily Pythoninae includes 15 species in five genera (Kluge 1993). The subfamily Boinae does not occur in Australia. Kluge (1993) proposed that the Pythoninae originated in the Australasian region.

HISTORY OF DISCOVERY

The earliest discoveries of Australasian pythonines are associated with early voyages of discovery and early European settlement in eastern Australia and the islands to the north. The first described species that is undeniably Australasian in distribution is *Morelia amethistina* (as *Boa amethistina* Schneider, 1801); the type is presumed lost and the type locality is not known (Cogger, Cameron & Cogger 1983), though it may have come from the Moluccas or Timor (Kluge 1993). *Morelia spilota* was the first species described from Australian type material (Cogger *et al.* 1983).

European-based workers described eight Australian species last century, and deposited the type specimens in European institutions. Two species of *Aspidites* were described by Australian-based zoologists last century. Krefft deposited the type specimen of one of these (*A. melanocephalus*) in the British Museum, while the type specimen of *A. ramsayi* (Macleay, 1882) is believed lost. Three of the five species described this century were recognised as a result of careful re-assessment of known species (see Cogger *et al.* 1983; Kluge 1993); two of these, *Morelia oenpelliensis* and *M. carinata*, are recently-discovered, spectacular and remotely distributed species.

During the past two decades Shine and his co-workers have investigated many aspects of the biology of most Australian pythons (summarised in Shine 1991a). The natural history of the Australian pythons was summarised by Ehmann (1992).

MORPHOLOGY AND PHYSIOLOGY

External characteristics

The Pythonines are robust, muscular snakes (Pl. 7). The tail is prehensile in many species, and moderate in length compared to the long tails of some arboreal colubrids and the short tails of burrowing elapids. The head is distinct from the neck in most species (except *Aspidites*) and the eyes are moderate (*Aspidites*) to large (*Morelia*) in size. The smallest adult pythonines are 0.45 m in length; the largest are reported to exceed 10 m (Kluge 1993). The streamlined, rounded head, with non-protrusive eyes of

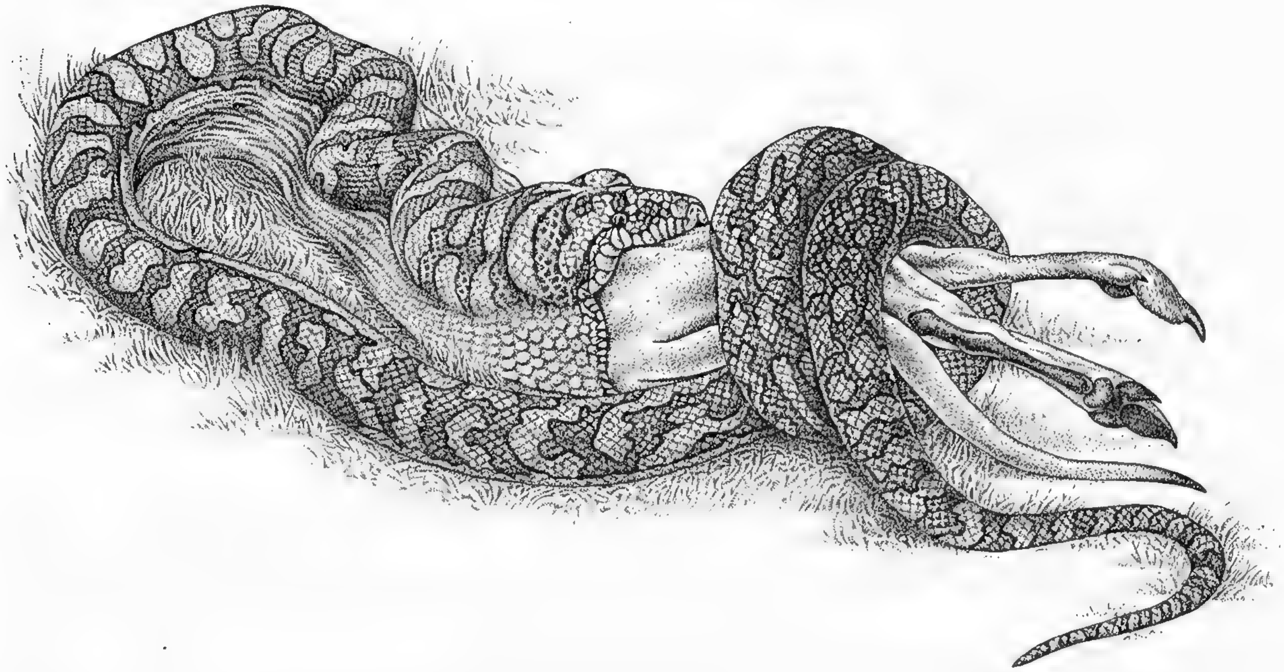

Figure 33.1 A large *Morelia spilota variegata* constricting and eating a young Whip-tailed Wallaby, *Macropus parryi*. (After photo by W. Farrugia/ANT) [K. Hollis]

Aspidites may be an adaptation for entering hollows, burrows and earth cracks for shelter and finding prey. The neck of adult *Antaresia* (= *Liasis childreni* group of Smith 1981) is distinctly slender while the body is often quite thickset. This combination allows rapid and long strikes at flying prey, such as bats entering caves, where anchor points are scarce and precarious (Shine 1991a; Ehmann 1992). The longest Australian python on record, *Morelia amethistina*, exceeded 8 m; Aboriginal people from Arnhem Land report that *Morelia oenpelliensis* may be longer, though more slender (Ehmann 1992).

The greatest range of colour variants is found in the widespread species *Morelia spilota* (Ehmann 1992). In *Morelia viridis* (formerly *Chondropython*; see Kluge 1993), juveniles may be rich yellow (Pl. 7.3), reddish orange or orange, and change between one to 12 weeks to the typical adult green colouration (Pl. 7.4) when they are one to three years old (Ross & Marzec 1990; Ehmann 1992).

Photographs of all Australian pythons appear in Wilson & Knowles (1988) and Ehmann (1992). Hoser (1989) published many photographs of variants, and Ross & Marzec (1990) provide photographs of many boids in Australia and elsewhere.

Body Wall

The dorsal overlapping body scales are rhomboidal in shape, and the single row of enlarged ventral scales is narrower relatively than those of colubrids and elapids. The body scales are small and mid-body scale row counts are high (mean 51, range 31 to 80; after Cogger 1992) for Australian species. These high counts reflect the need for greater stretching of the skin between semi-rigid scales to accommodate bulky mammalian prey, especially in the larger species (Fig. 33.1). The smallest species (*Antaresia* spp.) have the lowest scale row counts.

Morelia carinata is the only pythonine with keeled scales (albeit weakly keeled), whereas rugose or finely keeled scales occur in many Boinines. Such scale carinations or keeling may provide grip and/or directional stability when moving through vegetation or over muddy substrata (*cf. Candoia*, *Tropidonophis*) or when restraining struggling prey, and may provide air channels that reduce suction attachment when crawling on soft muds.

The frequency of skin-shedding in some captive boids was reported by Hoser (1982). Banks (1985a) reported a sloughing cycle of 10 to 250 days, and an exceptional period of 645 days in an adult male of *Antaresia childreni*, the longest sloughing cycle ever reported. Generally boids shed less frequently than the more active elapids and colubrids.

SKELETAL SYSTEM

The skull (Fig. 33.2) is long compared to colubrids and elapids, especially in the snout and temporal regions. The extensive gape of boids reflects the posterior elongation of the supratemporal, quadrate and the lower jaw, which is enhanced by the mobility of the anterior bones of the upper snout (especially the maxilla and its associated bones). The supraorbital bone, which forms the upper margin of the orbit in pythonines, is absent in boinines (McDowell 1987). The osteology of boids and a detailed morphological study of the skull bones and dentition of pythonines are described by McDowell (1975) and Kluge (1993), respectively.

Solid, long, pointed and razor-sharp teeth are present on the maxillary and dentary, on the palate (palatine and pterygoid) and on the premaxilla (except in *Aspidites*). The numerous teeth gradually decrease in size posteriorly, except on the very short median premaxilla. There is no diastema, nor are there large teeth or fangs as in some other snakes.

The vertebrae are procoelous with well-developed condyles. Accessory articulating facets, namely the zygosphene and the zygantrum are present, as are zygopophyses and small, inconspicuous accessory prezygopophysial processes (McDowell 1987; Underwood 1976). The ribs have tuber costae and simple terminal cartilages.

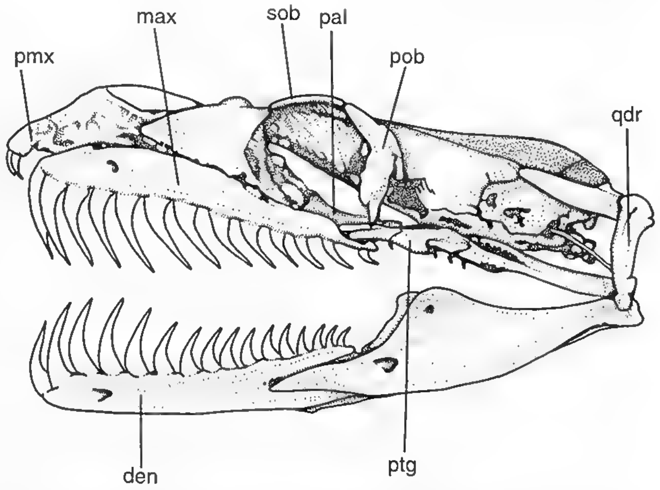

Figure 33.2 Lateral view of the skull of *Morelia amethistina*, illustrating the supraorbital and the arrangement of the teeth. **den**, dentary; **max**, maxilla; **pal**, palatine; **pmx**, premaxilla; **pob**, postorbital; **ptg**, pterygoid; **qdr**, quadrate; **sob**, supraorbital. (After McDowell 1979) [T. Wright]

The vestigal hindlimbs and pelvic structures, seen in live pythons as a spur-like projection on either side of the vent, are important appendages during mating (see Reproduction; Shine 1991a).

LOCOMOTION

The following summary of locomotion in boids is based partly on Gans (1974) and Cundall (1987). Boids, like other terrestrial snakes, use lateral undulation in swimming, in rapid movement on land and sometimes in hasty climbing during escape. In this mode of locomotion all parts of the snake are in motion.

Rectilinear locomotion ('belly walking') is most commonly used by boids for slow forward progress when stalking prey or foraging. In concertina locomotion, one third to two thirds of the body is held static in relatively tight 'S' bends while the remainder, which appears much straighter, moves forward. Then the previously static part of the body is moved forward in similar fashion, so there is an alternation of movement of the front and the hind portions of the body. This mode is mostly used during arboreal activity when moving between or along widely spaced elevated branches and vines or inside naturally occurring vertical hollows and channels.

Morelia viridis is the only truly arboreal Australian boid. Most are at least partly terrestrial. All pythonines swim, although species of *Aspidites* and *Anteresia* do so only when necessary, for example when the ground is flooded. Species of *Morelia* occasionally enter the water, and *Liasis mackloti* (previously *L. fuscus*; Kluge 1993) and *Liasis olivaceus* habitually enter the water (Ehmann 1992).

FEEDING AND DIGESTIVE SYSTEM

Detection and capture of endothermic prey in many boids (including most pythonines) is facilitated by the heat sensitive labial pits. Active ectothermic prey, especially reptiles, may have a body temperature that is significantly higher than the ambient temperature or that of the substratum, and therefore is presumably detectable by pythons. The absence of labial pits in *Aspidites* (Kluge 1993) and the boinines *Eryx* and *Charina* (Parker & Grandison 1977; Ross & Marzec 1990) is perhaps not surprising in view of the semi-fossorial lifestyle and/or hunting behaviour of these genera. *Morelia viridis* and *Aspidites ramsayi* (Pl. 7.2) may attract potential prey by caudal luring (Murphy, Carpenter & Gillingham 1978; Wilson & Knowles 1988).

Prey constriction in snakes is best developed in the Boidae. Most boids use three to eight body coils to constrict prey. As in other snakes, prey ingestion involves major relocations of the lower jaw bones, particularly in adult snakes taking in a large meal (Fig. 33.1). Cundall (1987) reviewed the functional morphology of snake feeding and provided many references to boids.

During digestion some pythons, for example *Morelia spilota*, may position the stomach in a warm spot thereby elevating its temperature (Webb in Heatwole & Taylor 1987; Slip & Shine 1988c).

CIRCULATORY SYSTEM

Underwood (1976) and Kluge (1993) reviewed some aspects of the circulatory system of boids, and the intercostal arteries in particular. Thermoregulatory aspects of circulation in Australian and New Guinean boids have been reported by Webb & Heatwole (1971) and Johnson (1975a, 1977). Thermoregulation is described under Behaviour below.

RESPIRATION

Oxygen consumption and energy metabolism during intense movement has been studied in one boid, the Desert Rosy Boa *Lichanura trivergata roseofusca*. Its energy output/consumption was the lowest of six snake species studied (Ruben 1976; Lillywhite 1987b). Bennett & Dawson (1976) reviewed snake metabolism (including oxygen consumption) and Lillywhite (1987b) has summarised research on snake cardiorespiratory function.

Several Australian pythons are known to be able to remain fully submerged in water for between 20 and 45 minutes (*Liasis mackloti, L. olivaceus, Morelia amethistina, M. spilota*; Ehmann pers. obs.). *Liasis mackloti* (as *L. fuscus*; Shine 1991a) and *L. olivaceus barroni* (Ehmann 1992) spend considerable periods of time partly or almost fully submerged. The submergence capacity of pythons is perhaps not unexpected since they are generally large-bodied, with large lungs and a relatively low metabolic rate (Andrews & Pough 1985).

EXCRETION

Australian pythons (except *Morelia carinata*) excrete nitrogenous waste as uric acid paste, usually with faecal material (Ehmann pers. obs.). Excretory and evaporative water losses are minimised by behavioural factors. Australian pythons usually are freely active on the surface only at night when relative humidity is usually high, or during overcast or rainy conditions by day (Ehmann pers. obs.). The arid-adapted pythons of the genera *Antaresia* and *Aspidites* may have more efficient excretory systems and water conservation mechanisms compared to their relatives from more mesic habitats (*Liasis* sp. and *Morelia* sp.).

SENSE ORGANS AND NERVOUS SYSTEM

The most noteworthy sense organs in many boids are the infra-red or heat sensitive labial pits that allow these snakes to detect, stalk and strike prey accurately in the dark. These pits (Fig. 33.3) are found within the labial scales (absent in *Aspidites*) in pythonines, and in boinines they are between the labial scales (present only in a few species). Kluge (1993) made a detailed morphological study of the labial pits in pythonines, and de Cock Buning, Terashima & Goris (1981) analysed the warmth reception of pit organs.

Many boids and especially pythonines have scale pits, or apical pits, that are believed to be sensory (McDowell 1975; Kluge 1993).

EXOCRINE AND ENDOCRINE GLANDS

Anal glands are reported in some pythons (McDowell 1975) and Ross & Marzec (1990) describe and illustrate probing the 'musk glands' for gender determination. Anal glands probably produce pheromones that act as mate attractants in adults (especially females). They may function as predator repellents in young snakes.

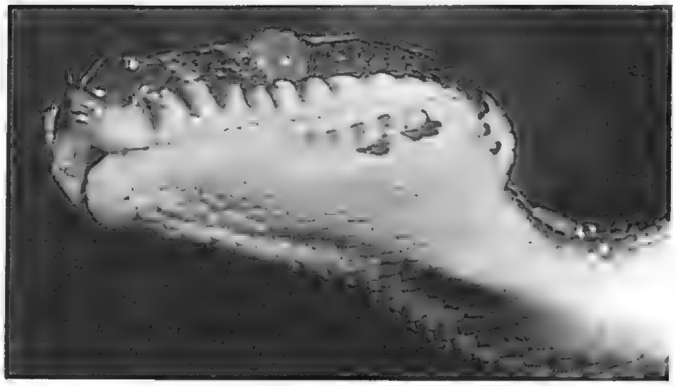

Figure 33.3 The labial pits of *Morelia spilota*, within the labial scales, sense the heat emitted by ectothermic prey. Note the opaque spectacle over the eye, indicative of incipient skin shedding. [Photo by H. Ehmann]

Seigel & Ford (1987) provided a comprehensive review of reproductive endocrinology in snakes. Testosterone levels in males of the cuban boa *Epicrates striatus* peak during mating (Seigel & Ford 1987).

REPRODUCTION

Observations on captive boids have contributed substantially to the literature on boid reproduction. A major review of snake reproduction by Seigel & Ford (1987) included some boid examples, especially concerning parental care. Heatwole & Taylor (1987) also reviewed many important aspects of reptilian reproduction.

Available information indicates that most Australian pythons are oviparous (Ross & Marzec 1990; Shine 1991a; Ehmann 1992); no information is available for *Morelia carinata*. McDowell suggested that all pythonines are oviparous (McDowell 1975), whereas the boinines as far as is known are viviparous (Parker & Grandison 1977; Ross & Marzec 1990).

In south-western Australia, spermatogenesis in *Morelia spilota imbricata* starts in late summer or autumn and culminates in November when mating is believed to occur (Kuchling 1991). In many species, the male must experience an episode of cooling to breed successfully (Ross & Marzec 1990). Mengden *et al* (1980) published photomicrographs of normal and heat-affected (abnormal) python spermatozoa.

The morphology of the paired hemipenes of boids has been extensively studied as an adjunct to systematics. Boids hemipenes lack spines, in contrast to those of colubrids and elapids. The club shape, flounces and terminal loops of the engorged everted hemipenes of *Liopython albertisi* are illustrated by Ross & Marzec (1990).

The seasonal timing of boid reproduction varies considerably (Shine & Slip 1990; Ross & Marzec 1990). In Australia, ovigenesis usually occurs from October to January, especially in the southern and eastern sections of the continent, at least in species for which there are sufficient data. In the monsoonal north, oviposition occurs earlier in *Liasis mackloti* (August-October) and possibly serves to avoid nest inundation by rains in the wet season from December onwards. A high proportion of non-reproductive females in large collections suggests that many female pythons probably do not reproduce each year.

Courtship and copulation of boids, mostly in captivity, is well documented (Goin, Goin & Zug 1978; Murphy, Carpenter & Gillingham 1978; Murphy, Lamoreaux & Barker 1981; Charles, Field & Shine 1985; Charles 1988; Ross & Marzec 1990; Shine 1991a; Vandermark 1992). During courtship the male crawls over the female, flicking his tongue, and frequently touches his chin on

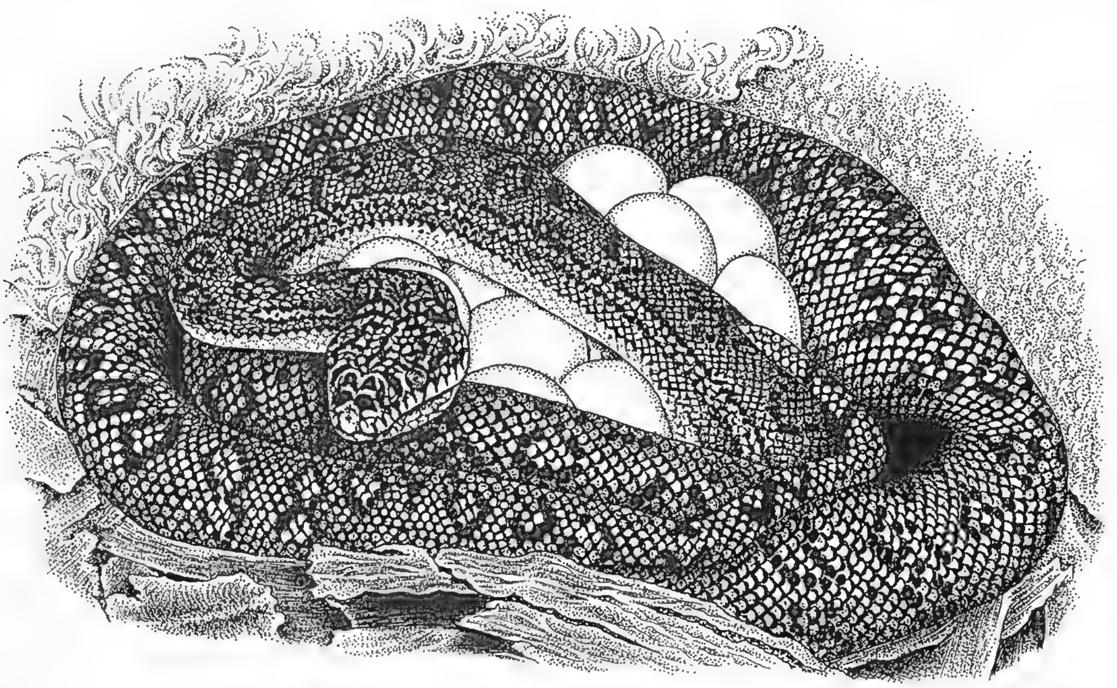

Figure 33.4 A brooding female *Morelia spilota* coils around her clutch of eggs to warm and protect them. (After Shine 1991) [K. Hollis]

the female's back. The male rakes his larger spurs (Shine & Slip 1990) back and forth (termed spurring) over the female's posterior body. In some boids, the male stimulates the female with his spurs to move her cloaca into an accessible position juxtaposed to his own cloaca. One of the male's two hemipenes is partly everted and inserted into the relaxed cloacal opening (vent) of the female, and is then fully everted and engorged with blood so that it swells in the female's cloaca and cannot be easily withdrawn (Ehmann pers. obs. of *Morelia spilota variegata*). Copulation may occur one to many times over several days and sometimes with several males, each copulation lasting between 10 and 150 minutes.

After copulation, many female boids refuse food or eat very little as eggs develop. In pythonines, the distended female often lies with her mid and posterior belly uppermost (Christian 1978; Murphy *et al.* 1978, 1981; Charles *et al.* 1985; Charles 1988; Ross & Marzec 1990).

Oviposition in pythonines occurs at a site presumably selected by the female. Seven nests of *Morelia spilota variegata* were associated with bales of hay, a pile of grass or densely matted vegetation (Charles *et al.* 1985; Slip & Shine 1988c, 1988e). Shine (1991a) reported oviposition by *Liasis mackloti* in goanna burrows on high ground near a swamp.

The clutch size of eleven Australian python species varied from five to 21. Mean clutch size was not significantly correlated with mean adult size, although three of the smallest pythons had consistently small clutches of five, six and seven eggs (Shine & Slip 1990; Shine 1991a). In a re-evaluation using data from Shine (1991a), a significant positive correlation was found between an estimator for reproductive effort (mean hatching size x mean clutch size) and mean female body size. The eggs (and hatchlings) of *Aspidites melanocephalus* are surprisingly large (Charles *et al.* 1985), but quite small in *Morelia spilota* (Ehmann pers. obs.).

After laying, the female python brings the eggs together firmly with a body loop and then coils herself around them. The eggs are soon stuck together into a coherent mass (Fig. 33.4). At this stage the females of some species become aggressively protective of their clutch (Charles *et al.* 1985; Ross & Marzec 1990), and lunge and bite at any threatening intruder.

In some species, female pythons are known to maintain relatively high and stable egg temperatures during incubation by leaving the eggs in the morning, basking nearby, and when warm, returning to their eggs to warm them. If temperatures fall to a certain point, a brooding female may 'shiver', producing heat by anaerobic respiration (Harlow & Grigg 1984; Charles *et al.* 1985; Slip & Shine 1988c). Females may also leave the brood to drink, and Shine (1991a) reported captive *Liasis mackloti* wetting her eggs on returning with water held in her cloaca, presumably to rehydrate them. Seigel & Ford (1987) and Shine (1988c) have reviewed parental care in reptiles, including the pythonines.

Hatching of pythonine eggs has been reported many times (Murphy *et al.* 1981; Sheargold 1979; Charles *et al.* 1985; Charles 1988; Ross & Marzec 1990). The hatchling first slits the leathery egg shell using its egg tooth. Kluge (1993) has summarised the egg tooth's occurrence and its attachment. The neonate may remain inside the slit egg for up to 48 hours, presumably absorbing remaining egg yolk and fluids. Sheargold (1979) reported that neonates of *Liasis maculosus* (as *L. childreni*) left their eggs in rapid succession, as if on cue, some time after the last egg had pipped. Such synchrony may improve each hatchling's chance of surviving predators. Shine (1991) provided data on the average lengths of neonates in eleven species of Australian pythons, and Ross & Marzec (1990) provided additional data for many boids bred in captivity.

Hybrids between genera, species and subspecies are known for captive snakes from Australia (Banks & Schwaner 1985; Hoser 1989; Kortlang 1989). In eastern Australia, *Morelia s. spilota* × *M. s. variegata* hybrids are sometimes found in the wild. Captive interspecific and intergeneric crosses, *Morelia spilota* × *M. amethistina*, *Morelia spilota* × *Liasis mackloti* and *L. stimsoni* × *L. childreni* are between species that are sympatric over much of their common ranges, yet hybrids have never been found in the wild. This suggests that there are strong pre-mating isolating mechanisms that operate between wild pythons, and that genetically even the genera are closely related, supporting McDowell's (1975) view of close relationships based on the morphology of the species.

EMBRYOLOGY AND DEVELOPMENT

Embryonic development in boinines occurs *in utero* and the young are born as small snakes, whereas in pythonines most embryonic development occurs *in ovum* following oviposition. A novel and potentially valuable technique for observing the later embryonic development of reptile eggs was developed by Barnett (1979, 1987) in response to *Liasis maculosus* eggs that split open during incubation through absorption of excess water. The wide open egg was suspended in an improvised humicrib and developed to full term.

The neonates of *Morelia viridis* and the very similar *Corallus caninus*, undergo similar dramatic colour changes as they grow (Ross & Marzec 1990). Changes in body shape are associated with the ontogenetic changes in diet, from lizards and/or frogs to endotherms, of some Australian pythons (Shine & Slip 1988), especially in some *Antaresia* (Ehmann pers. obs.)

NATURAL HISTORY

Life History

The size or age at which boids become sexually mature is known for a few species. Shine & Slip (1988) determined that sexual maturity is attained at approximately 70 to 75% of mean adult length in most of 13 species of Australasian pythons. Males are consistently smaller than females at maturity. *Liasis mackloti* reaches sexual maturity about one year after hatching (Shine 1991a). Pythonines generally reach maturity in 18 months to four years, whereas boinines mature in 18 months to seven years; in both subfamilies males often mature earlier than females (Ross & Marzec 1990).

Longevity in captivity was summarised for some boids by Ross & Marzec (1990), but these data may not apply to wild animals. Growth curves have been published for *Liasis mackloti*, in which size-biased mortality occurs in larger animals (Shine 1991a).

Ecology

The diet of the small and more xeric-adapted *Antaresia* comprises frogs and lizards. Reptiles predominate in the diets of medium to large sized, xeric-adapted *Aspidites*, and form 92% of all dietary items in *A. melanocephalus* (Shine 1991a). Mammals and birds are major dietary items of the larger Australian boids. Murid rodents predominate and possums, bandicoots, rabbits and bats also eaten (Shine & Slip 1990). Macropods, especially wallabies, are also eaten by large pythons. The eggs of magpie geese, *Anseranus semipalmata*, are eaten by large, mostly female, *Liasis mackloti* (Shine 1991a). At Humpty Doo in the Northern Territory, *Liasis mackloti* shows habitat and dietary lability, and assumes a semi-aquatic, terrestrial or arboreal life style, depending on the availability of water and associated prey (Shine 1991a). In this area, the population density of *Liasis mackloti* was estimated at hundreds of snakes per hectare (Shine 1991a). The diet of many species changes ontogenetically (Shine & Slip 1990; Ross & Marzec 1990; Shine 1991a; Ehmann 1992).

Shine & Slip (1990) proposed that sparse vegetation cover and a scarcity of large endothermic prey has, through lack of habitat and prey selection, resulted in the evolution of smaller species (especially *Antaresia*) and reptile eating (*Aspidites*) specialists.

Worrell (1963) described winter concentrations or aggregations of *Morelia amethistina* on open ground in deep rainforest gorges of the Atherton Tableland. These aggregations disperse with the onset of warm weather. Webber (1978) reported a large mass of adults and at least one juvenile *Morelia s. spilota* in the Grose Valley, New South Wales, and aggregations of one large female and one to three courting males of this species are common (Shine 1991a). Two spring breeding aggregations of four and five *M. spilota* were observed on the Murray River near Blanchetown (Ehmann pers. obs.).

Many diseases and parasites are known from captive boids (see Ross & Marzec 1990), but their impact on wild populations is unknown. Shine (1991a) outlined some examples for snakes generally, including pythons.

Dispersal and migration of boids is poorly documented. It is likely that neonates and young boids disperse into and through areas unsuited to adults, where smaller, suitable shelter sites and lizard or frog prey are available.

Behaviour

Male-male combat under captive conditions is well documented in some boids. Such behaviour may be rare in free-ranging snakes. In such combat, two male *Aspidites melanocephalus* tightly entwine their tails, align and overlay their bodies loosely, and elevate the head and forebody. Each rakes his spurs on his opponent's body 0.5 to 2 times per second; no biting was seen (Barker, Murphy & Smith 1979; Murphy *et al.* 1981; Ross & Marzec 1990). In contrast, Charles *et al.* (1985) observed tight coiling and biting by a larger male when a smaller male was substituted for a female mate. Male-male aggression is reported in *Liasis olivaceus*, *Morelia spilota variegata* and *Morelia viridis* (Moran 1988; Charles *et al.* 1985; Walsh 1985; Ross & Marzec 1990), but is believed to be absent in *Morelia spilota spilota* (see Shine 1991a).

Thermoregulatory behaviour has been extensively studied in Australian and New Guinean boids. Cogger & Holmes (1960) first reported basking and coiling to elevate and maintain body temperature in *Morelia spilota variegata*. Coiling into a tight ball-like mass significantly reduces loss of stored heat and extends the time that digestion and ambush hunting can occur. This behaviour has been reported in several species (Johnson, Webb & Johnson 1975; Johnson 1975a; Slip & Shine 1988b).

The patterns of heat distribution within the bodies (and associated thermoregulatory behaviour) of several Australian and New Guinean boids has been studied (Webb & Heatwole 1971; Johnson 1975a, 1977). Most species showed elevated head temperatures while warming, with more precise temperature control in the head region. When overheated, boids maintain head temperatures lower than that in the body. These physiological controls are linked to behavioural/position adjustments.

Slip & Shine (1988a, 1988b, 1988c, 1988d, 1988e) reported the first detailed study of thermoregulation and associated behaviour in boids (see also Feeding and Digestive System, and Reproduction). They reported that *M. s. spilota* are mostly solitary (Slip & Shine 1988d). In warm weather, these snakes bask once in the morning to elevate body temperature before seeking shelter for the rest of the day, where heat loss is minimised, assisted usually by body coiling. At night, snakes relocated sometimes to a new foraging area or ambush site.

Defensive behaviours in boids are described by Bustard (1969f), Johnson (1975b) and Delean & Harvey (1982). Boids, like many other snakes, give warning by body inflation, hissing, and making bluff strikes with a closed or partly open mouth. *Liasis stimsoni* rolls into a ball with the head concealed, if aggressive posturing and striking fails to deter a human offender (Delean & Harvey 1982).

Aspidites is the only pythonine to exhibit burrowing behaviour. Murphy *et al.* (1981) reported that four captive *A. melanocephalus* excavated gravel by bending the head and neck into the shape of a 'J', moved the head and neck sideways into the loose substratum and then pulled the entrapped material towards the posterior body. Fyfe & Harvey (1981) observed six captive *A. ramsayi* using the chin and anterior ventral area to scoop out large quantities of sand, and suggested that wild snakes probably 'enlarge existing animal burrows for shelter or while hunting'. Captive specimens also completely buried their anterior 0.5 m under loose sand for 15 to 20 minutes, leaving the rest of the body exposed, emerging for about one minute before repeating the behaviour (Fyfe & Harvey 1981).

Economic Significance

In Australia and elsewhere there are extensive husbandry and breeding programs for boids by private keepers, researchers and institutions such as zoos and animal parks. Boids, especially those species that are easily tamed, are used most widely in public education (Ross & Marzec 1990). Captive husbandry and breeding of boids is an important adjunct to research and conservation efforts.

No Australasian boid species is considered to be threatened, but some races of *Morelia spilota* are vulnerable due to habitat loss and alteration, especially from extensively cleared areas of southern Australia. The race from the Murray-Darling drainage (see Ehmann 1992) is threatened and has been the subject of a Conservation Action Statement in Victoria (Allen 1993). Populations of *Morelia spilota imbricata* and *Aspidites ramsayi* in south-western Australia are similarly threatened (Smith 1981) and have been given additional protective status in Western Australia. A detailed study of the cryptic and secretive *Morelia s. spilota* around Sydney (Slip & Shine 1988a, 1988b, 1988c, 1988d, 1988e) showed that the species is not as threatened as was previously believed, and it has since been removed from Schedule 12 of the New South Wales National Parks and Wildlife Act.

Some Australian python populations could be threatened by over-collecting. The insular populations of St Francis Island in South Australia (Schwaner, Francis & Harvey 1988), and the small populations of *Antaresia stimsoni* (Pl. 7.5, as *Liasis stimpsoni*) in isolated rocky outcrops and small ranges in southern Australia may be at risk, and require monitoring and possibly management.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

The distributions of Australian pythons are mapped in Cogger (1992) and Ehmann (1992), and Shine (1991a) provided a species density map for Australian pythons. Species density is highest (eight species) on eastern Cape York and Torres Strait, and six species occur in the warm tropical areas of the western Kimberley and in Arnhem Land, where rainforest, relictual rainforest patches or deep mesic gorges occur. Pythons are absent from the cold winter areas of the south-eastern Australian mainland and Tasmania.

The distribution of 11 species of boids in New Guinea, Indonesia, and the Western Pacific is provided by McDowell (1975, 1979). Of particular interest are the four species shared with Australia: *Liasis mackloti* and *Morelia amethistina* are widespread in New Guinea and Indonesia; *Morelia viridis* is widespread in New Guinea and is restricted to small pockets of rainforest on eastern Cape York; *Morelia spilota* is widespread in Australia, and in southern New Guinea restricted to drier habitats. The first two species probably reached Australia by southward invasions, *L. mackloti* being first, followed by some evolutionary divergence. The last two species are most likely a reciprocal exchange northwards across the Torres Strait landbridge in Pleistocene times (see also McDowell 1975).

Beyond Australasia, pythonines occur in greater Asia and Africa, whereas the boinines occur in Europe, Africa, Central and South America and the West Indies (Cadle 1987). Cadle (1987) also discussed the various hypotheses and evidence explaining boid distribution in the Australasian Region.

Affinities with other Groups

McDowell (1987) concluded that the superfamily Booidea is a well-defined group without clear relationships to any other, and without clear palaeontological evidence of being particularly ancient. However, pelvic vestiges, premaxillary teeth and other osteological peculiarities suggest this is an old group. McDowell places the group into the infraorder Alethinophidia containing six superfamilies (and 16 families) of snakes, which were previously classified into the infraorders Henophidia and Caenophidia, with a total of eight families (Parker & Grandison 1977).

Affinities within the Boidae

The Boidae comprise two subfamilies: the distinctive Pythoninae, and all other snakes historically referred to as boinines, namely the Boinae and Erycinae of McDowell (1987). McDowell (1987) recognised a superfamily Booidea comprising the Pythonidae and the Boidae (Boinae plus Erycinae); three of the boinine subfamilies of Parker & Grandison (1977) were removed to other superfamilies. This scheme has not been fully accepted and is still the subject of study and debate.

On the basis of a detailed systematic study using both behavioural, and external and internal morphological characters, Kluge (1993) reassigned six of the 15 Australian species to three other genera and synonymised *Liasis fuscus* with *L. mackloti*. These are significant changes to recent Australian usage (*cf.* Wilson & Knowles 1988; Ehmann 1992; Cogger 1992). Kluge (1993) developed a phylogeny of the Pythoninae and found that '*Aspidites* is the sister lineage of all other pythonines, and the remaining Australia-New Guinea taxa constitute a paraphyletic assemblage. The southeast Asia-Africa *Python* forms a highly derived clade'.

Fossil Record

Before McDowell's (1987) transfer of the Madtsoiidae (Madtsoiinae of Boidae) to the infraorder Chlorophidia, *Wonambi* from Naracoorte Caves Pleistocene, was the first and most impressive 'boid' fossil from Australia (Smith 1976a). The oldest Australian snake fossils are the Miocene boids *Montypythonoides riversleighensis*, approximately 14 million years old, and *Morelia antiqua*, some 12 million years old, from Queensland and the Northern Territory, respectively (Smith & Plane 1985). Archer, Hand & Godthelp (1991) reported the occurrence of many boid remains in the Riversleigh deposits.

Kluge (1993) reassessed these Miocene boids and concluded that the first was *Morelia spilota* and the second *Liasis olivaceus*. He cast doubt also on the assignment of three snake fossils from elsewhere to the Pythoninae by Rage (1984). Rage (1987) reviewed ophidian fossil history and disagreed strongly with the removal of madtsoiines from the Boidae. He presented an overview of snake evolution based on fossil remains including many species he assigned to the Boidae.

34. FAMILY COLUBRIDAE

Harald Ehmann

DEFINITION AND GENERAL DESCRIPTION

The family Colubridae is distinguished from other snakes primarily by the dentition, which usually comprises solid teeth on the maxilla, palatine, pterygoid and dentary, but never on the premaxilla. A few species have enlarged and/or grooved posterior maxillary teeth, which channel venom from the supralabial (Duvernoy's) gland. Envenomation is effected by chewing rather than by injection, and serves to subdue struggling prey and to initiate digestion (Goin, Goin & Zug 1978; McDowell 1987). Within Australia, the members of this family are characterised by a combination of attributes — enlarged ventral scales in a single row, a more or less cylindrical tail in which all subcaudals are divided, fewer than 30 mid-body scale rows, and the presence of a loreal scale (see Fig. 34.1) in all species except *Fordonia leucobalia* (Pl. 8.3).

Approximately 300 colubrid genera in nine subfamilies were recognised by McDowell (1987), including three subfamilies in Australia (Colubrinae, Homalopsinae and Natricinae). However, the subfamily classification of Cogger (1992), which includes the two subfamilies Homalopsinae and Colubrinae, is followed here (see also Affinities within the Taxon). Eight genera, *Boiga*, *Cerberus*, *Dendrelaphis*, *Enhydris*, *Fordonia*, *Myron*, *Stegonotus*, and *Tropidonophis* are found in Australia. These genera also occur in New Guinea and beyond. Although the family Colubridae comprises over 1600 species, or approximately two thirds of the world's living snakes, only 11 species are found in Australia, where they are considered to be relatively recent invaders from islands to the north.

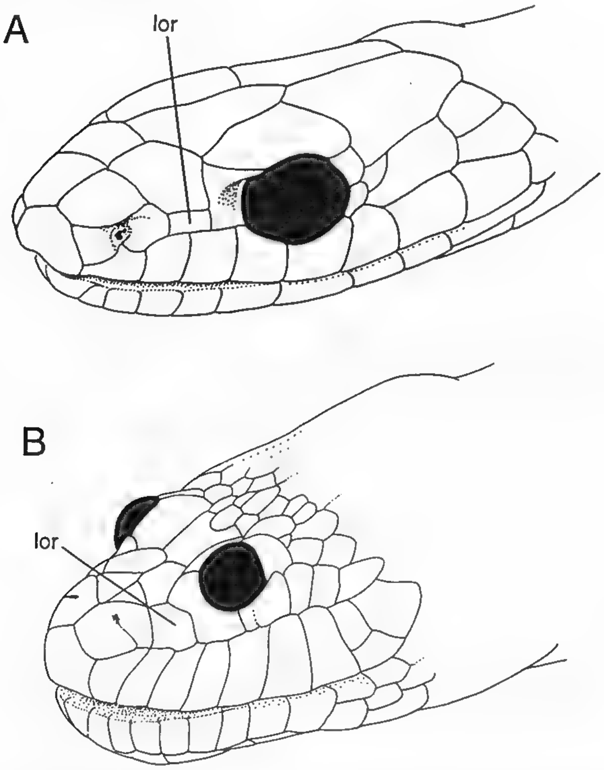

Figure 34.1 Oblique dorso-lateral views of the heads of A, a colubrine, *Dendrelaphis punctulata* and B, a homalopsid, *Cerberus rynchops*, comparing the form of the nostrils, eye and loreal scale. [R. Plant]

HISTORY OF DISCOVERY

The Australian colubrids were described over a century ago in Europe and their type specimens, several of which have been lost or destroyed, were lodged in European museums (see Cogger, Cameron & Cogger 1983a). *Ceberus rynchops*, described by Schneider in 1799 (as *Hydrus rynchops*), is the earliest described species occurring in Australia. Although the whereabouts of the type material and the type locality are unknown (Cogger *et al.* 1983a), the distribution of *Ceberus rynchops*, from northern Australia to India, suggests that the type material may have originated from outside Australia. The first colubrid to be described from indisputably Australian material was *Dendrelaphis punctulata* (as *Leptophis punctulatus*) by J.E. Gray (1826), based on a specimen from Careening Bay in Western Australia. Between 1826 and 1854, four species and two genera of currently recognised taxa were described by Gray, and two further species were described by Schlegel and by Duméril, Bibron and Duméril. Günther, Fischer and Meyer each described species between 1867 and 1886 that occur in Australia, of which only *Dendrophis calligastra* was based on Australian type material.

All but four of the 23 species that have been described from type material collected in Australia have been synonymised. The most prolific describer of Australian and New Guinean colubrids was William Macleay, who described 17 species and two genera more than a century ago, all of which are currently in synonymy. Several authors described between two and four separate species from type material which currently is considered to be conspecific (Cogger *et al.* 1983a). This in part reflects the significant morphological variability in the more common species that are widely distributed in northern Australia, south-eastern Asia and the intervening archipelagos.

There have been relatively few taxonomic studies of the Australian colubrids although their ecology and zoogeography have attracted considerable interest (Shine 1991c).

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Australian colubrid species are medium-sized snakes ranging from 500 to 2000 mm in adult total length. The two species in each of the genera *Boiga* (Pl. 8.1) and *Dendrelaphis* show slight to moderate lateral compression, and all other Australian species have relatively rounded bodies.

The head is moderately to obviously distinct from the narrower neck. The eyes are moderately large and set high on the head in the Homalopsinae, larger and set laterally in the Colubrinae. The external nares are valvular and on top of the snout in the Homalopsinae, but permanently open and on the side of the snout in the Colubrinae (see Fig. 34.1).

The tail is apparently prehensile in the four species of tree snakes (*Boiga* and *Dendrelaphis*), although the tail of *Dendrelaphis* does not have the extensive musculature near the tip of the tail present in arboreal pythons (McDowell pers. comm.)

Colouration within a species can vary remarkably. *Dendrelaphis punctulata* may be green, blue, black, golden yellow, or an intermediate colour. Dorsal patterning in *Enhydris polylepis* may consist of small blotches of pigment, large blotches, or the entire back may be dark. In *Fordonia leucobalia* (Pl. 8.3), the combination of variable body colouration and dorsal patterning is complex, ranging from fawn to grey to orange with scattered small blotches, large blotches, to a near absence of any paler colour.

Body Wall

The body and head scales of colubrids are similar to those of other terrestrial and arboreal Australian snakes. Colubrids of moist habitats have very glossy, water repellent scales, which presumably reduce the risk of microbial attack. The dorsal and lateral scales of the aquatic species *Cerberus rynchops* and *Tropidonophis mairii* are strongly keeled. These keels may aid in maintaining directional stability and reduce friction during rapid movement, especially on slippery, muddy substrates. In *Dendrelaphis* species, the lateral ends of each ventral scale are angled abruptly to form a pair of latero-ventral keels. These provide purchase even on fine irregularities of a twig or branch, and allow a secure grip that facilitates rapid body movement in a precise direction.

Skeletal System

The skull (Fig. 34.2) is highly kinetic between the anterior elements and the braincase. Solid teeth are present on the upper and lower jaws and on the palate, but not on the premaxilla. Both *Dendrelaphis* species (Fig. 34.2A), both *Stegonotus* species and the sole *Tropidonophis* have numerous, ungrooved, fine, pointed teeth. The two *Boiga* species and all four homalopsines have two enlarged, grooved teeth on the posterior maxilla that are associated with prey envenomation (Fig. 34.2B). The homalopsine *Fordonia leucobalia* is unusual in having relatively short and blunt teeth (Gyi 1970) which facilitate the capture, holding and swallowing of crabs (Savitzky 1983).

The skeletal anatomy of Australian species was described by Gyi (1970) (*Cerberus rynchops rynchops* and *Fordonia leucobalia*) and Malnate & Underwood (1988) (*Tropidonophis mairii*). Bellairs & Kamal (1981) reviewed the development of the skull in snakes extensively and provided access to earlier literature.

The axial skeleton consists of pre- and post-cloacal vertebrae and ribs; there are no vestigial girdles or limb bones. The vertebrae are procoelous with well-developed condyles, and accessory articulating facets, namely the zygosphene (anterior) and the zygantrum (posterior), are present in addition to the zygapophyses found in other amniotes.

One rarely reported feature of *Tropidonophis mairii* is the ease with which it can break its tail distally when it is firmly grasped. Tail autotomy is not known in other Australian snakes (Lyon 1973; Ehmann pers. obs.). Tail fragility may be a characteristic of the genus, as incomplete tails are common in many overseas *Tropidonophis* (Malnate & Underwood 1988). There is no tail regeneration.

Locomotion

Lateral undulation is the most common type of locomotion used by Australian colubrids. It is used in swimming, movement on land, and in climbing. Concertina locomotion is often used by arboreal snakes when moving between or along widely spaced elevated branches and vines or inside naturally occurring vertical hollows and channels. Sidewinding occurs in *Fordonia*, *Cerberus* and *Myron* (Cogger & Lindner 1974; Jayne 1987, Wall 1919) but rarely in *Tropidonophis* (Ehmann pers. obs.). Rectilinear locomotion has been observed in all Australian colubrids (Ehmann pers. obs.).

Feeding and Digestive System

Constriction, or a modification of it, is used in some species to subdue and/or hold prey. Species of *Boiga*, *Fordonia*, *Myron* and *Stegonotus cucullatus* are all known to constrict prey (Irvine 1954; Shine & Schwaner 1985). Australian *Boiga* species constrict prey with anterior body loops (Ehmann 1992) whereas several overseas colubrids, including *Boiga*, use the tail and posterior body (Murphy 1977). The most bizarre feeding in any Australian colubrid is that of *Fordonia leucobalia* which has very effective crab venom (Kopstein 1931). It constricts its crab prey or clamps it into the muddy substrate with an overbearing body loop, and then proceeds to break off and partly crush and crack individual appendages, before swallowing them. When the crab's overall size and defences are suitably reduced, the snake partly crushes and swallows the body (Savitzky 1983; Shine & Schwaner 1985). Savitzky (1983) indicated that *Fordonia* has hypertrophied gastric musculature that presumably aids in coping with the hard and often jagged crab exoskeletons. At least six of Australia's eleven colubrids can envenomate their prey, in some cases apparently as an aid to digestion rather than to subdue the prey (Irvine 1954). Other Australian species have venom which is highly effective in subduing/immobilising prey (Kopstein 1931; Parker & Grandison 1977; Shine 1991c).

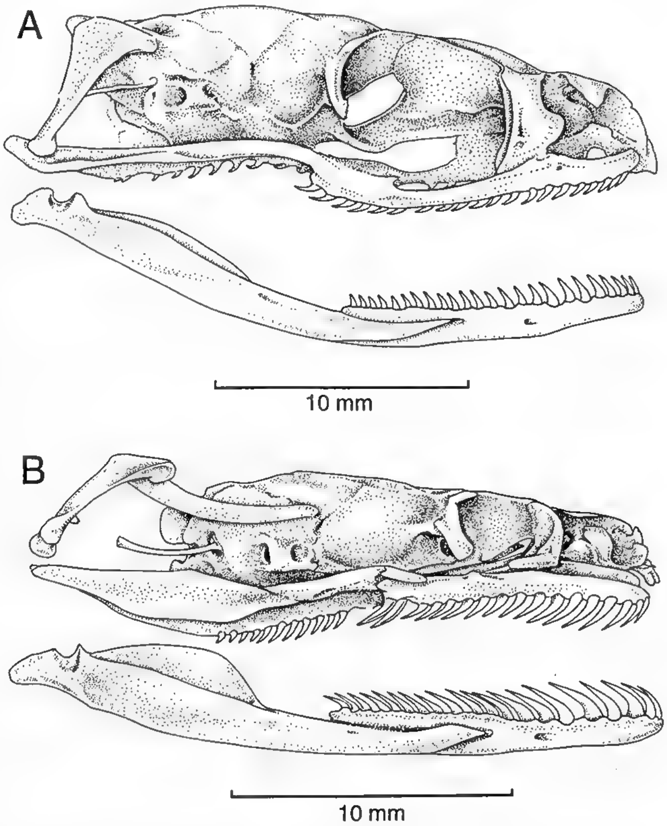

Figure 34.2 Lateral view of the skull of colubrid snakes. **A**, the solid-toothed species, *Dendrelaphis punctulata*; **B**, a rear-fanged colubrine species, *Cerberus rynchops*. [R. Plant]

Cundall (1987) reviewed the functional morphology of feeding and envenomation in snakes and Mushinsky (1987) reviewed several specific aspects of foraging ecology in snakes, including non-Australian colubrids.

Respiration

The Australian homalopsine snakes possess some specialised, aquatic adaptations. These include valvular nostrils on the top of the snout (see Fig. 34.1). The oxygen carrying capacity of blood in *Cerberus rynchops*, a frequent inhabitant of mangroves, is close to the lower end of the range for land snakes (Feder 1980; Heatwole 1987). Its ability to take in oxygen through the skin is lower than other snakes (Heatwole 1987). The concurrent low transport rate of carbon dioxide would be advantageous in mud of mangroves, which has high carbon dioxide levels (Heatwole 1977a).

Heatwole (1987) provided an excellent overview of the respiratory/circulatory function in aquatic/marine snakes, and

Johnson (1975a) has reported on head-body temperature differences in *Boiga irregularis* as a function of circulation.

The respiratory physiology of Australian colubrine snakes has yet to be investigated. One interesting observation is that *Tropidonophis mairii* can remain submerged for 20 to 30 minutes (Lyon 1973).

Excretion

The Australian terrestrial colubrine snakes, and at least the homalopsines *Cerberus* and *Fordonia*, all excrete nitrogenous waste as uric acid paste, usually with faecal material (Ehmann pers. obs.). It is possible that the freshwater-inhabiting *Enhydris polylepis* can excrete primarily urea, as it is not subject to the same desiccation risks as the terrestrial colubrines or to the salty environments of other homalopsines.

A premaxillary salt gland in the anterior roof of the mouth of coastal and estuarine homalopsines excretes excess salt. In *Fordonia*, the salt gland is extremely large, probably as an adaptation to the relatively high salt content of crabs (Savitzky 1983). These snakes also have significantly reduced rates of cutaneous water loss (Heatwole 1987).

Sense Organs

The slightly elevated placement of the eyes in the homalopsines is the only obvious difference from the position and function of sense organs of terrestrial snakes. Otherwise the five senses are believed to be similar to those found in other relatively unspecialised terrestrial forms. The pupils are vertically elliptical in nocturnal species of *Boiga* and *Stegonotus* and round in diurnal species of *Dendrelaphis* and *Tropidonophis*. Scale pits present in many head shields, dorsal scales and sometimes in the subcaudals of *Tropidonophis mairii* (Malnate & Underwood 1988) may have a sensory function,

Exocrine and Endocrine Glands

As well as the premaxillary salt gland in the homalopsines (see Excretion) the colubrines *Dendrelaphis* and *Stegonotus* are known to produce distinctively odoriferous secretions from the cloacal glands. These are particularly obvious when a snake is first handled. Normally docile captive snakes become quite agitated when exposed to their species' smell, for example, on a contaminated hand. These odours are surprisingly strong (relatively nutty-sweet in *Dendrelaphis punctulata* but offensively pungent in *Stegonotus cucullatus*) in newly hatched and juvenile snakes. They probably occur in response to stress and serve as a pheromonal danger signal to nearby conspecifics (Ehmann pers. obs.). *Stegonotus* produces scent from anal glands (Cogger 1992).

The most significant exocrine gland in some colubrids is associated with prey envenomation (see Feeding and Digestive System). Duvernoy's gland (in the supralabial gland) secretes a venom that drains to the vicinity of the teeth (sometimes grooved and/or enlarged) of the posterior maxilla (see Cundall's 1987 review). The studies by Kopstein (1931) demonstrated the high specificity and effectiveness of two colubrid venoms, and the importance of relating functional venom studies to the natural prey species.

For a comprehensive review of reproductive endocrinology in snakes, including non-Australian colubrids, see Seigel & Ford 1987.

Reproduction

A major review of snake reproduction by Seigel & Ford (1987) covered many non-Australian colubrid studies, and included *Cerberus rynchops*, studied outside Australia. Reproduction in Australian colubrids is discussed by Shine (1991c) and Ehmann (1992).

All Australian colubrines are oviparous whereas the homalopsines are viviparous. The mean litter or clutch size ranges from 5.5 to 13.0 per female, and is significantly correlated with maternal body size in four species. Some Australian colubrids exhibit reproductive seasonality. Oviposition in *Boiga* species throughout Australia occurs in summer; east coast *Dendrelaphis punctulata* have a similar pattern, but in the Northern Territory the species shows no obvious seasonality. Gravid *Fordonia* have been collected from July to October, gravid *Cerberus* in February and August, and gravid *Enhydris* in June and November. *Tropidonophis* can reproduce almost year-round, even in southern populations, although no gravid females have been recorded from August to October, probably because these months are relatively dry within the species' range.

Embryology and Development

Shine (1991c) published data on artificially incubated eggs of four Australian colubrids. The most notable feature of these data is that in *Tropidonophis* the egg size, mass and incubation time are all remarkably lower than in *Boiga*, *Dendrelaphis* and *Stegonotus*. In the wild, the eggs of *Boiga*, *Dendrelaphis* and *Tropidonophis* are laid in moist or very humid sites that are not exposed to temperature extremes (Lyon 1973; Ehmann 1992). During development, eggs of *Boiga* and *Dendrelaphis* absorb moisture and increase in size, sometimes becoming strongly cohesive and constrained within rigid-sided oviposition sites (Ehmann pers. obs.).

NATURAL HISTORY

Life History

The only Australian colubrid for which information on growth and longevity is available is *Cerberus rynchops*. Two small specimens from Burma, 19.4 and 20 cm long, doubled their lengths in the first year and by the end of the second year were approximately three times their original length (Wall 1921).

A detailed, recent review of snake life histories, based substantially on North American colubrids, is provided by Parker & Plummer (1987).

Ecology

The habitats of the Australian colubrids are summarised in Ehmann (1992). All Australian colubrids occur in mesic, moist, or wet habitats associated with permanent watercourses, swamps, estuaries or bays. *Boiga* species can inhabit drier habitats probably because their surface activity is nocturnal and the risk of desiccation is less. Shine (1991c) suggested that the colubrids in Australia are not in significant competition with the endemic elapids and pythons because they have invaded Australia with ecological specialisations that are rare amongst the endemics.

The diets of Australian colubrids are diverse. Homalopsines feed largely on fishes and crustaceans, *Tropidonophis* consumes mostly frogs, *Dendrelaphis* eats mostly frogs and lizards, *Boiga* takes birds, lizards and mammals (Green 1989), and *Stegonotus* feeds mainly on reptile eggs, frogs and lizards (Shine 1991c).

Frog-eating Australian colubrids frequently have subcutaneous swellings that contain the sparagana stage of tapeworms (Ehmann pers. obs.).

Australian *Boiga irregularis*, *Dendrelaphis punctulata*, *Tropidonophis*, *Cerberus*, *Enhydris* and *Fordonia* are sometimes locally abundant and aggregated (Worrell 1963b; Covacevich & Limpus 1973; Lyon 1973; Cogger & Lindner 1974; Gow 1976; Ehmann pers. obs.).

Behaviour

Aggregations of Australian colubrids are relatively small compared to those in the large dens seen in some higher latitude species in the northern hemisphere (Gregory 1984). In a long-term opportunistic study of *Boiga irregularis* at Calga, north of Sydney, Ehmann (1992, unpub. data) found two females associated with egg clutches laid in deep recesses in rock crevices. Both females remained in the vicinity of their eggs for 18 and 27 days. Habitation of spring-summer refuges by adult males or females averaged two days (range one to four days, n = 4).

The defensive behaviour of Australian colubrids towards humans varies from the pugnacious (if mildly aroused) members of *Boiga* and *Stegonotus*, to the less easily provoked *Dendrelaphis*, *Tropidonophis*, *Cerberus*, *Fordonia* and *Enhydris*. *Myron* is not inclined to bite even when provoked (Ehmann 1992).

The arboreal, diurnal *Dendrelaphis* species bask in sunlight, usually using elevated, leaf-camouflaged platform sites, such as forks, dense twigs and/or vines (Thompson 1935; Ehmann pers. obs.), whereas the terrestrial and semi-aquatic diurnal *Tropidonophis* basks on low vegetation, open ground and even lying on the surface of shallow still water (Lyon 1973; Ehmann 1992). The aquatic crepuscular and nocturnal homalopsines also may engage in thermoregulatory behaviour by emerging in the late afternoon either to bask or to lie in shallow warm water. The nocturnal *Boiga irregularis* north of Sydney, basks one or more body loops in full morning or afternoon sunlight usually remaining within a recess or crevice (Ehmann pers. obs.). Colubrids, and especially colubrines, restrict their surface activity during dry or drought conditions, but the same species become quite active and mobile during very humid warm weather or soon after warm rains. This behaviour minimises the risk of desiccation.

Gillingham (1987) reviewed courtship and mating behaviour, social aggregation, and aggression in snakes including many North American colubrids. Mushinsky (1987) summarised the behaviours associated with foraging, and Lillywhite (1987b) reviewed the behavioural components of the thermal ecology of snakes.

Economic Significance

The Australian colubrids are not dangerously venomous to humans. Some homalopsines in South East Asia and India are important predators of invertebrate pests, frogs and fishes in the natural food chains of rice cultivation areas.

None of the Australian colubrids is considered to be endangered (Ehmann 1992). The conservation status of *Stegonotus parvus* on Murray Island (its only Australian occurrence, based on four collected specimens) is unknown, but the species appears to be common in Papua New Guinea (McDowell 1972b). All Australian colubrids are potentially put at risk by habitat change and aquatic or marine pollution.

The limitations of *Tropidonophis* as a potential biological control organism for *Bufo marinus* were outlined by Shine (1991c). Shine indicates that they eat *Bufo marinus*, and therefore may have the capacity to overcome the toad's toxicity.

In Australia, *Boiga* species are known to prey on aviary birds on rare occasions, but appropriate caging easily excludes them. However, the accidental introduction of *Boiga irregularis* to Guam, probably from the Admiralty Islands in salvaged materials from World War II, has resulted in a population explosion of the species and the extinction or endangering of most of Guam's native vertebrates, especially birds. There is no doubt that *Boiga irregularis* potentially poses a severe conservation threat to the native faunas of other Pacific islands (Rodda, Fritts & Conry 1992; Fritts 1988).

BIOGEOGRAPHY AND PHYLOGENY

Distribution

The Australian colubrid populations are outliers of much wider distributions in the islands of New Guinea, south-eastern Asia and further north. *Myron* and some *Enhydris* are endemic to Australia and New Guinea while *Cerberus* and *Fordonia* are distributed widely throughout the Indo-Australian region. Of the colubrines, some *Tropidonophis* and *Dendrelaphis* are also endemic to Australia – New Guinea, while *Stegonotus* (Philippines, Borneo, Moluccas, New Guinea and Australia) is a possible recent arrival in the Australasian region. Most *Boiga* are widespread in the Indo-Australian region (Cadle 1987); *Boiga fusca*, currently considered a synonym of *B. irregularis* by some authors, may be an Australian endemic.

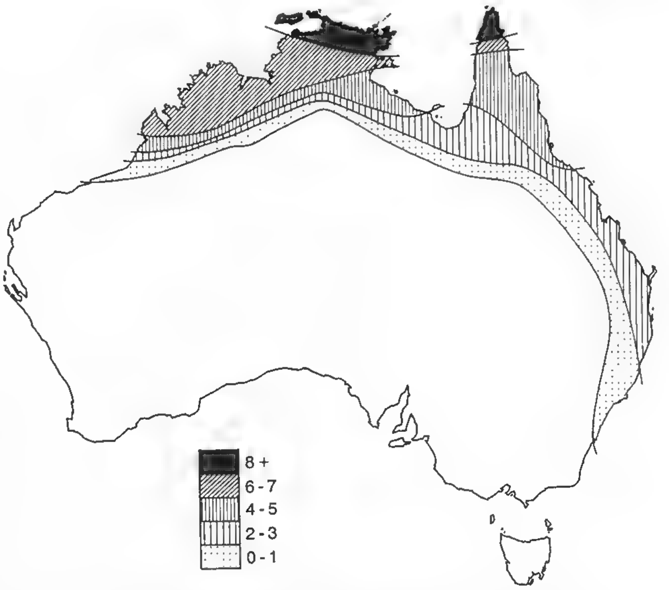

Figure 34.3 Species density map of colubrids. (After Shine 1991c)
[W. Mumford]

Australian colubrids are restricted to mesic habitats in the northern tropical and eastern tropical, subtropical and temperate regions (Fig. 34.3) (Ehmann 1992). *Boiga irregularis* and *Dendrelaphis punctulata* have the southernmost and furthest inland populations, and *Enhydris polylepis* is the homalopsine most highly adapted to freshwater (Wilson & Knowles 1988; Cogger 1992; Ehmann 1992).

The colubrines are almost cosmopolitan in distribution whereas the homalopsines occur in southern Asia, the Indo-Australian Archipelago and Australia (Cadle 1987).

Affinities with Other Groups

The Colubridae are placed in the superfamily Colubroidea which is considered to comprise two series. The more primitive Proteroglypha contain the Elapidae, *Calliophis*, *Atractaspis* and some other African genera, and the Opisthoglypha contain the Colubridae and Viperidae. The systematics and phylogeny of the Colubroidea are uncertain. The available morphological, anatomical, cytogenetic and molecular data are conflicting, but the greatest promise for resolution probably lies with immunological investigations (Cadle 1987; McDowell 1987).

Affinities Within the Taxon

The number and definition of subfamilies in the Colubridae is uncertain (Cadle 1987). In this account the Australian colubrids have been treated conservatively as belonging to two subfamilies, but other authors have suggested four: Homalopsinae, Natricinae (for *Tropidonophis*), Boiginae (for *Boiga*), and Colubrinae (Cadle 1987; McDowell 1987; Cogger 1992). Furthermore, Cadle (1987) places *Enhydris polylepis* in the Colubrinae.

The colubrids radiated extensively in all zoogeographic regions other than the Australian region, with some minor radiation in New Guinea (Cadle 1987). Cogger & Heatwole (1981) postulated that the colubrids arrived recently in Australia by land-bridge migration or by swimming, and Storr (1964a) suggested that of the homalopsines, *Enhydris* entered from the north-east and the other three genera entered from the north-west. Some ecological preadaptations that may have facilitated and ensured the successful invasion of Australia by colubrids were discussed by Shine (1991c).

Fossil Record

As yet no colubrid fossils have been reported from Australia, but the vast Riversleigh fossil deposits in northern Queensland may yield fossils, as they include many snake remains yet to be identified (Archer, Hand & Godthelp 1991).

The earliest known colubroid fossils date from the Late to Early Eocene of Italy, the Early Eocene of France and Portugal; there are possible primitive colubroids from the upper Eocene beds of England (see Rage 1987). However, the first undisputed colubrid fossils date from the middle Oligocene of Europe and North America, and are at least 30 million years old. By the Miocene — times that have been referred to as the 'Age of Colubroidea' (Rage 1987) — an astonishing array of colubrids existed in North America and Europe; other areas are poorly studied, but a few are known from Morocco, Asia and South America.

35. FAMILY ELAPIDAE

Glenn Shea, Richard Shine & Jeanette C. Covacevich

DEFINITION AND GENERAL DESCRIPTION

Recent studies indicate that the Australian terrestrial front-fanged snakes or proteroglyphs, traditionally assigned to the family Elapidae, are more closely related to the viviparous marine proteroglyphs assigned to the family Hydrophiidae than to non-Australian elapids. These relationships are described in more detail under Affinities with Other Groups. Acceptance of the hypothesis of a sister-group relationship between the Australian elapids and hydrophiids requires the placement of the Australian 'elapids' in a subfamily, the Oxyuraninae, within the family Hydrophiidae. However, some studies have suggested that the relationships of the hydrophiid sea snakes lie within the Australian terrestrial proteroglyph radiation, which would require still further modification to this nomenclature. Because the term 'elapids' remains widely used for the Australian terrestrial proteroglyphs covered by this chapter, while the more correct 'oxyuranines' is, as yet, little used, we retain elements of the more traditional terminology by referring to 'Australian elapids' in the text, and we retain Elapidae as the family name.

The rostral location of the venom delivery apparatus in the oral cavity distinguishes elapids and sea snakes from all other snakes, and as a group they are referred to as proteroglyphous snakes. The terrestrial and marine proteroglyphous snakes of the Australian region differ from other proteroglyphs in the mechanism of fang movement. They are 'palatine draggers' rather than 'palatine erectors' (McDowell 1970; see Feeding and Digestive System for a detailed description). All Australian proteroglyphs have at least one pair, and sometimes several pairs, of fixed, hollow, elongate fangs on the rostral region of the maxillae. More posteriorly, there are varying numbers of small maxillary teeth which are solid in most species. However, in *Oxyuranus microlepidotus* they are hollow, and appear to be functional fangs (Covacevich, McDowell, Tanner & Mengden 1981).

The absence of a loreal scale readily differentiates Australian proteroglyphs externally from other Australian snakes, with the one exception of the aquatic colubrid *Fordonia leucobalia* of tropical Australia (Pl. 8.3).

Venoms of Australian elapids have a predominance of pre- or post-synaptic neurotoxins. Some are extremely potent to humans. Venoms also have significant myotoxic, coagulant, and anti-coagulant effects, and less significant impacts on platelet function and haemolytic activity (White 1987a).

Though Australian elapids and hydrophiids are similar morphologically, the elapids are readily distinguished by the cylindrical, tapering tail, the lack of valvular nostrils and lingual fossae.

Many species of Australian elapid are viviparous, but the most common form of reproduction amongst them is oviparity. All hydrophiids are viviparous; the other marine proteroglyphs, the laticaudids, are oviparous.

The Family Elapidae is the most diverse of the seven families of snakes in Australia. Close and moderately close family relatives of the Australian elapids occur widely in the tropics and subtropics of Asia, Africa and the Americas.

HISTORY OF DISCOVERY

In his recent checklist of Australian elapid snakes, Hutchinson (1990b) recognised 81 species, in 20 genera. Two additional species of *Austrelaps* have been recognised subsequently (Rawlinson 1991). Some composite species, such as *Pseudonaja nuchalis*, require division into several species (Mengden 1985b). Other species are yet to be described, for example, in the genus *Demansia*. Thus new species are likely to be added slowly to the checklist of Australian elapids for several years to come.

Mengden (1983) and Cogger (1985) summarised the history of taxonomy and nomenclature of the Australian elapids. Earliest accounts of Australian elapids are of two well known, common species from the Sydney region. *Vermicella annulata* and *Pseudonaja textilis* are described, but not named, in White's (1790) journal. The first formal descriptions are by Shaw (1794, 1802) of *Coluber porphyriacus* (= *Pseudechis porphyriacus*) and *Boa palpebrosa* (= *Acanthophis antarcticus*) (Cogger, Cameron & Cogger 1983a).

Not surprisingly, the periods of greatest discovery and description of elapids coincide with the most intense exploration of Australia. Close to 50% of the taxa currently recognised were described in the period 1830–1880. British and European researchers shared the excitement of new species from a new land. Albert Günther, John Edward Gray, Constant and Auguste Duméril, along with Gerard Krefft, of the Australian Museum, Sydney, are prominent as authors in descriptions of species (Adler 1989).

The catalogues of George Albert Boulenger (1893, 1894, 1896), published soon after the great era of discovery and description of Australia's elapids, stood as a standard starting point for taxonomists working with this family until the 1960s. In Australia, late in the 19th century and early this century, the work of describing and reviewing the elapids continued primarily in the hands of Sir William Macleay, Edgar Waite and Charles de Vis. Macleay and de Vis are remembered more for the quantity of their work than for its consistent high quality. Each described many new species of snakes, few of which are still recognised. Waite's review (1898) of the Australian snakes is admired still, and like the earlier monograph by Krefft (1869), is much sought today by collectors.

The reptile work of de Vis has been the subject of much criticism, initiated by Boulenger in a scathing assessment of his works, and repeated several times since, for example, by Covacevich (1971) and Cogger (1985). In a recent review of de Vis' overall contribution to understanding Australia's past and present fauna, Ingram (1990) noted parallels with the works and styles of Macleay, and that Macleay's work, generally, has escaped criticism. Ingram concludes that, despite many shortcomings, de Vis's contributions were substantial.

The 20th century has been characterised by few new species, but a wealth of 'new', often resurrected, genera. The number of genera peaked in the early 1960s and most of the species described in recent years have been the result of splitting previously widespread species, for example, *Pseudechis butleri* and *Suta ordensis* (Cogger 1985). Though declining numbers of new species and fairly consistent numbers of genera in recent decades should have produced a reasonably stable taxonomy, this has not been the case, more from nomenclatural changes than from refinement of knowledge (Cogger 1985).

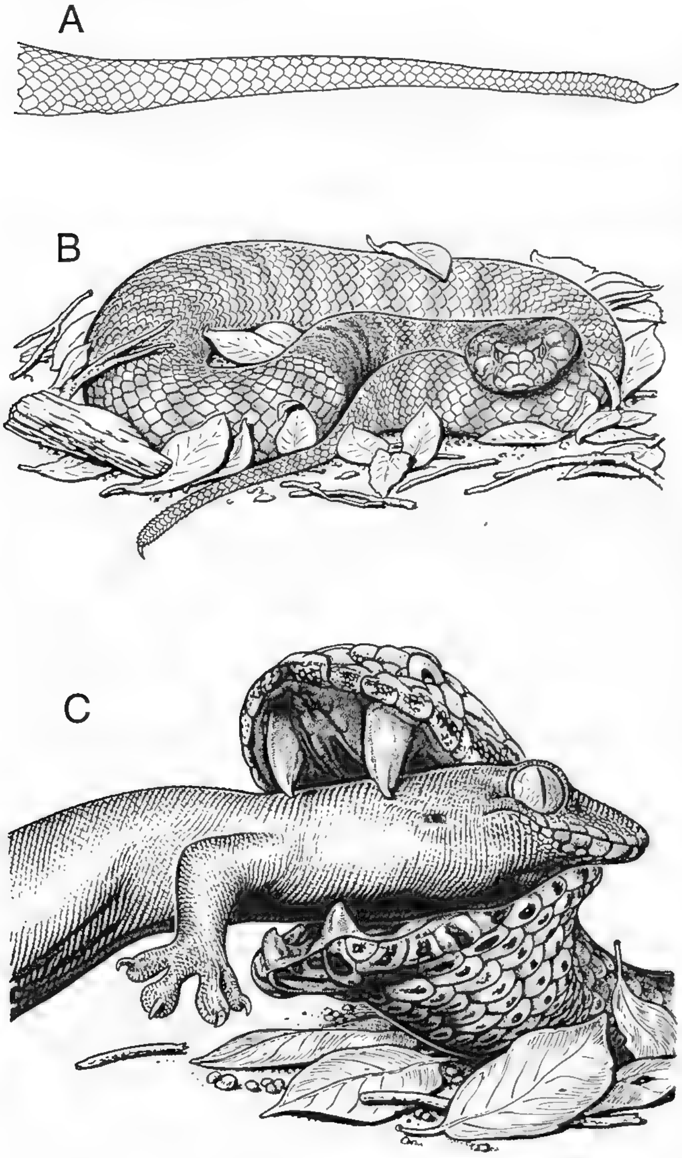

Figure 35.1 The stocky build of *Acanthophis antarcticus* enables it to capture large prey, which are immobilised by deeply injected venom. The use of the tail as a lure assists capture. **A**, details of scalation of tail, including caudal lure; **B**, camouflaged amongst leaves, waiting to ambush prey; **C**, at the moment of capture, the *vagina dentis* covers each large fang. (B, after photo by C.B. Banks/NPIAW; C, after photo by J. Wombey/Auscape) [B. Jantulik]

Historically, Australian elapid nomenclature at both generic and species levels has been extremely unstable, particularly before the mid 1980s. Subsequently, there has been a major swing away from traditional taxonomic techniques to biochemical methods of analyses of variations within, between, and beyond the species boundaries.

Intuitive analyses of traditional characters produced a plethora of names and hotly-defended concepts of generic allocations. Mengden (1983), Cogger (1985), McDowell (1985), Mengden (1985a), Wallach (1985), and Hutchinson (1990b) have contributed significantly to the rationalisation of concepts of species and genera, and to the production of a stable taxonomy, now based on a consensus from many different fields. Hypotheses regarding relationships within the Australian elapid radiation and between related families, have been proposed recently based on karyology and alloyzme electrophoresis (Mengden 1985a), immunological comparisons of serum proteins (Schwaner, Baverstock, Dessauer & Mengden 1985) and soft part anatomy (Wallach 1985). Most species were covered and the results are generally compatible. From them, Hutchinson (1990b) produced the much needed '... taxonomic scheme in which the included genera can be defined so as to be monophyletic as well as morphologically cohesive...'.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Australian elapids vary greatly in length. The longest accurately reported in the literature are 2.31 m snout–vent length (SVL) for *Pseudechis australis* (Shine 1987e) and 2.26 m SVL and 3.66 m total length for *Oxyuranus scutellatus* (Gow 1973; Shine & Covacevich 1983). Other *Pseudechis* and *Oxyuranus* species, together with *Notechis* and *Pseudonaja* species, attain a maximum SVL of over 1.5 m. The smallest species are *Drysdalia mastersii, Simoselaps anomala, S. calonota* and possibly *S. minima* (maximum SVL 271, 194, 251, 194 mm respectively; Shine 1981b, 1984b), with several other species in the genera *Cacophis, Furina* and *Simoselaps* attaining maximum lengths of less than 350 mm. The smallest reported neonates are those of *Simoselaps littoralis* (70 mm SVL; Shine 1984b).

Mass of adult elapids is rarely reported. However, large adult *Notechis ater* from Chappell Island weigh nearly 1.7 kg (Schwaner & Sarre 1988). Neonates of small elapid species may weigh as little as 0.8 g (*Rhinoplocephalus*; Shine 1984a) and 1.2 g (*Hemiaspis*; Shine 1987a).

Elapids show a variety of body forms. Some taxa, such as *Acanthophis* (Pl. 8.9), are very short-bodied and robust. At the other extreme, the elongate whip-snakes (*Demansia*; Pl. 8.6) have slender bodies and long tails, up to 36% of SVL (Storr 1978c). The head is usually not much broader than the neck, although there are some exceptions (for example, *Acanthophis*). The tail tip is pointed, except in *Vermicella* (Pl. 8.4) and to a lesser extent in some *Simoselaps* (Pl. 8.5). In *Acanthophis*, the distal part of the tail is very narrow, the more distal caudal scales are mucronate, and the apical scale is modified into a soft slender curved spine

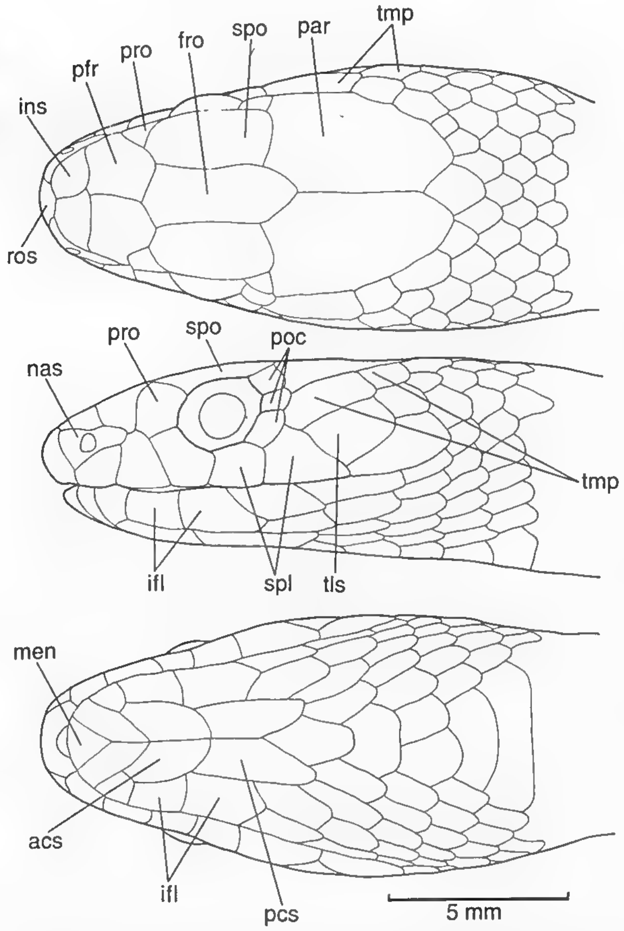

Figure 35.2 Dorsal, lateral and ventral head shields of a typical Australian elapid (*Demansia torquata*). **acs**, anterior chin shield; **fro**, frontal; **ifl**, infralabials; **ins**, internasal; **men**, mental; **nas**, nasal; **par**, parietal; **pcs**, posterior chin shield; **poc**, postoculars; **pfr**, prefrontal; **pro**, preocular; **ros**, rostral; **spl**, supralabials; **spo**, supraocular; **tls**, temporolabial; **tmp**, temporals. [B. Jantulik]

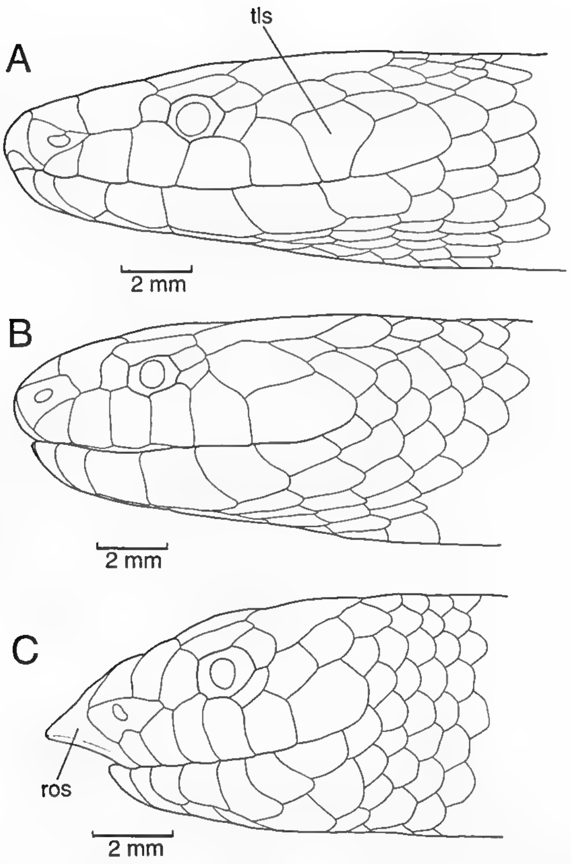

Figure 35.3 Head shields in lateral view. **A**, *Furina ornata*, in which the temporolabial reaches the lip; **B**, *Cacophis krefftii*, which lacks the temporolabial; **C**, *Simoselaps roperi*, a burrowing species in which the rostral shield is modified to form a cutting edge. **ros**, rostal shield; **tls**, temporolabial. [B. Jantulik]

(Fig. 35.1A). This structure forms a lure for attracting prey (Fig. 35.1B, C).

All elapids have a regular pattern of large head shields (Fig. 35.2). Along the head dorsum, these are the rostral, paired internasals, paired frontonasals, frontal, and paired parietals. Laterally, each nostril lies within a nasal scale, which may be deeply grooved. In *Rhinoplocephalus bicolor* and *Vermicella multifasciata* the internasals are fused to the rostral and nasals respectively. There is no loreal scale, a structure usually present in Australian colubrid snakes. The eye is typically surrounded by a single preocular, a single large supraocular, two to three postoculars, and two of the supralabial series. In *Acanthophis* the supralabial scales are excluded from the orbit by two to three subocular scales. The exclusion of the penultimate supralabial from the lip line, by contact of the last and third-last scales in the series, is characteristic of Australopapuan elapids. This produces a large 'lower anterior temporal' or temporolabial scute (McDowell 1967, 1970), and leaves only two true supralabials, of five or six, behind the level of the eye. In some *Acanthophis*, *Tropidechis* and *Furina* (Fig. 35.3A) the temporolabial retains contact with the lip line (Krefft 1863; van Lidth de Jeude 1911; Kinghorn 1939; McDowell 1984). In other genera (*Cacophis*, *Pseudonaja*, *Simoselaps*, *Vermicella*) the pattern is modified by loss of the temporolabial, usually to the last true supralabial (Fig. 35.3B; Scanlon 1985; Cogger 1992). Along the lower lip, there are usually seven infralabial scutes.

The shape of the snout is modified in two groups of elapids. In burrowing elapids of the *Simoselaps semifasciatus* species group, the rostral shield forms a shovel-like cutting edge to the snout (Fig. 35.3C). In *Pseudonaja nuchalis* the rostral shield is flattened and 'strap-like' in dorsal profile, in contrast to the rounded rostral apex seen in other elapids.

The scales on body and tail are imbricate dorsally but more juxtaposed ventro-laterally (Storr 1985) and are arranged in longitudinal rows. Dorsal and lateral scales are generally rhomboidal and smooth, although they are keeled and more lanceolate in *Tropidechis*. Weak to strong keels are also seen in *Acanthophis* and *Oxyuranus scutellatus* (Wallach 1985). The number of longitudinal rows of scales at midlength is of significance in identifying elapid species (Fig. 35.4). The normal range of variation is 15 to 23 rows, and lower values predominate in smaller species. The scales in the most ventral row on the lateral surface are much larger than the adjoining lateral scales in some taxa. The unpaired ventral scales on the body are generally at least three times as broad as adjacent lateral scales. The anal plate is either single or paired, sometimes varying within species (Fig. 35.5). Subcaudal scales are either single (in live-bearing species; Shine 1985c) or paired (mostly in egg-layers), although in *Pseudechis* species the more proximal scales are single and the more distal paired. Similar variations occur occasionally in some *Pseudonaja* species (Annable 1985).

Most Australian elapids have a brown to grey dorsal and lateral ground colour (Pl. 8.7–8.12), with little pattern on the body, apart from darker edges to the individual scales. A number of the larger elapids show great variation in the ground colour. *Pseudechis australis* varies geographically from uniform pale yellow-brown to red, to almost black in the south of the range, and with further variation in the occurrence of pale spots and dark edges to scales (Smith 1982). Extreme variation in pattern, partly the result of the existence of cryptic species, is known for *Pseudonaja nuchalis* (Gillam 1979b; Mengden 1985b). A red/grey dimorphism in dorsal ground colour occurs in *Acanthophis antarcticus* (Hoser 1985; Shine 1991a). Seasonal darkening of colour in cooler months is known for both species of *Oxyuranus*, *Acanthophis antarcticus* and *Pseudonaja nuchalis* (Banks 1981, 1983a; Mirtschin 1982; Shine 1991a).

Vermicella (Pl. 8.4) and many *Simoselaps* species have a strong body pattern of alternating brightly coloured light and dark transverse bands. Transverse bands, often less distinct, narrower or less regular, also occur in *Acanthophis*, *Denisonia devisi*, *Hoplocephalus bungaroides*, *H. stephensi*, *Suta fasciata*, most *Pseudonaja modesta*, many individual *Notechis* and *Pseudonaja nuchalis* and juvenile *P. textilis*. Though rare in Australian elapids, a dark longitudinal stripe occurs in *Simoselaps calonota* and *Rhinoplocephalus nigrostriatus*, and some *Demansia psammophis* have paired russet stripes on the forepart of the body. Other taxa (*Rhinoplocephalus bicolor, Suta nigriceps*) show a less differentiated darker mid-dorsal region. The degree of polish on dorsal scales differs between species and genera (Storr 1985). The colouration of the skin between the scales, often revealed when the snakes inflate their lungs in threat displays, is also variable between species, and is of diagnostic value (Storr 1985).

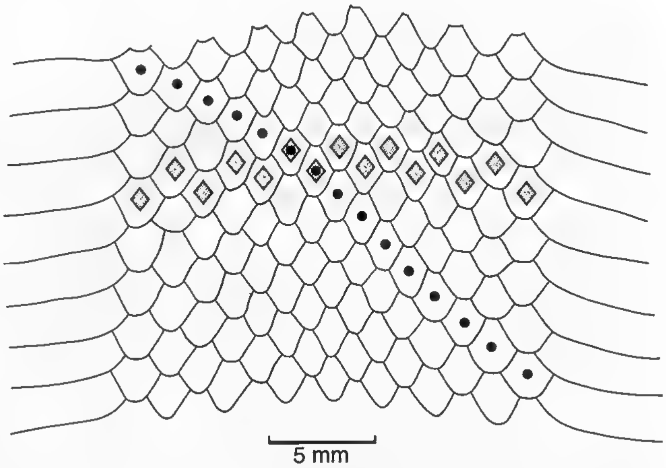

Figure 35.4 Arrangement of dorsal and lateral body scales of *Rhinoplocephalus nigrescens*. The flattened skin has been cut along the ventral midline, dividing the broad ventral scales. The 15 longitudinal rows of scales are characterisitc of this species. Alternative methods of counting scale rows are indicated by round and rhombic symbols. [B. Jantulik]

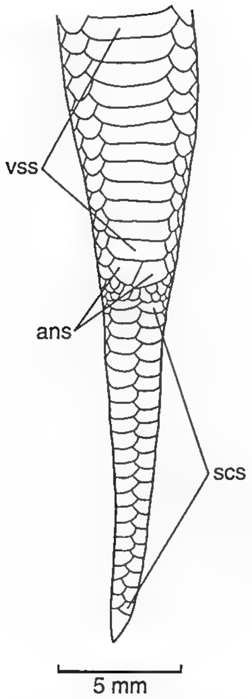

Figure 35.5 Arrangement of scales on the ventral surface of the tail in *Simoselaps littoralis*. **ans**, paired anal scales; **scs**, paired subcaudal scales; **vss**, ventral scales. [B. Jantulik]

The ventral surface, usually pale, may bear yellow to brown spots, dark margins to scales or extensions of dark lateral bands. Several small species have yellow to pink venters, and in others the venter may be uniformly dark.

The head pattern of Australian elapids is often diagnostic for species or genera, and may include bands, patches, bars or rings of various colours over the face, snout or across the eye, as in the genera *Drysdalia*, *Demansia*, *Furina*, *Simoselaps* (Pl. 8.5), *Suta* and *Cacophis*. Pale margins to the labial scales give a barred appearance to the lips of *Acanthophis* (Fig. 35.1), *Austrelaps* and *Denisonia*. A narrow longitudinal pale stripe along the supralabial scales characterises several *Drysdalia* species, while a second pale stripe behind the eye is seen in *Hemiaspis signata*.

Sexual dimorphism is evident in several aspects of elapid morphology. Adult males are similar in size to adult females or a little smaller in most species. However, in several species and genera, especially larger taxa (Shine 1989), males grow much larger than females, correlated with the occurrence of male combat (Shine 1978b, 1991a). Such forms include *Austrelaps*, *Demansia*, *Hemiaspis signata*, some *Notechis* populations, *Oxyuranus scutellatus*, *Pseudechis*, large *Pseudonaja* species, some *Rhinoplocephalus* and *Suta*. In at least *Notechis*, males also have a greater muscle mass (Schwaner & Sarre 1988).

In those species examined, females have more ventral scales and fewer subcaudal scales, and a correspondingly longer body and shorter tail than males (Boulenger 1896; Mackay 1956; Rawlinson 1965; Storr 1967b; Hay 1972; Parker 1972; Gillam 1979b; Turner 1992). This has been imputed to be the result of space requirements for embryos/eggs in females and the hemipenes in males, although evidence for this is limited (Kluge 1974). Certainly, the tail base of males is broader than in females in those species with long slender tails.

Sexual dimorphism in head size relative to body length occurs in several species. Males have significantly larger heads than females of the same body length in *Austrelaps*, *Rhinoplocephalus*, *Suta*, *Furina*, *Pseudechis* and *Simoselaps*, but head sizes tend to be larger in females in some other taxa (Shine 1991b). The shape of the head is also sexually dimorphic in *Pseudechis porphyriacus* (Camilleri & Shine 1990), in which elements of the feeding apparatus of males are larger.

Body Wall

Elapid body scales are epidermal. The keratinised layer is sloughed regularly, generally in a single piece (Banks 1985). The skin is tightly bound to the superficial musculature by connective tissue, with little subcutaneous fat present. The musculature of the body wall of *Acanthophis antarcticus*, *Drysdalia coronata*, *Notechis scutatus*, *Pseudechis porphyriacus* and *Pseudonaja textilis* has been described (McKay 1889; Mosauer 1935; Rosenzweig 1989). A third supracostal muscle, *m. supracostalis lateralis medius*, is present in *Pseudechis* (Rosenzweig 1989).

Skeletal System

Australian elapid skulls have been illustrated by a number of authors, including Fairley (1929), Thomson (1933), Worrell (1956a, 1956b, 1961, 1963a, 1963b), Scanlon (1985) and Scanlon & Shine (1988). Despite the relative abundance of illustrations, and the use of osteological characters in phylogenetic reconstructions (Boulenger 1896; Kinghorn 1923a), there are few detailed descriptions of the cranial osteology of any Australian elapids. Notable exceptions are the descriptions and illustrations of *Acanthophis* by McKay (1889) and *Vermicella* by McDowell (1970).

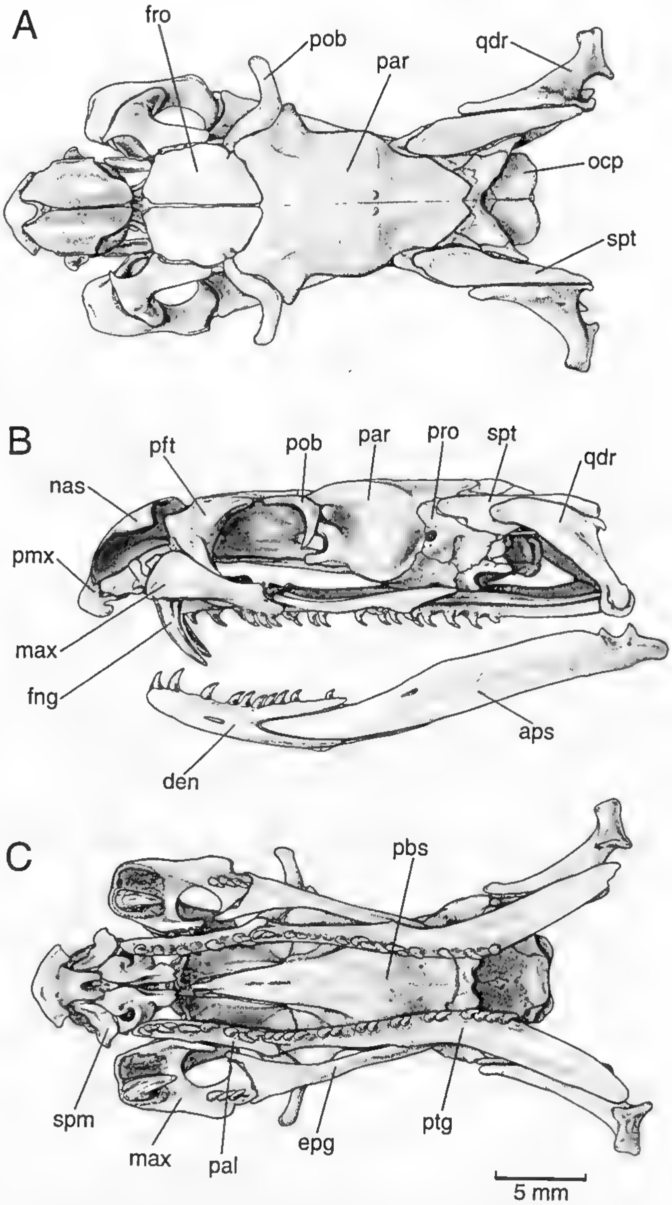

Figure 35.6 The skull of *Pseudechis guttatus*. **A**, dorsal view; **B**, lateral view; **C**, ventral view. **aps**, fused articular, prearticular and surangular; **den**, dentary; **epg**, ectopterygoid; **fng**, fang; **fro**, frontal; **max**, maxilla; **nas**, nasal; **ocp**, otoccipital; **pal**, palatine; **par**, parietal; **pbs**, parabasisphenoid; **pft**, prefrontal; **pmx**, premaxilla; **pob**, postorbital; **pro**, prootic; **ptg**, pterygoid; **qdr**, quadrate; **spm**, septomaxilla; **spt**, supratemporal. [B. Jantulik]

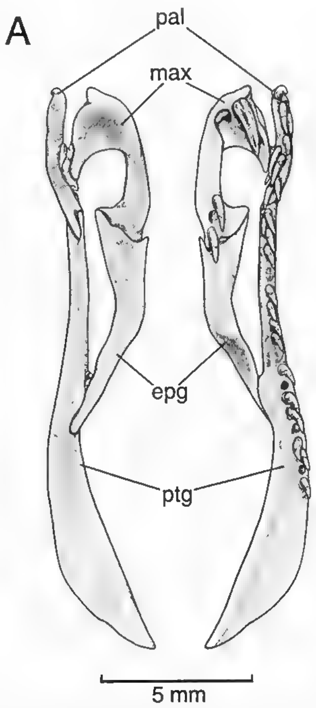

Figure 35.7 Left palatal complex of *Echiopsis curta*. **A**, dorsal view; **B**, ventral view. **epg**, ectopterygoids; **max**, maxillae; **pal**, palatines; **ptg**, pterygoids. [B. Jantulik]

The highly kinetic skull (Fig. 35.6) can be divided into several largely discrete components (Hoffstetter 1939; Romer 1956; Underwood 1967). The snout complex is composed of a single premaxilla and paired nasals, vomers and septomaxillae. The vomers occasionally fuse into a single element. The snout complex articulates with the rostral part of the braincase by variably developed contact between nasals, septomaxillae and frontals.

The rostral part of the braincase is almost entirely enclosed by paired frontals, dorsally and laterally and by the rostral process of the parabasisphenoid ventrally. The paired prefrontals do not articulate with the nasals (Romer 1956), unlike those of more primitive snakes, although there may be fascial connections between the two. The caudal part of the braincase is composed of a single large parietal, a single supraoccipital, paired prootics and paired otoccipitals (formed by fusion of exoccipital and opisthotic), a single parabasisphenoid (the fused parasphenoid and basisphenoid) and basioccipital (Fig. 35.6). Laterally, between rostral and caudal parts of the braincase, is a large cavum epiptericum or optic fenestra, bordered by the frontal, the parietal, and usually by the parabasisphenoid ventrally (Romer 1956; Underwood 1967), although the latter element may be secondarily excluded and the fenestra very reduced in some burrowing elapids (McDowell 1970). Along the rostro-lateral margin of the parietal, and usually just contacting the frontal are paired postorbitals. The paired supratemporals articulate with the caudo-lateral aspect of the braincase, and with the quadrates. Columellae are present.

The left and right palatal complexes are quite separate from each other. Each consists of a medial rod, composed of a palatine and a pterygoid, and a convex lateral component, composed of maxilla and ectopterygoid (Fig. 35.7). The caudal end of the ectopterygoid articulates with the pterygoid, but the rostral elements of the lateral and medial components are attached to each other only by ligaments. The short maxilla is hooked rostro-medially. McDowell (1970) stated that *Vermicella* is unique amongst Australian elapids in possessing a lateral process of the palatine. However, this process was not reported by Boulenger (1896) and Scanlon (1985), and is absent in two dried skulls examined in the Australian Museum (*V. annulata*, unregistered; *V. multifasciata*, R12882). The palatal complex is attached to the more dorsal elements of the skull by ligaments between pterygoid and quadrate, and a sliding articulation between maxilla and prefrontal (Fairley 1929). The palatine extends immediately ventral to the vomer, but is connected to it only by a loose fascia.

Each mandible is composed of the dentary, a caudal element formed by the fusion of articular, prearticular and surangular (Fig. 35.8), and, interposed between these on the medial surface of the mandible, the splenial and the angular bones. A distinct coronoid is absent. The left and right mandibles are loosely connected by an elastic ligament, while each articulates caudally with its respective quadrate.

The hyoid forms an inverted Y, with a short lingual process (sometimes absent) and long, paired cornua (McKay 1889; Underwood 1967; Langebartel 1968).

The postcranial skeleton of Australian elapids is poorly studied, except for McKay's (1889) account for *Acanthophis*. The postcranial skeleton consists solely of vertebrae and ribs. The vertebrae have the same range of articular and muscular processes as in other snakes (McKay 1889; Underwood 1967), and hypapophyses are present throughout the vertebral column in the trunk region (McDowell 1968).

Locomotion

As in most other limbless squamates, surface-active elapids move by lateral undulation. In this method of progression, controlled waves generated by the axial musculature pass caudally along the body and tail. The caudally-directed free edges of the body scales assist in gaining a purchase on surface irregularities, and propulsive forces are generated by the caudally-facing portions of the convex surfaces of the bends (Gans 1985b). Similar lateral undulations are shown by fossorial, sand-swimming elapids (*Simoselaps*), and by elapids swimming over water surfaces. Elapids swim well, and *Pseudechis porphyriacus*, at least, has been observed sheltering and foraging for fish below the surface (Gilbert 1935; Webb 1981a; Roberts 1984).

While most Australian elapids are surface-active, some genera, such as *Hoplocephalus* and *Tropidechis* are at least semi-arboreal (Shine 1983a; Shine & Charles 1982). The related tigersnakes (*Notechis*) may also climb bushes and trees, sometimes using

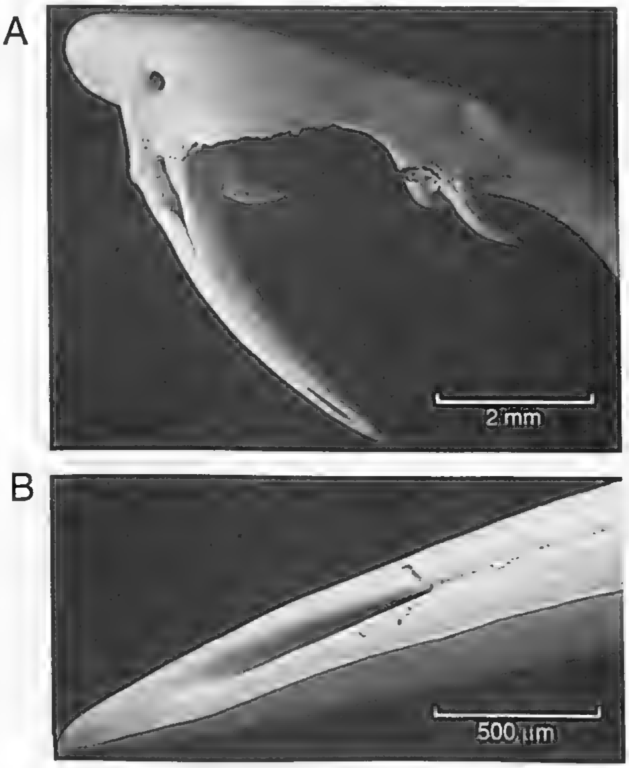

Figure 35.8 Photomicrographs of **A**, fang, illustrating the groove along the greater curvature between the orifice at each end and **B**, close-up of fang tip. [Photo by Geoff Ahern]

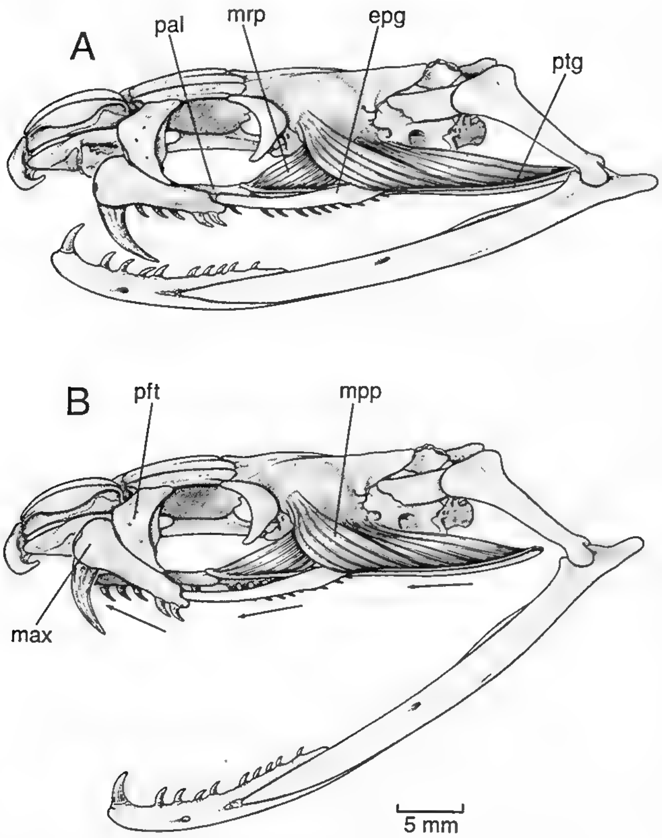

Figure 35.9 Fang erection mechanism in the taipan, *Oxyuranus scutellatus*. **A**, The palatal complex is drawn caudally by the *m. retractor pterygoidei*, when the mouth is closed; **B**, when preparing to bite, the mouth is opened and the palatal complex is drawn rostrally by the *m. protractor pterygoidei*. As a result, the maxilla is drawn rostrally and rotates around the prefrontal bone, thus raising the fang. Arrows indicate direction of movement of the pterygoid, ectopterygoid and maxilla. **epg**, ectopterygoid; **max**, maxilla; **mpp**, *m. protractor pterygoidei*; **mrp**, *m. retractor pterygoidei*; **pal**, palatine; **pft**, prefrontal; **ptg**, pterygoid. [B. Jantulik]

concertina movements, and *Pseudonaja textilis* climbs low bushes to prey on nestling birds (Kitson 1905; Warham 1958; Eckert 1965; Heatwole, Minton, Whitten, Dick, Parmenter *et al.* 1973; Shine 1977a; Webb 1981b; Gans 1985b). Even the heavy-bodied death adder (*Acanthophis antarcticus*) may be active in low bushes (Serventy 1951; Shea pers. obs.).

Feeding and Digestive System

Teeth are present on the maxillae, palatine, pterygoid and dentary bones. Implantation is pleurodont, and tooth replacement occurs throughout life. The maxillary teeth (Fig. 35.8) are grouped into enlarged rostrally-located fangs and a row of smaller teeth caudally on the bone. A diastema between the fang and subsequent teeth is characteristic of the elapids (McCarthy 1985). There are usually at least two fangs on each maxilla at any one time, although only one of these is in use and ankylosed to the bone (Scanlon & Shine 1988). The others are reserve fangs.

The number of maxillary teeth behind the fang varies (for examples, see Boulenger 1896; Kinghorn 1921, 1923a, 1939; Fairley 1929; Coventry & Rawlinson 1980; Covacevich *et al.* 1981). In most genera of Australian elapids, there are several teeth (Underwood 1967). Very large numbers (up to 13 teeth) are seen in *Demansia* and *Pseudonaja*, while very low numbers (one to three) are characteristic of *Acanthophis*, the sand-swimming *Simoselaps* species, *Oxyuranus scutellatus*, and *Vermicella*. *Elapognathus*, *Simoselaps approximans* and *S. bimaculata* lack maxillary teeth apart from the fangs. In most genera, there is little variation between species in the number of maxillary teeth. A notable exception is *Cacophis*, in which larger species have more teeth.

Lying medial to the maxillary tooth row, the more numerous palatine and pterygoid teeth form a single longitudinal row usually beginning at the rostral end of the palatine, although in *Oxyuranus scutellatus* the rostral end of the palatine is edentate (Kinghorn 1923a). In a similar way, the dentary teeth lie in a single row between maxillary and palatine/pterygoid rows, when the mouth is closed. Some data on the number of palatine, pterygoid and dentary teeth are available (Thomson 1933; Mackay 1955; Covacevich *et al.* 1981; Scanlon & Shine 1988; Greer pers. comm.; Worrell 1955, 1956b, 1961a, 1963a, 1963b). There are two to 16 palatine teeth. Species of *Simoselaps* and *Vermicella* have the least. The number of pterygoid and dentary teeth ranges from four to 33 and six to 30 respectively, and counts below seven and ten are restricted to *Simoselaps bimaculata* and *Vermicella annulata*, respectively.

As in other snakes, all teeth are strongly caudally recurved. The pterygoid teeth of oophagous species of *Simoselaps* are enlarged, compressed and tilted medially, as modifications for opening eggs. Enlargement of the rostral dentary teeth occurs in other elapids (Scanlon & Shine 1988).

The fangs of elapids are canaliculate (Fig. 35.8). The canal is formed by overgrowth of the walls of a groove lying along the rostral margin of the tooth. A suture usually marks the position of the canal, which is open at both base and apex of the tooth. A gingival sheath, the *vagina dentis*, normally covers the fangs, and slides down to the base of the tooth during biting. The duct from the venom gland opens near the basal aperture of the fang canal deep within the *vagina dentis*.

The mechanism of fang erection in Australian elapids (Fig. 35.9) has been described in detail by McKay (1889) and Fairley (1929). The entire palatine-pterygoid-ectopterygoid-maxilla apparatus is protracted by the *m. protractor pterygoidei* (Fig. 35.9A), which inserts on the pterygoid. As the palatal complex passes rostrally, the maxilla, which is attached to the prefrontal by ligaments, is drawn rostro-dorsally around the prefrontal, with flexion occurring at the maxillo-ectopterygoid joint. Additional protraction of the palatal complex rotates the prefrontal rostro-dorsally on the frontal, further elevating the maxilla, particularly in the death adder (*Acanthophis*). Following a bite, the palatal complex is retracted by the *m. retractor pterygoidei*, *m. pterygoideus* and *m. pseudotemporalis* (muscle nomenclature follows Haas 1973).

In the Australian elapids (the 'palatine draggers' of McDowell 1970), the palatine, which lacks any articulation or ligamentous attachment to the neurocranium or snout complex, is simply drawn rostrally during protraction of the palatal complex, and plays no part in envenomation. However, alternate protraction and retraction of the palatal complex and the mandibles is important in prey ingestion. The mandibular musculature has been described in detail by McKay (1889), Fairley (1929), Kesteven (1944) and McDowell (1967, 1970), while Haas (1973) has attempted to standardise the nomenclature of the muscles.

In addition to the injection of venom, many Australian elapids restrain prey by constriction, in a fashion similar to pythons (Fig. 35.10; Shine & Schwaner 1985; Morley 1987; Shine 1991a). Such constriction prevents the escape of prey following envenomation, and assists in ingestion.

The gastrointestinal tract is simple and relatively straight. The oesophagus is thin-walled, and extends almost to the caudal end of the liver. The stomach lies dorso-sinistral within the body cavity, and may be differentiated from the oesophagus by its much thicker muscular wall and stronger mucosal folds. Although there is little evidence of a sharp change in diameter or a sphincter to indicate the cardia of the stomach, the pylorus is pronounced. In *Pseudonaja textilis*, the cardia lies at approximately 55% of SVL, while the pylorus is located at approximately 65% of SVL. There is little evidence of a differentiated large intestine or a caecum. The lumen of the caudal-most part of the intestine may be sacculated by semilunar folds. The intestine is closely invested

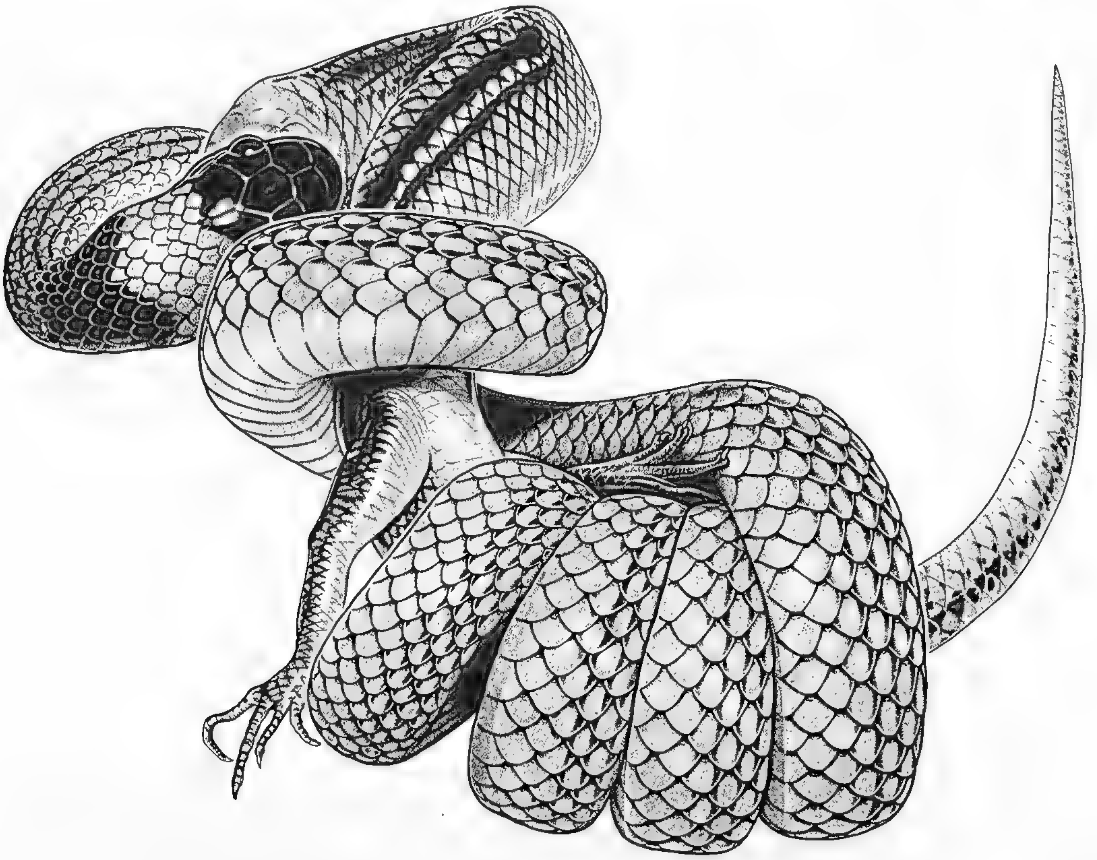

Figure 35.10 Constriction of prey following envenomation by a juvenile *Furina ornata*. [B. Jantulik]

with thick fat bodies throughout its length. As in other reptiles, the intestine enters the coprodaeum of the cloaca.

The liver is elongate, tapered at each end and shows little evidence of external lobation, although Wallach (1985) recognised two longitudinal sections and varying degrees of asymmetry. It lies ventrally and slightly dextrally in the body cavity, and ranges in overall length from 19 to 34% of SVL (Wallach 1985). The gall bladder lies close to the pylorus, well caudal to the liver. The cystic duct passes caudo-dorsally from the base of the gall bladder, then ventrally around the apex, to enter the intestine near the pylorus, between the lobes of the pancreas.

Circulatory System

Little has been published on the cardiovascular system of Australian elapids. Webb, Heatwole & de Bavay (1974) examined cardiac morphology in *Notechis*, *Pseudechis porphyriacus* and *Suta* as part of a critique of the literature on the reptile heart, but no further details of elapid morphology were given, and the elapid heart must be assumed to be similar to that of other snakes, in turn reportedly similar to the varanid heart (Webb 1979a).

The position of the apex of the heart varies between species and genera, from 20 to 32% of SVL (Wallach 1985). The relative position of the junction of right and left systemic arches forming the aorta, and the relative diameters of the two arches are also variable (Wallach 1985). Only a left common carotid artery is present (Underwood 1967). The spleen lies in contact with the pancreas (Underwood 1967).

The blood composition and erythrocyte morphology and biochemistry of several Australian elapids have been studied (Cleland & Johnston 1912; Cleland 1915; Saint Girons & Saint Girons, 1969; Saint Girons 1970b; Agar, Board, Gruca & Shine 1977; Board, Roberts & Shine 1977).

The thymus is represented by paired cranial and caudal lobes. It lies lateral to the jugular vein and extends cranially from the base of the heart (Bockman 1970; Shea pers. obs.). Its structure has not been studied in elapids.

Respiration

There is much variation in lung morphology in snakes, and consequently it has been well studied in elapids (Cope 1894; Underwood 1967; Wallach 1985). The right lung is well developed and large in all Australian elapids, and ranges in length from 31 to 74% of SVL. The length of the very reduced left lung is less than 2.5% of SVL, and it is even absent in several species. Additional lung tissue is also present in some Australian elapids along the dorsal margin of the trachea, between the ends of the tracheal cartilages. This 'tracheal lung' is also seen in the related sea snakes.

The right lung consists of a cranial vascular portion with numerous faveolae, where gas exchange takes place, and an avascular saccular portion caudally. The vascular portion is thicker walled and bears smaller faveolae cranially.

Gaseous supply to the right lung is via a right bronchus from the trachea. This may enter the lung near the cranial apex, or more caudally.

Excretion

Paired kidneys are present, but their structure has not been studied in Australian elapids. The length of the kidneys varies from 7 to 23% of SVL (Wallach 1985). Each kidney is supplied by several renal arteries (Underwood 1967), and a single ureter from each kidney passes caudally to enter the urodaeum dorsally. As in other snakes, a bladder is absent. Nitrogenous wastes are excreted as uric acid.

Sense Organs and Nervous System

Like that of other snakes, the elapid eye is covered by a transparent spectacle and lacks scleral ossicles, scleral cartilage and paraboloids in the visual cells (Underwood 1967). Eye size is variable (Shine 1991a), the iris may be pale or dark (Gillam 1979b; Hutchinson 1990b) and the pupil may be round or vertically elliptical (Storr 1985; Hutchinson 1990b). Although the variation in eye size parallels activity patterns, with larger eyes in diurnal species (Shine 1991a), iris colour and pupil shape show no such correlation; however they are generally consistent within genera. The retina of *Acanthophis* resembles that of rattlesnakes in lacking type C cones, but has rods as well as type A and B cones. In contrast, the few other Australian elapids that have been studied lack rods, but have type A, B and C cones (Underwood 1967, 1970).

The tongue is long and slender, with a deeply forked apex, and is withdrawn into a sheath in the floor of the oral cavity when not in use. The tongue is used primarily for chemoreception, in conjunction with the vomeronasal organ, which lies in the roof of the mouth, enclosed by the septomaxillae and vomers (Parsons 1970). Little is known of the nasal cavity and olfactory tissues of elapids. However, given the small variation in the anatomy of the nasal cavity of other snakes (Parsons 1970), it is likely that the elapid nasal cavity is similar to the rather simple structure of other snakes.

There are no external traces of an ear and the tympanic membrane and tympanic cavity of the middle ear are absent. Instead, the columella is related laterally to the quadrate (Baird 1970), although the footplate reaches the vestibular window to transmit vibrations to the inner ear as in other squamates. Some aspects of the inner ear of several Australian elapid genera have been studied by Miller (1968), who concluded that variation in the cochlear duct was correlated with habitat utilisation rather than phylogeny in snakes.

The central and peripheral nervous systems of elapid snakes have been little studied. The distribution of the spinal nerves of *Acanthophis* has been described by McKay (1889), and Proske (1969) described the cutaneous nerve endings in *Pseudechis*.

Endocrine and Exocrine Systems

The elapid hypophysis is similar to that of most other higher snakes (Caenophidia), but differs from that of viperids (Saint Girons, Bassot & Pfeffer 1964). Gross anatomical and cytological features of the caenophidian hypophysis have been described by Saint Girons (1970a).

A rounded, unpaired, plaque-like thyroid is present on the ventral surface of the trachea, slightly anterior to the heart base (Lynn 1970; Shea pers. obs.). Two pairs of parathyroids have been reported in *Notechis* (Clark 1970). Adrenal glands are present as paired, attenuate, yellow to orange bodies lying medial to the gonads (Gabe 1970). The adrenal histology of four Australian elapids (*Acanthophis antarcticus*, *Hemiaspis signata*, *Oxyuranus scutellatus* and *Pseudechis australis*) is similar to other squamates (Gabe, Martoja & Saint Girons 1964; Gabe 1970).

The compact, triangular pancreas is similar to that of other snakes (Underwood 1967; Shea pers. obs.); however, its histological structure and physiology have not been unstudied. It lies dorso-dextrally along the duodenum, immediately caudal to the pylorus, and is perforated by the bile duct.

A number of exocrine glands are associated with the head (McDowell 1967, 1968, 1969b, 1970; Kochva 1978; Saint Girons 1988). Five salivary glands have been reported. The superior and inferior labial glands are large, and the rostral and caudal sublingual glands and the premaxillary gland are small. All but the premaxillary gland are paired, and all are polystomatic. The sole ocular glands are the Harderian glands, which are restricted to the orbit in elapids (McDowell 1968). A large lateral nasal gland is also present.

Elapids possess a large venom gland caudodorsal to the oral margin (Fig. 35.11). In the Australian elapids, the caudal extremity of the venom gland does not pass ventrally around the angle of the mouth, unlike many other elapids (McDowell 1969b). The venom gland is invested by a tough tendinous connective tissue capsule, and its secretions are transmitted to the base of the *vagina dentis* by a single duct passing ventro-lateral to the orbit.

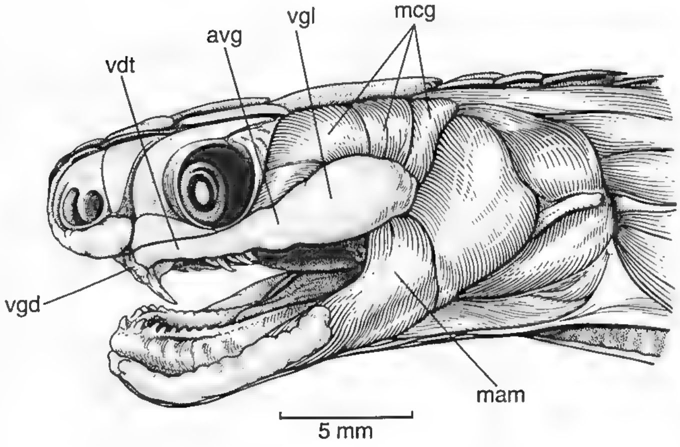

Figure 35.11 Venom gland and associated muscles in *Notechis scutatus*. The lateral and caudal parts of the *vagina dentis* covering the fang, and some superficial structures covering the venom gland have been removed. **avg**, accessory venom gland; **mam**, *m. adductor mandibulae externus 1b*; **mcg**, *m. compressor glandulae*; **vdt**, venom duct; **vgd**, *vagina dentis*; **vgl**, venom gland. [B. Jantulik]

Surrounding the caudal part of the venom duct is a small accessory venom gland, with a mucous secretion (Rosenberg 1967).

The composition of elapid venoms has been well studied for many species, particularly the more dangerously venomous taxa. Sutherland (1983) assembled the data available at that time, and a bibliography of the literature on Australian snake venoms and snake bite was compiled by Campbell (1976).

Amongst the toxic compounds identified in Australian species are both pre- and postsynaptic neurotoxins, myotoxins (especially in *Austrelaps*, *Rhinoplocephalus*, *Notechis*, *Pseudechis* and *Tropidechis*), procoagulants (especially in *Notechis* and *Pseudonaja*) and anticoagulants, haemolysins (especially in *Pseudechis*) and phospholipases with other functions. Some constituents have more than one action, and the venoms of different elapid species show varying combinations of effects (Sutherland 1983; White 1987a; Tan & Ponnudurai 1990). Different populations of tiger snakes (*Notechis*) show markedly different venom toxicities and effects (Worrell 1963c; Sutherland 1983; John & Kaiser 1990; Yang, Chang & Wu 1991). Variation in venom properties between individuals in the same population has also been reported for other species (Williams & White 1990), and even in the same individual over time (Williams & White 1992).

Notexin, the primary neurotoxin of *Notechis* venom, has been well studied (Sutherland 1983). It is a protein of 119 amino acid residues with molecular weight of 13 574 daltons, and has both myotoxic and presynaptic neurotoxic effects. The major neurotoxin from *Pseudonaja textilis* venom, textilotoxin, is the largest and most complex snake toxin known, with a molecular weight of 88 000 daltons, and has presynaptic neurotoxic effects (Sutherland 1983; Tyler, Barnett, Nicholson & Spence 1987), although two other neurotoxins isolated from the same species, pseudonajatoxin a and pseudonajatoxin b, have postsynaptic effects (Barnett, Howden & Spence 1980; Tyler, Spence, Barnett & Howden 1987). Taipoxin, another large presynaptic neurotoxin with a molecular weight of 45 600 daltons, has been isolated from *Oxyuranus scutellatus* venom (Fohlman, Eaker, Karlsson & Thesleff 1976). A short-chain myotoxin (122 amino acid residues, molecular weight 13 484 daltons) lacking neurotoxic effects, mulgatoxin, has been isolated from *Pseudechis australis* venom (Leonardi, Howden & Spence 1979). Although the venom of this species has been reported to be primarily myotoxic in action (Sutherland 1983), a number of neurotoxins and haemolytic and anticoagulant phospholipases have been isolated from it (Nishida, Terashima, Shimazu, Takasaki & Tamiya 1985; Takasaki & Tamiya 1985; Sharp, Berry, Spence & Howden 1989; Takasaki,

Table 35.1 Relative toxicity of Australian elapid snake venoms to mice (from Broad *et al.* 1979). LD_{50} is the minimum dose (mg venom/kg mouse) required to kill 50% of a sample of mice. Thus the more toxic venoms have the lowest LD_{50} values. Toxicity is also dependent upon the diluent used for the venom. The two values are for venom in: (a) 0.85% saline; (b) 0.1% bovine serum albumin in saline.

Species/subspecies	LD_{50} (a)	LD50 (b)
Oxyuranus microlepidotus	0.025	0.010
Pseudonaja textilis	0.053	0.041
Oxyuranus scutellatus	0.09	0.064
Notechis scutatus scutatus	0.118	0.118
Notechis scutatus niger	0.131	0.099
Notechis scutatus occidentalis	0.194	0.124
Notechis scutatus serventyi	0.338	0.271
Acanthophis antarcticus	0.400	0.338
Pseudonaja nuchalis	0.473	0.338
Austrelaps superbus	0.560	0.500
Pseudonaja affinis	0.660	0.560
Pseudechis papuanus	1.09	1.36
Hoplocephalus stephensii	1.36	1.44
Tropidechis carinatus	1.36	1.09
Pseudechis guttatus	2.13	1.53
Pseudechis colletti	2.38	–
Pseudechis australis	2.38	1.91
Pseudechis porphyriacus	2.52	2.53
Cryptophis nigrescens	2.67	–
Demansia olivacea	>14.2	–

Suzuki & Tamiya 1990). Recently, a number of additional toxins have been identified and characterised from other Australian elapids (Fohlman 1979; Sheumack, Howden & Spence 1979; Sheumack, Spence, Tyler & Howden 1990; Vaughan, Scully & Tirrell 1981; Tamiya 1985; Speijer, Govers-Riemslag, Zwaal & Rosing 1986; Bernheimer, Linder, Weinstein & Kim 1987; Masci, Whitaker & de Jersey 1988; Williams & White 1989; Schmidt & Middlebrook 1989; Francis, John, Seebart & Kaiser 1991).

Venom yields from Australian elapids are extremely variable, even from an individual snake over time. In general, however, of the dangerously venomous species, the lowest yields are from the brownsnakes (*Pseudonaja*), with a mean yield of 4 mg per milking for the best studied species, *P. textilis*. The highest yields are from the taipan, *Oxyuranus scutellatus*, with a mean yield of 120 mg, and the mulga snake, *Pseudechis australis*, with a mean yield of 180 mg and maximum of almost 600 mg (Sutherland 1983).

Venom toxicity also varies between species, and is not correlated with venom yield. In terms of LD_{50} of mice, the most toxic Australian elapid venoms occur in the two *Oxyuranus* species and *Pseudonaja textilis* (Table 35.1).

The mechanism of venom injection is largely independent of fang erection, and consequently bites may not necessarily result in envenomation (Sutherland 1983). In elapids, the venom gland is largely surrounded caudally by a superficial belly of *m. adductor mandibulae externus*. This muscle is divided further into a dorsal compressor of the venom gland, *m. compressor glandulae*, and a ventral portion, *m. adductor mandibulae externus 1b* (Fairley 1929; Rosenberg 1967; Haas 1973; the nomenclature used here follows Haas 1973). Patterns of variation in the venom gland musculature of Australian elapids have been described by McDowell (1967, 1969b, 1970), and the homologies of this musculature are considered by McDowell (1986). Contraction of these muscles compresses the venom gland, and results in expulsion of venom into the venom duct, and further, into the fang canal via the *vagina dentis*. Further compressive effects on the venom gland may be provided by contraction of the pterygoid musculature during mouth closure (Fairley 1929).

Reproduction

In Australia, elapids may be oviparous or viviparous, the latter mode of reproduction being characteristic of '... a relatively recent, but extensive and diverse, adaptive radiation of elapids in southern Australia ...' (McDowell 1985). Reproduction in all elapids is sexual.

The chromosomes of Australian elapids have been studied intensively by Mengden (1981, 1982, 1985a, 1985b) and Mengden, Shine & Moritz (1986). Diploid number ranges from 30 to 42, usually with a distinct division between macrochromosomes and microchromosomes. Pairs one and three are metacentric, with a prominent secondary constriction on one arm of the first in all but *Demansia*, while pair two is submetacentric. Pairs four or five (the latter in *Denisonia* and most *Drysdalia*) are sex chromosomes, and the morphology of the W chromosome is highly variable between species (Mengden 1981, 1985a). The chromosomal data may be divided into ten karyomorph groups (Mengden 1985a). Some currently recognised species are chromosomally polymorphic (Mengden 1982, 1985a, 1985b) and may be composite.

Electrophoretic and immunological analyses of blood and liver proteins have also been carried out for several groups of Australian elapids (Mengden 1985a, 1985b; Schwaner *et al.* 1985; Mengden *et al.* 1986; see Mengden 1983 for a review of the earlier literature), and have proven to be useful in hypothesising phylogenetic relationships, both within the Australian radiation, and to other elapid groups.

The gonads in both sexes are paired, and lie dorsally in the body cavity, the right extending towards the head more than the left. In the female, the ovaries lie a short distance caudal to the pylorus. In *Pseudonaja textilis*, the cranial end of the right ovary is at approximately 65% of SVL. The ovaries are very elongate and are suspended from the dorsal midline by a short mesovarium. The oviducts are paired, and each passes dorso-lateral to the respective ovary but ventro-lateral to the kidney, before passing dorso-medially again to enter the urodaeum. The infundibulum of each oviduct opens near the cranial end of the ovary, but does not enclose it.

The anterior end of the right testis is at approximately 75% of SVL in *Pseudonaja textilis*. Each testis is suspended from the dorsal midline by a short mesorchium. The epididymides lie dorso-medial to the testes, suspended by their own peritoneal fold. Each ductus deferens passes ventrally over the surface of the kidney, inclines laterally along its ventro-lateral margin lateral to the ureter, and opens dorso-laterally into the urodaeum. Only the terminal post-renal portion of the ductus deferens is non-convoluted.

The male copulatory organs are paired hemipenes, as in other squamates. The hemipenes of Australian elapids are ornamented with strong spines and often flounces, and the *sulcus spermaticus* is forked (Worrell 1961b; McDowell 1967, 1969b, 1970; Wallach 1985). The hemipenis itself may also be forked, and in Australian elapids, the calyces, present in other elapids, are usually poorly developed to absent (McDowell 1967).

The reproductive cycles of female elapids have been studied in most Australian species by Shine and his co-workers (see Shine 1991a for summary). In general, most non-tropical species, including both egg-layers and live-bearers, show strongly seasonal reproduction, with vitellogenesis in spring, ovulation in late spring/early summer, oviposition in summer and parturition (in live-bearing species) in summer or autumn. Some evidence suggests that northern species and populations may breed a little earlier than cold-climate species (Shine 1981b, 1984a). There are also occasional records of individual females with enlarged ovarian follicles or oviducal eggs or young outside this period (Shine 1984b, 1988a). Greater variation in the seasonality of the female reproductive cycle occurs in tropical elapids. In some genera with both tropical and temperate species, the tropical taxa follow the same seasonal pattern as their southern congeners (*Pseudonaja*, *Rhinoplocephalus*; Shine 1984a, 1986e, 1988a, 1989). In other genera, the tropical species and populations apparently show little or no seasonality (*Demansia*, *Pseudechis*; Shine 1980d, 1987e). Aseasonal reproduction may also occur in the arid-adapted *Oxyuranus microlepidotus* (Shine & Covacevich 1983).

In contrast to the data on timing of female reproduction, data on the male reproductive cycle are scant and largely limited to six species from south-eastern Australia (Shine 1977b, 1991a). In *Pseudechis porphyriacus*, the male cycle closely parallels the female cycle, with testicular recrudescence beginning in autumn, but spermiogenesis is restricted to spring. In the brownsnakes examined (*Pseudonaja textilis*; note that one population was incorrectly identified as *P. nuchalis* in Shine's 1977 papers), the gonadal cycle is similar, but abundant spermatozoa are present throughout the year. In *Austrelaps ramsayi*, both *Hemiaspis* species, *Notechis scutatus* and *Suta dwyeri*, testicular size varies little throughout the year (although generally maximal in summer), spermiogenesis is postnuptial in midsummer, and spermatozoa are retained in the male tract until at least late autumn. The epididymides of *Simoselaps* species carry spermatozoa throughout the year (Shine 1984b).

Embryology and Development

Almost nothing is known of the embryological development of Australian elapids. Brief observations on the development of the orbitotemporal skeleton in *Pseudechis* were made by de Beer (1926). Amongst the live-bearing species, omphaloallantoic placentation (Stewart & Blackburn 1988) has been described for *Austrelaps* and *Suta* species (Weekes 1929, 1935). Foetal membranes closely invest a uterine wall that is locally infolded close to the main uterine vascular supply. The allantois completely invests the yolk sac at an early stage of development. Partial breakdown of maternal and foetal epithelium results in close apposition of the two circulations (Weekes 1935). Extraembryonic circulation is via left and right umbilical arteries and veins, and a single vitelline artery and vein (Weekes 1935). Placental transfer of nutrients has been demonstrated for several species of elapid (Shine 1977c).

The young of live-bearing species are born enclosed in their foetal membranes, which they penetrate almost immediately after birth. *Pseudechis porphyriacus* gives birth to young enclosed in a thicker membrane, from which emergence is often delayed (Schofield 1972; Craig 1978; Banks 1987b; Cogger 1992). This mode appears to represent an independently evolved instance of live-bearing.

Neonates of several elapid species show marked differences in colouration from adults. In *Pseudonaja* species, the young have dark head and nape patches, and in some species and populations, narrow dark rings on body and tail (Gillam 1979b; Bush 1989; Cogger 1992). These fade with age, and are usually absent in adults. Several *Drysdalia* and *Pseudechis* species and *Rhinoplocephalus bicolor* also show marked ontogenetic changes in body colour and pattern (Coventry & Rawlinson 1980; Shine 1986e, 1991a).

NATURAL HISTORY

Life History

Longevities of elapids in the wild are not known, though some captive specimens have lived for at least 20 years (Shine 1991a). Growth patterns and ages at sexual maturation are known for a few species, mostly from analysis of monthly distributions of body sizes of museum specimens (Shine 1978a, 1980a, 1980c, 1980e). Growth rates estimated in this way are relatively high, and suggest maturation at two to three years of age in most of the taxa studied to date. Some species may mature even earlier, and captive male *Oxyuranus scutellatus* are reported to mature in less than two years (Shine & Covacevich 1983). Hence, ages at maturation in Australian elapids tend to be slightly lower than in colubrid and viperid snakes studied in other countries (Seigel & Ford 1987; Dunham, Miles & Reznick 1988). Species of *Acanthophis* and *Vermicella* may be exceptions to this general pattern, and mature at four or five years of age (Shine 1980c, 1980e), although well-fed captive snakes may mature considerably earlier (Johnston 1987). As is usual in snakes, male elapids tend to mature earlier, and at smaller body sizes, than do conspecific females (Shine 1978b; Parker & Plummer 1987). The only detailed capture-mark-recapture study on elapids is Schwaner's (Schwaner 1985; Schwaner & Sarre 1988) work on island tigersnakes (*Notechis ater*).

The reproductive output of a female elapid depends on her body size. Interspecific comparisons indicate that smaller elapids produce fewer offspring per clutch, and probably reproduce more frequently (Shine 1977c, 1985b). In small species of elapids, the offspring at birth (or hatching) are small in absolute terms, but are larger relative to maternal size than is the case in larger species. Clutch size increases with maternal body size within a species, as well as among species. Thus, the tiny *Suta* species generally produce about three to four neonates, each about 40% of the mother's body length, whereas the much larger *Oxyuranus scutellatus* produces about 11 offspring, each about 20% of maternal length. Shine (1991a) provided data on average clutch sizes, offspring sizes and adult body sizes for most species of Australian elapids.

Although oviparity is the ancestral reproductive mode within the Australian elapids, viviparity has arisen independently in two lineages. One is represented by a single species, *Pseudechis porphyriacus*; all of its congeners are oviparous. The other viviparous lineage contains a wide range of genera. These include many taxa restricted mainly to southern and/or eastern Australia, such as *Tropidechis*, *Austrelaps*, *Notechis* and *Drysdalia*, but some viviparous taxa occur over a much larger area, for example, *Acanthophis* and *Suta*. Viviparous species constitute a higher proportion of the total elapid fauna in cooler areas (Shine & Berry 1978; Shine 1985b, 1985c). Offspring sizes and litter sizes appear not to differ significantly between oviparous and viviparous species of similar body sizes (Shine 1987e).

Ecology

Most Australian elapids are active, searching foragers, feeding mainly on relatively small prey. Prey types vary among species, depending on several factors including geographic distribution, habitat preference, foraging behaviour and body size. Several taxa have extremely specialised diets. *Vermicella* species feed mainly or even exclusively on typhlopid snakes, and the *Simoselaps semifasciatus* group feeds only on reptile eggs.

Reptiles and/or frogs are the main prey types for most elapid species. Diurnally-active lizard species are the usual prey of small nocturnal elapids (for example, *Cacophis*, *Furina*, *Suta*) that locate the sleeping lizards and seize them inside their nightime retreats (burrows, hollow logs, *etc*.). Prey location by these taxa is presumably mainly by scent, as nocturnal elapids have smaller eyes than diurnal species (Shine 1991a). Small elapids tend to have relatively specialised diets, consisting mostly of scincid lizards, although some genera (for example, *Hemiaspis*, *Denisonia*) feed mainly on frogs. Specialised anurophagy occurs also in some larger elapids (especially, some populations of *Notechis*), but most larger elapids (for example, *Pseudechis*, *Austrelaps*, *Pseudonaja*) have more generalised diets. Juveniles of these taxa feed mostly on frogs and lizards, but larger specimens also consume small mammals or birds. The largest elapids (genus *Oxyuranus*) feed exclusively on endothermic prey, mostly small mammals (Shine & Covacevich 1983). Diets are also relatively generalised in a few smaller species, such as *Echiopsis curta* and *Acanthophis* species. The latter genus is remarkably convergent in morphology and general ecology with viperid snakes, as well as in its reliance on 'ambush' predation. The tail-tip of death adders is brightly-coloured (especially in young snakes) and is wriggled as a lure to attract potential prey (Carpenter, Murphy & Carpenter 1978).

Significant geographic variation in dietary composition has been documented for several wide ranging Australian elapid species, presumably in relation to geographic shifts in prey abundance and availability (for example, Shine 1987e, 1989). Perhaps the most remarkable example is recorded from the small islands off South Australia, where islands separated by only a few kilometres often differ substantially in prey availability, depending mostly on whether or not the island supports breeding colonies of seabirds. The endemic tigersnakes on these islands thus differ enormously in diet, and in body size (Schwaner & Sarre 1990). The gross dietary composition of most elapid species is summarised by Shine (1991a). Details of diet are provided by Orange (1991), Rose (1974), Webb & Rose (1985) and Webb (1987) and in a series of papers by Shine (1977a, 1980a, 1980c, 1980d, 1980e, 1981a, 1981b, 1982, 1983a, 1983c, 1984a, 1984b, 1986e, 1987a, 1987d, 1987e, 1987f, 1988a, 1989), Shine & Charles (1982) and Shine & Covacevich (1983).

Habitat selection has rarely been studied in detail in Australian elapids, but many species are known to prefer particular habitat types. Thus, for example, syntopy is rare among several broadly sympatric elapid species in the New England region of New South Wales, because each species prefers slightly different biotopes (Shine 1977a). Preferences for specific types of shelter seem to constrain the geographic distributions of some species: for example, *Hoplocephalus bungaroides* apparently depends upon weathered sandstone outcrops, where it lives under exfoliated sandstone boulders (Krefft 1869; Hersey 1980; Shine & Fitzgerald 1989). Similarly, most *Rhinoplocephalus bicolor* have been found in abandoned stick-ant nests near swamps (Christensen 1972; Shine 1986e). Most 'sand-swimming' species of the genus *Simoselaps* are restricted to areas of loose, windblown sand. Other taxa are more catholic in their requirements, and a few have adjusted well to increasing human modification of the environment. For example, the larger *Pseudonaja* species are most abundant in areas disturbed by agricultural activities, and feed mostly on the introduced house-mouse *Mus domesticus* (Shine 1989). Habitat use by a particluar species seems to relate primarily to availability of prey and cover (Schwaner 1991).

Both internal and external parasites are common in Australian elapids. Among the external parasites are ticks of the genera *Amblyomma* and *Aponomma* (Roberts 1970; Sharrad & King 1981), trombiculid mites (*Guntheria*: Domrow 1978a) and paramegistid mites (*Ophiomegistus*: Domrow 1978b). Amongst the internal parasites are haematozoa, including several species of *Haemogregarina* and a possible trypanosome (Mackerras 1961), and other protozoa (*Eimeria*, *Cryptosporidium*, *Sarcocystis*: McFetridge & Burrell 1991). Acanthocephalans include *Sphaerechinorhynchus rotundicapitatus* (Johnson & Deland 1929a, 1929b; Daniels 1990). Lingatulids of the genus *Porocephalus* (Johnston 1912, 1918), cestodes of the genus *Acanthotaenia* (often cited as *Proteocephalus*: Johnston 1912; Smales 1984) as well as immature encysted cestodes (*Piestocystis*: Hill 1894), and many nematodes have been recorded, including *Abbreviata* (often reported as *Physaloptera*), *Capillaria*, *Diaphanocephalus*, *Dioctowittus*, *Hastospiculum*, *Kalicephalus*, *Moaciria*, *Ophidascaris*, *Polydelphis* and *Trichosomum* (Johnston 1912; Johnston & Mawson, 1942, 1948; Jones, 1978a, 1978b, 1979, 1980; Sprent 1988; McFetridge & Burrell 1991).

The trematode *Dolichopera macalpini* commonly parasitises anurophagous elapids, and has been reported to cause high mortality in captive collections (Johnston & Angel 1940; Giddings 1978; Rosenzweig 1984). Also commonly seen in elapids are subcutaneous swellings containing spargana, encysted larvae of the cestode *Spirometra* (Johnston 1912). Only occasionally do these appear to result in significant mortality (Purvis 1989). Studies on nematodes from the guts of elapids have revealed significant differences in infestation rates in different geographic areas (for example, Jones 1980). Ascarid worms may cause substantial mortality in free-living elapids, especially in elongate animals such as *Demansia psammophis* (Pl. 8.6) that are unable to forage successfully because of the enormous swelling induced by the ascarid infestation (Shine 1991a).

Home ranges and daily movements of elapids are poorly known, although the apparently low population densities and high vagility of many species suggest that individuals may sometimes cover huge areas. Studies with miniature radio transmitters showed that home range sizes of common blacksnakes (*Pseudechis porphyriacus*) were highly variable in space and time (Shine 1987c). Movements were largest in mate-searching males, and one animal covered an area of more than 90 ha over a period of only a few weeks. In contrast, home ranges were generally small outside the mating season, and typically less than 2 ha in extent during the summer months. Males grow larger than females in this species, and generally have larger home ranges (Shine 1987c). Limited radiotelemetric data suggest that home ranges are small (< 2 ha) in *Notechis scutatus* (Shine 1979).

Behaviour

Snakes are solitary animals, and elapids rarely interact with each other except during reproductive activities. In cooler regions of Australia, limited availability of suitable overwintering sites may result in local aggregations, such as in rabbit holes (*N. scutatus*; Shine 1979), in piles of rubble (*Austrelaps ramsayi*; Shine 1979), under concrete blocks (*P. porphyriacus*; Kinghorn 1956), or under exfoliated rocks and sheets of tin (for example, *Rhinoplocephalus nigrescens*; Jenkins & Bartell 1980; Shine pers. obs; Hoser 1980, 1991). However, many Australian elapids mate in both autumn and spring, and observations of male/female pairs during winter (for example, *Suta dwyeri*, *S. flagellum*; Shine 1979; Fyfe & Booth 1985) may reflect mating activity rather than communal overwintering. Large basking aggregations of *Pseudechis porphyriacus* and *Austrelaps ramsayi* have also been reported, the former in early summer (Sault 1977). There are no reports of social interactions among snakes under these conditions. Parental care of the offspring after hatching or birth has never been reported reliably in Australian elapids (Shine 1988c).

The only other circumstance where elapids are known to aggregate is during reproductive activities. Several males may converge on a receptive female, or females may aggregate at communal oviposition sites (for example, *Demansia psammophis*; Covacevich & Limpus 1972). Female viviparous snakes may also aggregate before parturition, as reported in *P. porphyriacus*, *Austrelaps ramsayi* and *Suta dwyeri* (Shine 1979). However, the most common reproductive interactions are courtship and male–male combat. Typically, a female is relatively sedentary during the mating season, and the pheromone trails she deposits on the substrate during her limited movements are detected by the actively searching males. Courting male elapids are very active, constantly flick the dorsal surface of the female with the tongue, and press their heads down against her dorsal midline (Rankin 1976b; Bush 1983; Orange 1984). The female finally signifies acceptance by elevating her tailbase so that the male can insert one of his paired hemipenes. The two snakes then remain locked together, with relatively little movement, for a prolonged period — often several hours (Charles, Whitaker & Shine 1980; Charles,

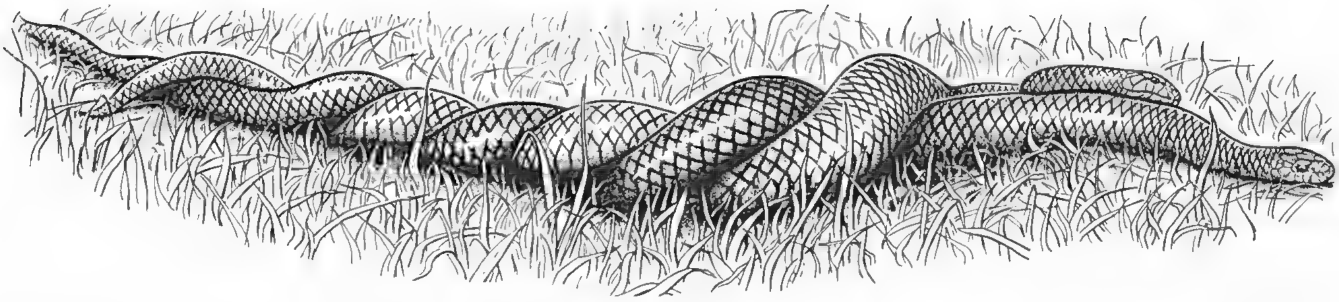

Figure 35.12 Male–male combat in *Austrelaps superbus*. (After photo by C. & S. Pollitt/ANT) [B. Jantulik]

Watts & Shine 1983; Charles 1984). The male's hemipenes are spinose in many taxa, and bleeding from the female's cloaca has been reported after copulation (Charles *et al.* 1980, 1983; Ehmann & Swan 1987).

Male–male interactions take a very different form. Territoriality (defence of a specific area) has never been convincingly documented in snakes anywhere in the world, but female defence polygyny (temporary defence of an area around a reproductive female) is widespread (for example, Duvall, Schuett & Arnold 1992). Although social behaviour of Australian elapids is poorly known, incidental observations confirm that male–male combat occurs in a wide variety of taxa including *Austrelaps* (Fig. 35.12), *Hemiaspis* and *Rhinoplocephalus* (Shine & Allen 1980), *Demansia* (Shine 1980d), *Oxyuranus* (Shine 1991a); *Pseudechis* (Fleay 1937; Baker 1969; Shine 1977b, 1987e; Shine, Grigg, Shine & Harlow 1981, Mirtschin & Davis 1992), *Pseudonaja* (Fleay 1937; Shine 1989, 1991a), *Notechis* (Shine 1977b; Bush 1983) and *Suta* (Turner 1992). The combat usually takes a highly ritualised form, where the two males intertwine their bodies and each attempts to force the other's head downwards. Vigorous biting has been observed in some taxa, such as *Pseudonaja nuchalis* (Fyfe pers. comm.). Although male–male combat has not been recorded in many Australian elapid species, the data are so scanty that the absence of records may mean very little.

The strongly seasonal climates over most of Australia mean that activity patterns of most elapids are also strongly seasonal. Although temperatures are high year-round in tropical Australia, precipitation is heavily concentrated in the summer months in this area, and hence reptilian activity tends to be most intense at this time as well (Friend & Cellier 1990; Braithwaite, Friend & Wombey 1991). In southern Australia, most elapids overwinter singly, under relatively superficial shelter, and may emerge to bask on unusually warm days even in midwinter. However, snake movements are very restricted in most of southern Australia over the period May to August.

Australian elapid snakes include diurnal, crepuscular and fully nocturnal species, but there is considerable flexibility in activity patterns even within single species. In many taxa, the time of day at which activity occurs shifts seasonally, with fully diurnal behaviour in spring and autumn but a trend towards crepuscular or nocturnal activity in hotter weather, for example, in *Notechis ater* (Schwaner 1989) and *Pseudechis porphyriacus* (Shine, 1979; Shine & Lambeck 1990). The same pattern occurs geographically, and tropical representatives of wide-ranging taxa (for example, *Pseudonaja nuchalis*, *Pseudechis australis*, *Demansia atra*) show much more nocturnal activity than their temperate-zone relatives. Temporal variations in food availability may also influence activity levels, with snakes becoming less active if foraging is unproductive (Shine & Lambeck 1990).

Despite this type of flexibility, however, most elapid species can be characterised fairly easily in terms of daily activity patterns. Many of the larger taxa, such as *Pseudonaja*, *Oxyuranus* and *Austrelaps*, are primarily diurnal, whereas most of the small species are nocturnal, including those of *Cacophis*, *Furina*, *Rhinoplocephalus* and *Suta* species (Fyfe & Booth 1984; Webb & Chapman 1984). Nonetheless, there are many exceptions to this trend, especially among the smaller species. For example, most whipsnakes (*Demansia* species) forage actively during daylight hours, even on very hot days. In a few cases, closely related species differ substantially in their activity patterns. Thus *Hemiaspis signata* is active both day and night, whereas *H. damelii* is strictly crepuscular.

Body temperatures of active elapids span a wide range, although most diurnal species appear to maintain temperatures between about 25° and 35°C (Shine 1979, 1987c; Lillywhite 1980; Saint Girons & Bradshaw 1981; Heatwole & Taylor 1987; Schwaner 1989; Shine & Lambeck 1990). Diurnal species typically bask in the sunlight for extended periods, often shuttling between sun and shade to maintain relatively constant body temperatures. Crepuscular and nocturnal taxa may rely more heavily on 'indirect basking', using heat transfer through sun-warmed cover objects, or 'protected basking' from within a crevice or other shelter.

Most Australian elapid snakes will defend themselves vigorously if attacked, and species-specific defence postures are common. The bandy-bandy, *Vermicella annulata*, slowly raises body loops and holds them off the ground (Bustard 1969b), whereas death adders, *Acanthophis* species, may inflate the body and form a tight spiral with the outer edges of the body raised. The curl snake, *Suta suta*, derives its common name from its habit of forming a tight coil when harassed. Crowned snakes, *Cacophis* species, flatten the head and arch the neck strongly, and then launch a series of rapid strikes with a closed mouth. The striking postures of brown snakes (*Pseudonaja*) show species-specific differences (Gillam 1979b) (Pl. 8.8). Many elapids flatten and broaden the neck and cranial portion of the body when threatened. This flattening is caused by elevation of the ribs, and is analogous to the 'hood' of cobras. Most of the larger elapids are less likely to keep their mouths closed while striking, and will often chew tenaciously to inject venom once they achieve a hold on the aggressor. Taipans (*Oxyuranus scutellatus*) are unusual in releasing their victim immediately after the strike (Shine & Covacevich 1983), although tigersnakes (*Notechis scutatus*) feeding on mammalian prey also employ this technique (Witten 1985a).

Economic Significance

Some 3000 cases of snakebite are reported in Australia each year (Sutherland 1983; White 1981, 1987b; Pearn 1988). In about 10% of these, antivenom is administered. Despite the fact that some of Australia's elapids have extremely potent venom, most victims of snakebite recover fully. Fewer than five human deaths are attributed to snakebite in Australia each year. Stock losses are not known. The high success rate in dealing with serious envenomation can be attributed largely to efficient, effective first aid and medical treatment (Sutherland 1983).

Mortality and morbidity are not the only costs of snakebite. Pearn (1988) has identified '... A number of factors (which) combine to make logistic costs of human envenomation of special significance in Australia — a large proportion of the world's most venomous snakes, a sparse population remote from skilled clinical help, ready access to outback radio and a high expectation of good medical care ...'. Costs of hospital admissions would be in excess of $2 million annually, assuming hospital costs of $800 per victim for an average stay of two days, for 3000 cases annually. To this must be added costs of venom kits and antivenom, and of any unused life-expired antivenoms. Annual productivity costs for the 300 serious cases of envenomation are more substantial, as each patient would be hospitalised, and out of the work/home force, for from one or two days to many months.

Snakes of the genera *Acanthophis*, *Austrelaps*, *Notechis*, *Oxyuranus*, *Pseudechis*, *Pseudonaja*, *Rhinoplocephalus* and *Tropidechis* are known to have inflicted fatal bites. Some species of *Demansia*, *Furina* and *Hoplocephalus* have been responsible for bites with serious sequelae, but not fatal outcomes. *Notechis scutatus* (Pl. 8.7) and *Pseudonaja textilis* are the species most frequently involved in fatalities (Covacevich, Davie & Pearn 1987). *Oxyuranus scutellatus* and *Pseudechis australis* have also been responsible for many fatalities in this country.

Pharmacological properties of Australian snake venoms have been investigated only recently. Stiles, Sexton & Weinstein (1991) have demonstrated a pronounced antibacterial effect in *Pseudechis australis* venom.

All Australian States except Tasmania currently have legislation in place to protect snakes. The regulations vary across the States, but all allow venomous snakes to be killed if they pose a threat to human life. In most cases, collection of snakes from the wild is prohibited without a permit, and such permits are generally issued only for scientific research or for a few exempted (common) species that may be kept by hobbyists. Wildlife protection authorities regularly confiscate illegally-taken 'pet' snakes from amateur keepers, and the courts impose substantial fines on these people. Unfortunately, this emphasis on protecting individual specimens is misplaced: very few snake species (if any) are threatened by collection for scientific research or by hobbyists. Instead, snakes are threatened by processes such as habitat destruction or the spread of feral animals, that are more difficult to control with legislation.

Although there have been relatively few attempts to breed Australian elapids in captivity, success in this respect has been reported for several taxa (for example, Charles *et al.* 1980, 1983; Fitzgerald & Pollitt 1981; Banks 1983a, 1983b; Charles 1984; Fyfe & Booth 1985; Mirtschin 1985; Turner 1985; Johnston 1987; Fyfe & Munday 1988; Fyfe 1991; Weigel 1992). Most attention has been devoted to the larger and more spectacular species, because these are valued as exhibition animals. They are also easier to keep in captivity, because of their willingness to eat rodents, than are most of the smaller species with specialised diets. Captive breeding may play some role in conservation efforts with a few endangered species such as the broad-headed snake *Hoplocephalus bungaroides* (Shine & Fitzgerald 1989), but is not a feasible substitute for increased emphasis on the preservation of native habitats.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

The detailed distributions of the 83 species of elapid snakes currently recognised from Australia (Hutchinson 1990b; Rawlinson 1991) are now both well known and well documented (Longmore 1986; Storr, Smith & Johnstone 1986; Swan 1990; Coventry & Robertson 1991; Ingram & Raven 1991). Major guides to the reptiles of Australia have been published recently, so broad distribution maps are also available for each species (for example, Wilson & Knowles 1988; Cogger 1992; Ehmann 1992), with data on habitat preferences.

Elapids are found in every habitat in this country. Their patterns of distribution and diversity differ quite markedly from those of other groups of reptiles (for example, agamids and geckos; Cogger & Heatwole 1981), reflecting their origins at different times and under different conditions of climate, soil and vegetation. There are three areas of very high species diversity: south-western Western Australia, south-eastern South Australia, and the region including eastern Queensland and extreme north-eastern New South Wales (Cogger & Heatwole 1981; Longmore 1986, Appendix 2). The last mentioned supports a greater diversity of elapid snakes than any other Australian area of comparable size. Longmore (1986) demonstrated a strong correlation between areas of predicted high diversity (based on habitat variability) and areas of actual high species diversity. Centres of high species abundance, while related to habitat diversity, are not necessarily areas of either origin or dispersal of species (Bishop 1981; Greer 1989).

In south-eastern Queensland, between Gladstone to the New South Wales border and west to about the Dalby area, there are 30 species. Eighteen species of elapid occur within the city limits of Brisbane and Ipswich, where the great bulk of Queensland's people also occur. South-eastern Queensland has a subtropical climate, so plants and animals which are adapted to both hotter and colder zones thrive in the area. A complex geological history has created a wide variety of soils and land forms in which has evolved a richly diverse mosaic of vegetation. Heaths, woodlands, grasslands and rainforests support habitat-specific elapids as well as species that range between all or several of these. In this region, *Hoplocephalus stephensii*, *Notechis scutatus* and *Tropidechis carinatus* range from sea level heaths to high level heaths and rainforests. *Pseudechis guttatus* and *Simoselaps australis* occur only in open woodlands and grasslands developed on black soils, while *Pseudonaja textilis* can be found anywhere, excluding dense rainforests, and has apparently adapted very well to lands modified by grazing or farming and to suburban development.

Outside the three areas of highest diversity, Cogger & Heatwole (1981) showed that diverse elapid populations (of at least 10 species, which vary with locality) occur over most of Australia. Exceptional areas, with low species diversity by Australian standards, are the north-western part of Western Australia, a small area in south-western Western Australia, and South Australia, and Tasmania. The areas of lowest species diversity are the temperate heaths of Tasmania and highland Victoria, where only two to four species occur. Broadly speaking, if diversity can be equated with evolutionary 'success' of a family, the elapids have been most successful in low and middle latitudes and near coasts where rainfall variability and other factors account for habitat variety. They are least 'successful' in more uniform arid and temperate areas.

Narrow ranges of occurrence and endemism related to particular, small habitat types or zones do not generally characterise Australian elapid distributions. There are several exceptions to this general rule: *Demansia simplex*, from sandstones of the Kimberleys area of Western Australia, *Denisonia maculata* and *Furina dunmalli*, from the brigalow forests of central, and southern Queensland, respectively, and *Elapognathus minor*, from heaths near swamps and wet sclerophyll forests in south-west Western Australia. *Hoplocephalus bungaroides* occurs in sandstone outcrops in the Sydney area, and *Simoselaps calonotus* inhabits coastal sands near Perth. Three species, *Echiopsis atriceps*, *Simoselaps minimus* and *Suta ordensis*, have been described recently, and are known from only very small numbers of specimens. All appear to have narrow ranges.

Taxa such as *Acanthophis* species, *Demansia psammophis*, *Furina* species, *Pseudechis australis*, *Pseudonaja modesta*, the composite species *Pseudonaja nuchalis*, *Pseudonaja textilis*, several *Simoselaps* species, *Suta suta* and *Vermicella annulata* are very widely distributed, although sometimes in pockets within a broad range.

Many species of elapid which occur in Australia are also found in New Guinea. The links between Australia and New Guinea, even recently in Holocene and Pleistocene times, are well documented (for example, Galloway & Kemp 1981). That Australian elapids were able to migrate north or south, when low precipitation and freezing of the polar ice caps resulted in reduced sea levels to join the two land masses, is reflected in the distribution of the elapids, and in many other groups. Periods of low precipitation also coincide, predictably, with the periods of minimum extent, or extinction in some places, of rainforests. This accounts for the absence of rainforest elapid species shared between New Guinea and Australia and for the high number of open forest species common to both, a pattern consistent with those of other groups.

Acanthophis species, *Demansia* species, *Furina tristis*, *Oxyuranus scutellatus*, *Pseudechis australis*, *Rhinoplocephalus boschmai* and *R. nigrostriatus* occur in both New Guinea and Australia. Amongst the rainforest species in both areas there is no overlap. No Australian elapids occur solely in rainforest, although several are largely dependent upon rainforest in north-eastern Queensland (for example, *Cacophis* species = *C. churchilli* of Wells & Wellington 1985, *Hemiaspis signata*, *Pseudechis porphyriacus*, *Rhinoplocephalus nigrescens* and *Tropidechis carinatus*). Many rainforest-dependent elapids occur in New Guinea but have not colonised Australia (Covacevich 1986).

Affinities with other Groups

Mengden (1983) noted that the one feature of elapid classification evident from its history is the inability of taxonomists to arrive at any unanimity. He attributed this to the problems of defining primitive and derived character states. As a result, the relationships of proteroglyphs and their possible colubrid ancestors are poorly understood.

Aparallactine, xenodontine and natricine colubrids have been suggested as ancestors for the elapids (*sensu lato*). Morphological and serological comparisons were the bases of these suggestions, but more recent molecular work is at variance with them (Mengden 1985a). Affinities between colubrids and elapids seem remote. However, despite the fact that origins of the elapids remain to be elucidated, family level relationships of the Australian elapids are now well understood and a matter of some, even considerable, unanimity among taxonomists.

The close affinity between Australia's terrestrial and marine proteroglyphs is supported by both biochemical and morphological data and it has been suggested by Smith, Smith & Sawin (1977), that they should be grouped in one family (Hydrophiidae) with two subfamilies — the terrestrial Oxyuraninae and the marine Hydrophiinae. Mengden (1983) adopted this approach, while posing key questions still to be resolved — how close phylogenetically are the elapids endemic to Asia, Africa, America and Australia; are the Australian elapids monophyletic; how close is the relationship of *Laticauda* to other marine species of proteroglyphs?

The work of Cogger (1985), Baverstock & Schwaner (1985), McDowell (1985), Mengden (1985a, 1985b), Molnar (1985), Schwaner *et al.* (1985), Storr (1985), Tamiya (1985) and Wallach (1985) has provided considerable data of use in answering these questions.

The Australian elapids are most closely related to hydrophiine sea snakes. Together, they form a monophyletic group, the Hydrophiidae, although relationships within this group remain unclear, particularly with respect to the affinities of the hydrophiine sea snakes, which may have evolved within the viviparous terrestrial lineage. The Hydrophiidae are also related, more distantly, to Asian and African elapids (family Elapidae, subfamily Bungarinae) and to American elapids (family Elapidae, subfamily Elapinae). The sea kraits (*Laticauda*) are also fairly closely related, firstly to Australian hydrophiines, secondly to Australian elapids (oxyuranines), and more distantly to Asiatic and African elapids. Their association with American elapids is presumed to be more remote.

Affinities within the Australian Elapid Radiation:

Intergeneric affinities. Until the early- and mid-1980s, the definitions of elapid genera were '... based on a high level of subjectivity resulting from the intuitive character weighting of morphological and other characters ...' (Cogger 1985). That, probably combined with a general lack of new species to be described, led many workers down a nomenclatural garden-path of new generic allocations, reallocations and re-reallocations.

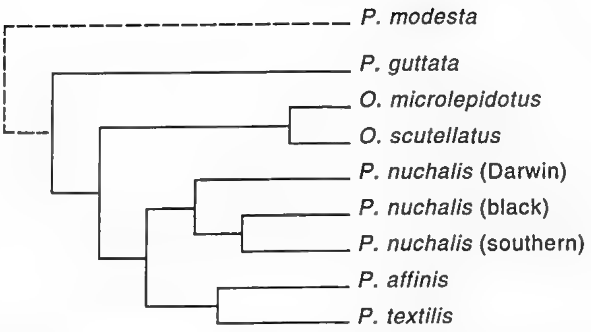

Figure 35.13 Relationships within *Pseudonaja*, based on electrophoretic studies by Mengden (1985b). The position of *Pseudonaja modesta*, not studied by Mengden, is based on Wallach (1985). *Pseudonaja inframacula* and *P. ingrami* were not available for these studies, and their relationships are unknown. Note the position of *Oxyuranus* within *Pseudonaja*. [D. Wahl]

This situation changed quite dramatically, with the work of McDowell (1967, 1969b, 1970, 1985), Mengden (1983, 1985a, 1985b), Baverstock & Schwaner (1985), Schwaner *et al.* (1985), Shine (1985c), Storr (1985) and Wallach (1985), culminating in Hutchinson's (1990b) widely accepted generic classification. In Hutchinson's synthesis, the many easily defined genera are identified, as are those for which there is still room for debate and refinement. In the former group are *Acanthophis*, *Demansia*, *Drysdalia*, *Echiopsis*, *Elapognathus*, *Hemiaspis*, *Hoplocephalus*, *Pseudechis*, *Pseudonaja*, *Oxyuranus*, *Rhinoplocephalus*, *Simoselaps*, *Suta* and *Vermicella*. Genera in the second group include *Austrelaps*, *Cacophis*, *Denisonia*, *Drysdalia*, *Furina*, *Notechis*, and *Tropidechis*.

Relationships between the genera have been hypothesised by Mengden (1985a), Schwaner *et al.* (1985), and Wallach (1985), on the basis of chromosomal and electrophorectic, immunological and anatomical comparisons, respectively. There is general accord between these, and between them and the Hutchinson synthesis, and other studies. For example, *Demansia* is a very distinct genus with its nearest relatives the well-defined genera *Pseudechis*, *Pseudonaja* and *Oxyuranus*. *Hemiaspis*, *Acanthophis*, *Hoplocephalus* are also distinct groups. *Notechis*, *Austrelaps* and *Tropidechis* have strong affinity.

Intrageneric affinities. Phylogenetic relationships within genera are not nearly so well understood as those between genera. The first examination of intrageneric relationships using many taxonomic tools was of the two monotypic genera *Oxyuranus* and *Parademansia* by Covacevich *et al.* (1981). On the basis of data on external and internal morphology, venom comparisons, karyotypes, and behaviour, they transferred *Parademansia* to the synonymy of *Oxyuranus*, in which two species *O. scutellatus* and *O. microlepidotus* (Pl. 8.10) were then recognised. This work was widely, but not totally accepted (for example, Cogger *et al.* 1983a). However, subsequent work (for example, Mengden 1985b) has strongly confirmed the transfer.

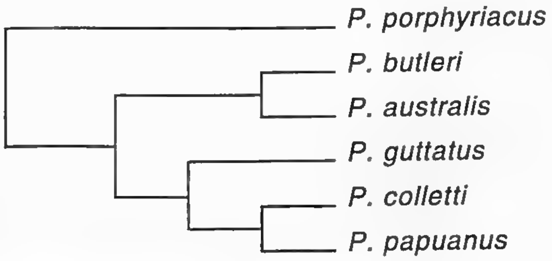

Figure 35.14 Relationships within *Pseudechis*, based on Mengden *et al.* (1986). [D. Wahl]

Phylogenies for two other genera, *Pseudonaja* (Mengden 1985b) and *Pseudechis* (Mengden *et al.* 1986), have also been proposed.

Pseudonaja comprises at least nine species, and possibly more (Fig. 35.13). Taxa which clearly warrant full species status are: *P. affinis*, *P. guttata*, *P. inframacula*, *P. ingrami*, *P. modesta*, *P. nuchalis* 'south', *P. nuchalis* 'black', *P. nuchalis* 'Darwin' and *P. textilis*. Mengden (1985b) showed unequivocally that the 'Darwin' *P. nuchalis*, and *P. nuchalis* 'black' and 'south' are as distinct from each other as established species like *P. affinis* and *P. textilis*, although the three species of *P. 'nuchalis'* form a monophyletic group.

Mengden's phylogenetic hypothesis for the genus, based only on electrophoretic data (Fig. 35.13) is in accord with the general picture of the group as determined from reviews of morphology and venoms. Exceptions, however, are the placement of *Oxyuranus* within the genus *Pseudonaja*, and the *P. nuchalis* complex, in which colouration morphs span the species definitions. The latter feature has not been observed in any other elapid group in Australia (Phillips pers. comm.).

Pseudechis is another genus in which phylogenetic relationships have been hypothesised (Mengden *et al.* 1986). Six species are assigned to the genus — *P. australis*, *P. butleri*, *P. colletti*, *P. guttatus*, *P. papuanus* and *P. porphyriacus*. Most species are endemic to Australia. *Pseudechis australis*, and the endemic *P. papuanus* are found in southern New Guinea (Whitaker, Whitaker & Mills 1982). Chromosomes, scale counts, general morphology, and blood protein electrophoretic patterns reveal that the viviparous *P. porphyriacus* is most divergent from the five oviparous species, which may be divided into two groups: *P. australis* and *P. butleri*, and *P. colletti*, *P. guttatus* and *P. papuanus* (Fig. 35.14).

Apart from a thesis, as yet unpublished, which explores relationships within the *Simoselaps*/*Vermicella* burrowing lineage (Scanlon 1985), relationships within the other genera have received only cursory attention, invariably based on phenetic and sometimes superficial ecological comparisons.

Fossil Record

Molnar (1984) listed the fossil elapids from Australia and has written extensively about their history and that of other Australian lepidosaurs (Molnar 1982b, 1985, 1991). The tangible record of the history of elapids in Australia is scant. All fossil elapid remains are of Pleistocene age and are unidentified, unidentifiable, or belong to the genera *Notechis*, *Pseudechis* or *Pseudonaja*. These remains shed no light on the origins of the elapids or on any aspect of the radiation of the group. In the absence of hard (fossil) data, there have been many proposals regarding the antiquity of the elapids here. Storr (1964a) thought that they could be a relict group, and one of the oldest elements in the Australian herpetofauna. Hypotheses invoking early origins were still the order of the day nearly twenty years later. Minton (1981) suggested that Australian elapids evolved in Australia or were early arrivals from another area of Gondwana, before the colubrids. Recent immunological studies (Schwaner pers. comm.; Schwaner *et al.* 1985) have suggested a more recent Pliocene or Pleistocene radiation following an initial separation of the Australian elapids from those of other continents approximately 20 million years ago (mid-Miocene).

36. FAMILY HYDROPHIIDAE

Harold Heatwole & Harold G. Cogger

DEFINITION AND GENERAL DESCRIPTION

The family Hydrophiidae, or true sea snakes, includes the majority of marine serpents and is the most completely marine of all extant reptilian taxa. Reptiles of other marine groups either lay their eggs on land (marine turtles, laticaudid snakes) or have freshwater or terrestrial species in addition to marine ones (acrochordids, colubrids, crocodilians). The Hydrophiidae never come out on land voluntarily and all live in salty water except two lake-locked species that have a marine origin.

The family is characterised by several features that reflect their adaptation to a marine environment. These include valvular nostrils, a lingual fossa and a vertically compressed, paddle-shaped tail; all species are viviparous (Cogger 1992). There are two subfamilies in Australian waters, the Ephalophiinae which comprises five genera and 11 species and the Hydrophiinae containing seven genera and 20 species.

Books dealing with the general biology of sea snakes include Dunson (1975a) and Heatwole (1987) and there are a number of review papers (Pickwell 1972; Heatwole 1977a, 1977c, 1978a; Cogger & Heatwole 1978; Minton & Heatwole 1978; Limpus 1987). Cantor (1841) and Bergman (1949, 1962) described the anatomy and/or presented meristic data. Hibbard (1975) reviewed their sensory perception. Vigle & Heatwole (1978) and Culotta & Pickwell (1993) compiled bibliographies on the Hydrophiidae. The Australian species have been reviewed (Cogger 1992) and catalogued (Cogger, Cameron & Cogger 1983), and faunas of Australian regions treated (Shuntov 1971; Dunson 1975b; Heatwole 1975c, 1977d; Limpus 1975b; Minton & Heatwole 1975; Redfield, Holmes & Holmes 1978).

HISTORY OF DISCOVERY

Sea snakes, along with marine turtles, were among the first Australian reptiles to be recorded by early European navigators and explorers. The abundance of sea snakes in our northern waters, especially the North-West Shelf, the Arafura Sea and the Gulf of Carpentaria, was noted as early as 1699 (Dampier 1703–1709).

The first of the species occurring in Australian waters to be described formally was the pelagic, yellow-bellied sea snake, *Pelamis platurus*, by Linnaeus in 1766, under the name *Anguis platura*. Not until 1804 was the first sea snake described based on an Australian specimen, the olive sea snake, *Aipysurus laevis* Lacépède, 1804. Only in 1869 was the first species, *Emydocephalus annulatus* Krefft, described by an Australian-based researcher.

Figure 36.1 *Aipysurus laevis* hiding in a crevice. Note the dorsally placed valvular nostrils, flattened tail and new skin. [Photo by C. Pollitt]

Throughout the 19th century species of sea snakes were occasionally described and named, although because of the great individual and geographic variation in these snakes, combined with small museum samples, many species were soon synonymised. Many species, though occurring in Australia, were described from Asian populations. Not until late in the present century was it found that many of these widespread species consisted of two or more species with strong regional endemism.

The first major study of local and regional sea snake distribution patterns was made by Soviet fisheries research vessels in the late 1960s (Shuntov 1971). In surveys ranging from the Gulf of Carpentaria to the Arafura and Timor Seas, Shuntov recorded 18 species of sea snakes. He found major regional differences in the taxonomic composition of sea snake catches, and significant seasonal differences in sea snake abundance. However, his results have not been corroborated by subsequent studies. Heatwole (1975d) reviewed the sea snakes of the Gulf of Carpentaria and between April and December 1976 surveys of sea snakes in eastern waters of the Gulf of Carpentaria were undertaken by CSIRO scientists as adjuncts to surveys of potential commercial penaeid prawn fisheries in the region (Redfield *et al.* 1978). These surveys found significant overall increases in sampling abundance in October, but there were different seasonal patterns of relative abundance between the different species sampled. Redfield *et al.* (1978) were unable to reconcile the significant differences between their results and those of Shuntov (1971) and Heatwole (1975d).

MORPHOLOGY & PHYSIOLOGY

External Characteristics

Sea snakes vary greatly in size and body form. The smallest Australian species (for example, *Ephalophis greyi*, *Hydrelaps darwinensis* and *Parahydrophis mertoni*) grow to only 0.5 m in total length, whereas the largest species (for example, *Astrotia stokesii*, *Aipysurus laevis*, *Hydrophis elegans*) may reach more than 2 m in length. Body form is highly variable. Generalist fish eaters are similar in form (apart from the flattened tail and some lateral compresson) to terrestrial snakes, whilst species that feed on burrowing eels (Ophichthidae, Congridae and Moringuidae) have small to minute heads and forebodies, followed by large, deep hindbodies up to 10 times the diameter of the head and neck.

Externally sea snakes have a suite of common features associated with a fully aquatic marine existence. These include the presence of fleshy, valvular nostrils and a fleshy lingual fossa, which together effectively seal the respiratory passages and prevent the entry of water into the lung when the snakes are submerged. The flaps of these valves are activated by spongy, erectile tissue. In most species the nostrils are situated on the upper surface of the snout (Fig. 36.1) to allow the snake to breath at the surface without exposing the rest of its body to aerial predators such as raptors.

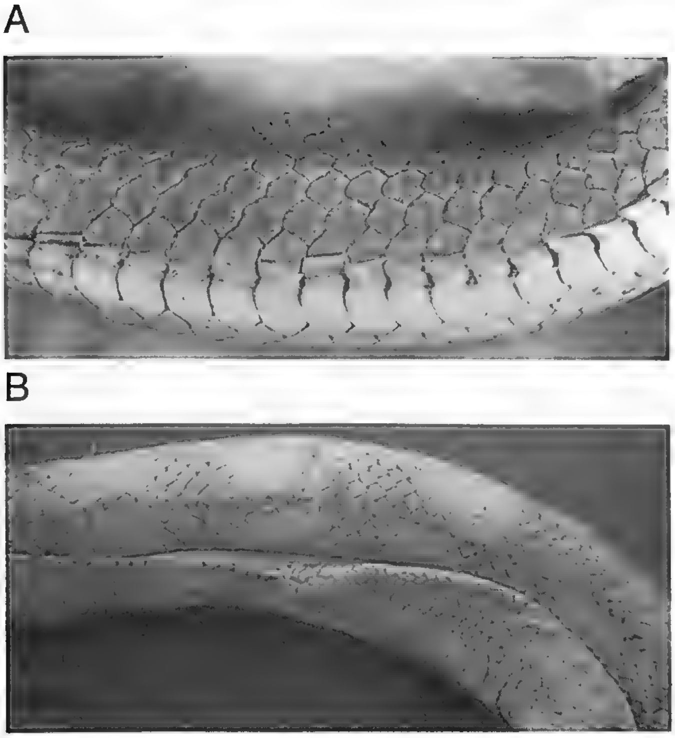

Figure 36.2 Ventral surface of two sea snakes showing different degrees of reduction of the gastrosteges. A, partly reduced gastrosteges of *Aipysurus laevis*, keeled centrally to enhance stability in the water; B, gastrosteges of *Hydrophis elegans*, reduced to the same size as the rest of the scales.
[Photos by H. Heatwole]

The scales are generally very small, arranged in 15 to 69 rows around the mid-body. The broad belly scales (gastrosteges) which characterise most terrestrial snakes and which are a primary mechanism in locomotion on land, are generally absent in sea snakes (Fig. 36.2). However, in some groups of sea snakes, notably members of the subfamily Ephalophiinae, the belly scales are much wider and appear to be used in terrestrial-style locomotion over mangrove and reef flats. This group also has much larger body scales than most other sea snakes.

The scales of sea snakes vary not only in size, but also in shape and relief. Many have scales which are keeled (Fig. 36.2A), tubercular or both, giving a very rough feel when handled. In many species, especially those of *Disteira*, *Lapemis* and *Hydrophis*, the rougher scales are restricted to the lower flanks and belly and are often much more developed in males. This suggests that scale tuberculosity is a secondary sexual character facilitating the male's hold on the female before or during copulation.

Locomotion

Sea snakes propel themselves through the water by the laterally compressed paddle tail which produces an undulatory movement of the body. This movement directs a rearwards force against the liquid medium, in contrast to terrestrial snakes which propel themselves by using small irregularities in the substrata for purchase by their broad, backwardly directed ventral scales. Morphological adaptations reflect these different modes of locomotion. For example, the vertebral column of many sea snakes is weak and does not provide sufficient strength to cope well with terrestrial conditions. Hydrophiids do not take purchase on the substrate and accordingly their gastrosteges are either somewhat narrowed or the same size and shape as other body scales (Fig. 36.2B). On the other hand, their propulsive surface has been increased by development of a broad paddle-shaped tail (Fig. 36.1; Pls 7.8-11) and in some species by a lateral flattening of the body until it is nearly ribbon-shaped (for example, *Astrotia stokesii*).

Feeding and Digestive System

Most hydrophiids are venomous. Venom is produced by a pair of modified salivary glands, which lie on either side of the face along the posterior part of the upper jaw (Fig. 36.3), and is stored in a central lumen of the gland. The larger posterior portion tapers anteriorly into an elongate region towards the fang, into which the gland empties (Limpus 1978a). Unlike viperid snakes, in which these regions are morphologically and functionally distinct (see Chapter 24; Fig. 35.11), the glands of sea snakes are indistinct and the protein-secreting and mucus-secreting functions not clearly separated. The proportion of the gland devoted to mucus production is lower in sea snakes than in most terrestrial elapids (Gopalakrishnakone & Kochva 1990) and is probably related to a lesser need for lubrication of food when swallowing underwater.

The fangs of hydrophiids are located in the front of the mouth (Fig. 36.3). Usually there is only one on each side of the head although sometimes a second, replacement fang may be present. They are sharply pointed, slightly recurved and have a central canal through which venom is extruded when the *m. adductor externus superficialis* applies pressure on the venom gland. In most sea snakes the fang is hypodermic-like, with a completely enclosed central canal exiting from a small orifice at the tip. *Astrotia stokesii* is an exception in that the venom canal opens through a groove in the fang throughout much of its length (Limpus 1978a).

Venom and the venom apparatus seem to have evolved in a feeding rather than a defensive context (Heatwole 1987). There are several lines of evidence for this. The few species (for example, *Emydocephalus annulatus* and *Aipysurus eydouxii*) that have secondarily adopted a diet of inactive food (such as fish eggs) and no longer need to subdue prey have nearly lost their venomous qualities and apparatus (Limpus 1978b; Minton 1983), though presumably they have as much need of defence as other hydrophiids. Also, some highly venomous species are reluctant to bite in defence; others do bite defensively but often fail to inject venom ('blank' bites).

Hydrophiid venoms are a mixture of a number of toxic proteins and polypeptides, spreading agents and lubricants. Venoms from several species have been fractionated and individual toxins purified and their chemical properties characterised (Tu & Toom 1971; Tu, Tzu & Beiber 1975), including amino acid sequences (Wang, Liu, Hung & Blackwell 1976; Maeda & Tamiya 1976, 1978; Fox, Elzinga & Tu 1977; Tamiya 1985). Common ingredients are short-chain toxins (60 to 62 amino acid residues) and long-chain toxins (66 to 74 amino acid residues) and

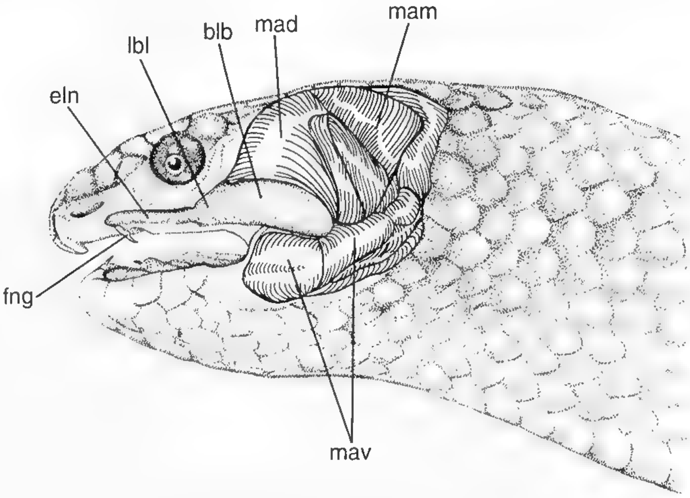

Figure 36.3 Head of *Aipysurus laevis*, dissected to show the venom apparatus. Venom gland terminology follows that of Limpus (1978a). **blb**, bulbous region of venom gland; **eln**, elongate region of venom gland; **fng**, fang; **lbl**, lower bulbous region of venom gland; **mad**, dorsal part of *m. adductor mandibulae externus*; **mam**, *m. adductor mandibulae externus medialis*; **mav**, ventral part of *m. adductor mandibulae externus*. (After Zimmerman 1991) [T. Wright]

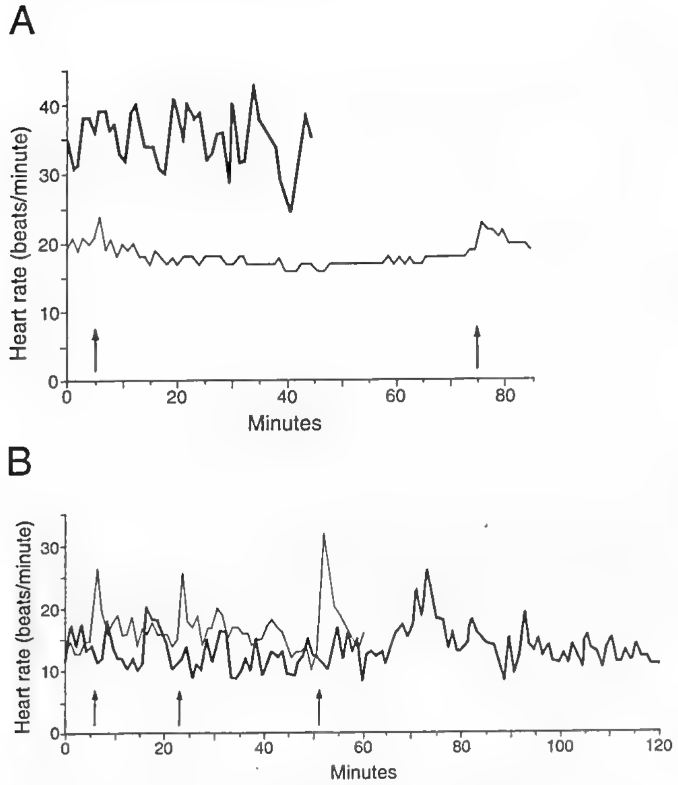

Figure 36.4 Comparison of the heart rates of an inactive snake (thin line) and one during nearly continuous activity (thick line). Arrows indicate breaths of the inactive snake. A, the hydrophiid, *Aipysurus laevis*; B, the laticaudid, *Laticauda colubrina*. (After Heatwole 1977b) [W. Mumford]

phospholipases (Tamiya 1985). The exact composition of venom varies interspecifically although some toxins are common to several species.

Sea snake venoms may function as neurotoxins (Fraser 1904; Carey & Wright 1961; Barber, Puffer, Tamiya & Shynkar 1974; Tu *et al.* 1975; Fohlman & Eaker 1977; Tamiya, Maeda & Cogger 1983), as myotoxins and as nephrotoxins. Unlike some terrestrial snakes, they have very little haemotoxic activity (Minton & Minton 1969). The most important and swiftest mode of action is neurotoxic (Sutherland 1983). The venom of *Aipysurus laevis*, a generalist predator (see below), has differing effects on prey species. Eels are especially resistant whereas experimentally envenomated fish show changes in ventilatory rate (Zimmerman & Heatwole 1992), impairment of the ventilatory system with incomplete mouth closure and eventual cessation of opercular movements (Zimmerman, Gates & Heatwole 1990). Death is probably by asphyxiation. Part of the interspecific differences in prey resistance may reflect mode of respiration. At high venom doses, fish known to employ cutaneous respiration (for example, blennies), and hence be less severely influenced by loss of ventilatory capability, survived longer than fish such as pomacentrids which rely more heavily on gill respiration (Zimmerman, Heatwole & Davies 1992). The locomotory system was also affected. There was progressive loss of coordination of the fins and the fish developed an inability to maintain position and buoyancy; they leaned to one side and tended to sink (Zimmerman *et al.* 1990). The action of the venom not only subdues prey, but aids in its recovery should the snake lose it.

Respiration, Circulatory System and Diving

Sea snakes can dive to depths as great as 100 metres (Heatwole 1978a) and regularly remain submerged for periods of half an hour to two hours (Heatwole 1978a; Graham, Gee, Motta & Rubinoff 1987b), and perhaps longer.

The metabolic rate of sea snakes is not greatly different from that of terrestrial snakes of equivalent body size (Table 37.1) (Heatwole 1978a) and lowered metabolism does not seem to be a major adaptation to diving. However, the temperature of sea snakes is nearly identical to ambient sea temperature (Graham 1974b; Heatwole 1981b) and cooler water at depth could retard metabolic rate and lengthen submergence time.

The blood of sea snakes has been compared with that of terrestrial snakes and other aquatic snakes. Differences in blood quality seem more related to activity and sluggishness than to diving capacity (Seymour 1976). Sea snakes have much lower blood volumes than the aquatic file snake, *Acrochordus granulatus* (Feder 1980), but blood volumes are not markedly different from terrestrial snakes; some species have a slightly higher blood volume than terrestrial snakes (Table 37.1; Pough & Lillywhite 1984; Heatwole & Dunson 1987). In general the similarities of haematology and metabolism of sea snakes and terrestrial snakes are more conspicuous than are the slight differences.

The lung of sea snakes, like that of terrestrial snakes, is a single tube that is longitudinally regionalised. The anterior end, known as the tracheal lung, is morphologically a modified trachea although functionally it acts as a lung, is highly vascularised and is involved in gaseous exchange (Heatwole & Seymour 1975b). The middle part of the lung, the bronchial lung, is the main avenue for gaseous exchange. It leads into a poorly vascularised section, the saccular lung, and serves mainly as an air storage compartment. In terrestrial snakes this part is thin and membranous, but in sea snakes it is muscular. Contraction of these muscles moves gas forward to the respiratory surfaces and mixes stored air with that of the anterior sections of the lung (Heatwole & Seymour 1975b).

Two evolutionary pathways are available to air-breathing diving vertebrates. Birds and mammals have the classic diving syndrome. This involves peripheral vasoconstriction of the blood (and hence oxygen) supply to the muscles and some internal organs, anaerobic metabolism of the blood-starved tissue with a resultant build-up of lactic acid, and diving bradycardia (lowered heart rate) with a reduced blood circuit, primarily to the heart, lungs and brain (see Elsner 1969). Diving bradycardia is independent of activity; strenuously active animals still have a lowered heart rate while submerged. By contrast, sea snakes have a higher heart rate while breathing (breathing tachycardia) than when not breathing, either submerged or at the surface (Fig. 36.4; Heatwole 1977e; Heatwole, Seymour & Webster 1979). The normal (resting) heart rate of sea snakes occurs when submerged; it is increased with activity in *Aipysurus laevis* (Fig. 36.4A), but changes little with activity in the laticaudid, *L. colubrina* (Fig. 36.4B) (Heatwole 1977b). Breathing tachycardia facilitates more effective transfer of oxygen to the blood during breathing.

Sea snakes usually surface for only a few seconds to take one or a few breaths (Heatwole 1978a); consequently they lack the time and ventilation that would be required to pay back an oxygen debt. Also, their blood has been shown to remain aerobic during voluntary diving (Seymour & Webster 1975). Sea snakes have solved the oxygen debt problem by using cutaneous respiration. Some species can absorb up to one-third of their oxygen requirements through the skin and lose up to 94% of their carbon dioxide production (Graham 1974a; Heatwole & Seymour 1975a). Elimination of carbon dioxide while underwater prevents it from building up enough to cause an acid imbalance in the blood. The capacity for cutaneous respiration is related to the degree of aquatic adaptation and to habitat. Hydrophiids generally respire more effectively through the skin than do other aquatic snakes, terrestrial snakes and most turtles (Table 37.1; Standaert & Johansen 1974; Heatwole & Seymour 1978; Seymour 1982).

Hydrostatic pressures in deep water can have a profound effect on air-breathing organisms. At depth, the lungs are hydrostatically compressed, and nitrogen is absorbed into the blood. During ascent, pressure decreases and dissolved nitrogen tends to come out as bubbles. These can cause serious discomfort, disability and

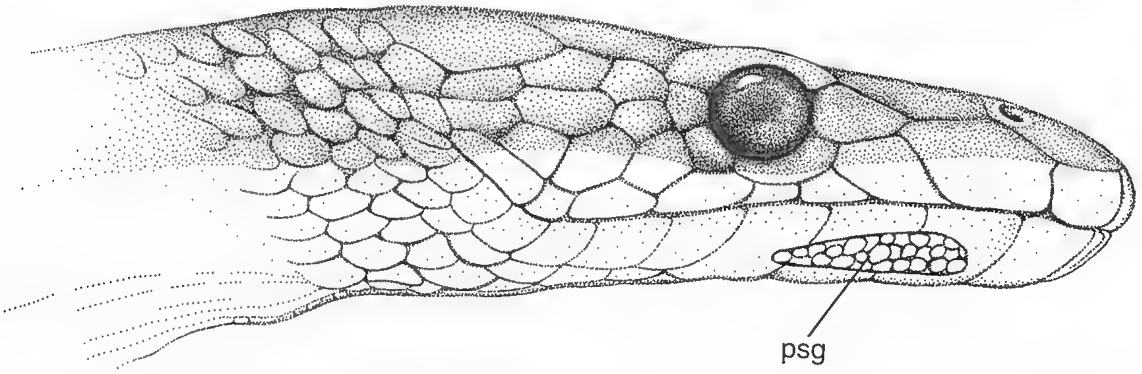

Figure 36.5 Head of *Pelamis platurus*, showing the posterior sublingual gland, or salt gland, in the lower jaw. It is located beneath the tongue sheath and empties into it. psg, posterior sublingual gland. (After Dunson 1979) [T. Wright]

even death in humans, a disorder known as Caisson's disease or the 'bends'. Sea snakes do not suffer the bends either because they normally stay on the surface for only a short time and dive to depth again before the symptoms appear or, more likely, because lung nitrogen dissolved under pressure dissipates through the skin into the sea and blood concentrations do not build up (Graham 1974a).

Cardiac shunts may also serve to reduce the danger of the bends. As explained in Chapter 24, the functional separation of oxygenated and deoxygenated blood in squamate hearts allows the systemic return to the heart to be shunted to the systemic output (right-to-left-shunt) and bypass the lungs during diving. This would result in slower uptake of gas and thus a reduced threat of the bends. The shunt in this direction would also enhance cutaneous respiration at the expense of pulmonary respiration. By employing such shunts a sea snake can regulate the relative contribution of lungs and skin to respiration according to immediate circumstances, as well as the rate of nitrogen absorption into the blood and thereby avoid the bends. (Seymour 1974, 1982; Seymour, Spragg & Hartmen 1981). *Hydrophis coggeri* (cited as *H. belcheri*) has extensive shunts with 76% of its blood flow bypassing the pulmonary circuit, almost three times the value for a laticaudid (Seymour 1978).

Terrestrial, and especially arboreal, snakes tend to have the heart situated close to the anterior end, thereby shortening the length of the blood column to the head and permitting maintenance of blood pressure in the brain when the head is lifted vertically. Because of the equalising effect of external hydrostatic pressure, snakes in water are less subject to gravitational gradients than those in air and require less control of axial blood pressures when in a vertical position. Accordingly, sea snakes have lower blood pressures and poorer regulation of blood pressure in compensation for postural changes than do terrestrial snakes and the heart is located closer to body midlength (Lillywhite 1976, 1987a, 1987c, 1988; Lillywhite & Pough 1983). When tilted in air their blood tends to pool in the posterior part of the body and they have problems in supplying blood to the brain.

The buoyancy requirements of sea snakes change with different activities. A snake ascending to breathe or maintaining position at the surface expends less energy if it is buoyant, whereas one foraging at the bottom exerts itself less if it is heavier than water. The lungs are the hydrostatic organs that assist in regulation of buoyancy (Graham, Gee & Robinson 1975; Graham *et al.* 1987b). At the surface, *Pelamis platurus* fills the lung sufficiently to float. Before diving it exhales some of the air but still maintains slightly positive buoyancy. Upon submergence buoyancy decreases through hydrostatic compression of the lung volume with depth and also metabolism of oxygen without equivalent replacement in the lung by carbon dioxide, which is dissipated to the sea via the skin as described above. Neutral or negative buoyancy is attained. These adjustments make for easier maintenance of position at depth and on the surface, although the snake still has to contend with a slight tendency to float during descent and to sink during ascent.

Excretion and Osmoregulation

Body fluids of sea snakes are hypotonic to sea water and thus there is a tendency to lose water and to gain salts. Mechanisms to counteract these tendencies are required to maintain a proper balance of salts and water in the body. Sea snakes, like other snakes (and birds), conserve water by being uricotelic, that is, the waste products of nitrogen metabolism are excreted as uric acid or urate salts. However, the kidneys of sea snakes do not play a major role in ionic regulation; the urine is hypo-osmotic to the blood plasma and less salt is excreted than through extra-cloacal routes (Dunson 1968, 1979). In hydrophiids most salt excretion is via the posterior sublingual gland, located in the lower jaw just beneath the tongue sheath (Dunson 1979) (Fig. 36.5). It actively transports cations as a brine into the tongue sheath. When the snake protrudes its tongue the brine is pushed out of the mouth into the sea. The sublingual gland has probably evolved independently into a salt-excreting gland in the Hydrophiidae, Laticaudidae and Acrochordidae (Dunson & Dunson 1973).

The effectiveness of this gland varies among species. Maximum concentration of the brine correlates positively with relative size of the gland. *Hydrophis semperi*, one of the two species of sea snakes now lake-locked, has retained a functional salt gland. On the other hand, some completely marine species have tiny salt glands with extremely low rates of secretion (Dunson & Dunson 1974). Other factors must be involved in their salt balance.

The skin of sea snakes is important in osmoregulation. The outer keratin layers act as a barrier against salts entering the body (Dunson & Robinson 1976). More salts move outward through the skin than inward (Dunson & Stokes 1983), thereby counteracting the tendency to accumulate salts from the environment. Water passes through the skin more easily than do salts, so that influx exceeds efflux and therefore assists the retention of water. The directionality of salt and water movement in sea snake skin is the reverse of that in freshwater snakes (Dunson 1978), which have opposite problems; they live in a dilute medium and need to get rid of water and gain salts from the environment.

Sense Organs and Nervous System

Hibbard (1975) reviewed the sense organs and optic tectum of sea snakes. In general, the retinal structure of hydrophiids suggest effective diurnal vision. However, there are interspecific differences. Species of *Aipysurus* probably have better vision than other taxa as they have more distinct stratification of the inner plexiform layer of the retina and better development of the optic tectum. *Astrotia stokesii* has a pure cone retina and small cone receptors. *Hydrophis elegans* probably has the poorest vision of the species studied.

Sea snakes are unique among reptiles in possessing cutaneous photoreception (Zimmerman & Heatwole 1990). Light-sensitivity in the tail of *Aipysurus laevis* is most highly developed on the upper side and toward the tip (Fig. 36.6). Detection of light by the tail warns the hiding snake to withdraw the tail along with the rest

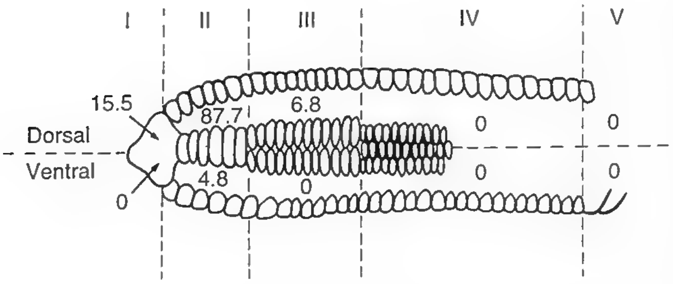

Figure 36.6 Sensory map of the tail of *Aipysurus laevis*. The numbers indicate the percentage of light stimulations to which the snake responded by moving its tail out of the beam. (After Zimmerman & Heatwole 1990)
[T. Wright]

of the body when hiding in crevices. Many sea snakes often hide in crevices among corals or other cover when not foraging for food or surfacing to breathe.

The olfactory epithelium of sea snakes is similar to that of other reptiles although some olfactory structures are reduced. The vomeronasal organ is well developed (Poran pers. comm.). Bowman's glands are present. The tongue is an important adjunct to olfaction through its use in transferring scented particles from the external medium to the sensory area of the vomeronasal organ. Taste buds may be present on the roof and floor of the mouth, but are absent from the tongue.

The inner ear of sea snakes has a well-developed sensory epithelium that senses both static and kinetic changes in equilibrium. However, the cochlear portions serving acoustic functions, especially the basilar papilla, are poorly developed in comparison to those of other reptiles. It is likely that sea snakes rely more heavily on vision and olfaction than on hearing.

Exocrine Glands

Sea snakes possess the same cephalic glands found in terrestrial snakes, including Harderian, sublingual, anterior sublingual, venom, labial and nasal glands (Burns & Pickwell 1972). The sublingual gland is a salt gland excreting concentrated brine and functioning in osmoregulation (see Excretion and Osmoregulation). The venom gland is discussed in Feeding and Digestion.

Pelamis platurus is known to have scent glands in the base of the tail. These actively secrete, although they are small in comparison to those of terrestrial snakes (Weldon, Sampson, Wong & Lloyd 1991). Their function is unknown. Little is known of the endocrine glands of sea snakes.

Reproduction and Development

All hydrophiids are live-bearers and, unlike the laticaudids, do not come out onto land to breed. Those that have been studied are truly viviparous in that after ovulation the developing eggs continues to receive nutrients from the mother via an allantoplacenta (Kasturirangan 1951).

Some sea snakes have strongly seasonal reproductive cycles, despite living in a relatively equable environment. The female gonadal cycle of *Aipysurus laevis* from the Great Barrier Reef is synchronous, with ovulation occurring in October and parturition in April, coinciding with the beginning and end of the monsoon season, respectively (Burns 1985). *Enhydrina schistosa* in Malaysia has a synchronous peak in gamete production by both sexes in September. Gestation extends over the warmer wet season from November to February–March (Voris & Jayne 1979). *Hydrophis brookii*, *Hydrophis melanosoma* and *Hydrophis torquatus* from the same locality and *Lapemis curtus* (= *Lapemis hardwickii*) from another Malaysian locality have similar reproductive cycles (Lemen & Voris 1981). Other species, however, have loosely seasonal or aseasonal reproduction. For example, the reproductive cycle of *Hydrophis caerulescens*, from the same locality as the *L. curtus* population mentioned above, was spread out over the year.

There may be regional differences in reproductive phenology. The conflicting reports of aseasonality and seasonality in *Pelamis* (see Kropach 1975) may arise from geographic differences in reproductive cycles. Lemen & Voris (1981) reported regional populations of several species being out of phase and Burns (1985) noted that in the Gulf of Carpentaria, gravid *A. laevis* are found in the cooler winter months as well as in summer and reproduction there must be less seasonal than on the Barrier Reef. Even in populations with synchronous reproduction not all mature individuals necessarily participate in each year's breeding activity. Only about half of the mature females of *A. laevis* breed in any one year. Burns (1985) suggested that it may take females two years to accumulate the energy required to produce young.

In general, sea snakes produce small numbers of young. The average clutch size ranges from three to nine for most species and larger females produce more young than smaller ones (Voris 1964; Voris & Jayne 1979; Lemen & Voris 1981). Considerable amounts of energy and materials are expended in reproduction. The young usually are large, with individual neonates in most species weighing 5 to 11% and entire clutches 28% to 38% of their mother's weight, an exceptionally large investment compared to that of terrestrial snakes (Table 36.1). *Enhydrina schistosa* is an exception, with clutch sizes averaging 18.3 and some numbering over 30. Reproductive effort per clutch is about the same as in other sea snakes (39%), but like terrestrial snakes,

Table 36.1 Reproductive characteristics of some sea snakes. Data from Lemen & Voris (1981).

Species	Mean clutch size	Mean reproductive effort (%)		Mean embryo weight (g)
		Per embryo	Per clutch	
Aipysurus eydouxii	4.4	6.6	28.9	10.8
Enhydrina schistosa	18.3	2.1	38.9	11.4
Hydrophis brooki	4.9	8.7	38.3	8.9
Hydrophis caerulescens	5.9	5.6	32.7	5.9
Hydrophis fasciatus	3.3	10.9	35.8	10.6
Hydrophis melanosoma	6.0	4.6	28.1	9.7
Hydrophis torquatus	5.5	6.3	34.9	6.2
Lapemis curtus	3.3	8.3	27.8	23.5
Thalassophina viperina	3.5	9.1	31.8	19.9

this species tends to produce many small young (neonates average 2.1% of their mother's weight), rather than few large ones.

Some of the effort expended in reproduction is wasted through infertility. Lemen & Voris (1981) reported that 5 to 20% of the oviducal eggs in nine species of hydrophiid were infertile, and that 6 to 60% of gravid females contained at least one infertile egg.

NATURAL HISTORY

Life History

Young snakes grow rapidly at first. Juvenile *Enhydrina schistosa* grow at an average rate of 0.5 g/day, without any seasonal decline (Voris & Jayne 1979; Voris 1985). They mature at about 18 months of age at which time growth rate declines. Females give birth for the first time at about 2 years of age. Only 10 to 20% of the newborn survive the first year and only about 6% of the females survive to reproduce. Only a tiny fraction of the population consists of animals four years of age or older (Voris & Jayne 1979).

Sea snakes often are locally abundant, yet few attempts have been made to measure population densities. The traditional mark/recapture method of estimating population size is difficult to use in a marine environment and has not always been successful. For example, Kropach (1975) marked 961 *Pelamis* but only four were recovered. Greater success was achieved for *Enhydrina schistosa* and an estimate of 900 to 1400 juveniles and about 1350 adults in an enclosed bay was obtained (Voris, Voris & Jeffries 1983; Voris 1985).

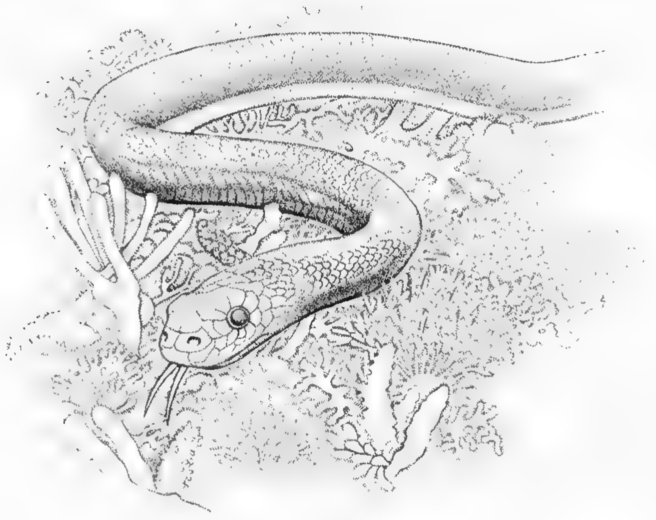

Figure 36.7 Diurnal foraging by *Aipysurus laevis* over a mixed coral bottom. (After photo by C. Pollitt) [T. Wright]

Ecology

The food of most sea snakes consists of fish and occasionally some marine invertebrates. Some are highly specialised and take only fish of one or a few types, or of a particular body form (Voris 1974). For example, *Enhydrina schistosa* feeds mostly on tachysurid and plotosid catfish and pufferfish (Voris, Voris & Liat 1978), *Microcephalophis gracilis*, and *Hydrophis melanosoma* eat eels almost exclusively and *Ephalophis greyi* and *Astrotia stokesii* seem to specialise on fish with a goby-like shape (Voris & Voris 1983). In general, most species of sea snakes feed primarily on sedentary fishes that either dwell on the bottom or inhabit burrows or crevices; eels and goby-like fish are especially prevalent in sea snake diets. Some species, however, are generalised feeders and take a variety of fish from many different families, including free-swiming ones (Voris & Voris 1983; Rasmussen 1989). Fishes from 19 families have been identified in the stomach of the pelagic *Pelamis platurus* (Kropach 1975). *Aipysurus laevis* is another generalist feeder. The works of McCosker (1975), Limpus (1975b), Voris & Voris (1983) and Burns (1984) collectively indicate that this species feeds on fishes of at least 17 families and six different body-shape types as well as fish eggs, prawns, squids, molluscs and moulting crabs. The fishes included bottom-dwelling as well as free swimming species and both diurnally and nocturnally active forms. *Aipysurus laevis* forages in crevices at night and during the day (Fig. 36.7; Heatwole, Minton, Taylor & Taylor 1978). The state of digestion of prey suggested that free swimming, nocturnal species are taken from crevices during daytime inactive periods, and that diurnal forms are taken from nocturnal retreats (McCosker 1975).

The habitat preferences of most sea snakes are largely unknown. Generally, individual species or species groups tend to have preferred habitats based on such factors as water depth, nature of bottom (coral, sand, mud), turbidity and season (Fig. 36.8). Many of these preferences simply reflect the occurrence of prey species. For example, many of the small-headed species of *Hydrophis* feed exclusively on garden eels which are restricted to sandy or some consolidated muddy substrates. The major habitats may be categorised as follows (the examples given are not exclusive to those habitats):

Coral reef habitats are selected by species which feed on crevice-dwelling fishes or fish eggs. Typically, such species browse the coral crevices looking for prey. Included in this group are *Emydocephalus annulatus* and most species of *Aipysurus*.

Coastal mangrove habitats are utilised by several smaller ephalophine species which feed on mudskippers and small crustaceans. This group includes *Hydrelaps darwiniensis*, *Ephalophis greyi* and *Parahydrophis mertoni*.

Turbid waters of estuaries and river mouths are the preferred habitat of *Enhydrina schistosa*, which may also travel long distances upstream into freshwater reaches of larger rivers.

Shallow inshore waters of moderate turbidity over mixed sandy/muddy substrata are the preferred habitat of many species, both ephalophiine and hydrophiine. It is typified by the productive shallow seas of the Gulf of Carpentaria. Species found commonly in this habitat complex are *Lapemis hardwickii*, *Hydrophis elegans*, *Hydrophis mcdowelli* and *Hydrophis ornatus*.

Deep (to 100 m), clear waters off coral reefs are preferred by many of the small-headed species such as *Hydrophis coggeri* and *Disteira kingii*, especially those which feed exclusively on burrowing eels.

Sea snakes often occur in mixed populations, sometimes in conjunction with other marine snakes such as laticaudids, homalopsines and acrochordids. Species richness varies widely and ranges from one to more than ten (Dunson 1975a; Dunson & Minton 1978). Ashmore Reef off northwestern Australia has ten resident species (plus a presumed stray), spatially separated into three zones: corals in shallow water, muddy or sandy substrata in deep water, and open surface water (pelagic) (Fig. 36.8; Minton & Heatwole 1975; McCosker 1975). There is further ecological segregation by diet; no overlap occurs in the prey taken at the species level (McCosker 1975). Smaller assemblages of three to five species in the southern Coral Sea show similar habitat separation (Heatwole 1975c). Two species widely occupying the same habitat had different food habits, *Aipysurus laevis* eating mainly fish and *Emydocephalus annulatus* feeding exclusively on fish eggs. In studies of assemblages from several localities, Glodek & Voris (1982) and Voris & Voris (1983) also found separation by habitat, but where overlap occurred, syntopic species tended to differ in diet.

Redfield *et al.* (1978) recorded 17 species in the sea snake assemblage of the Gulf of Carpentaria; *Lapemis curtus* (= *Lapemis hardwickii*) accounted for 61% of the individuals. Previous reports by Shuntov (1971) and Heatwole (1975d) from the Gulf found other species dominating and it was suggested that those differences might reflect an effect of the prawn-fishing industry in the intervening time between studies. However, biased sampling

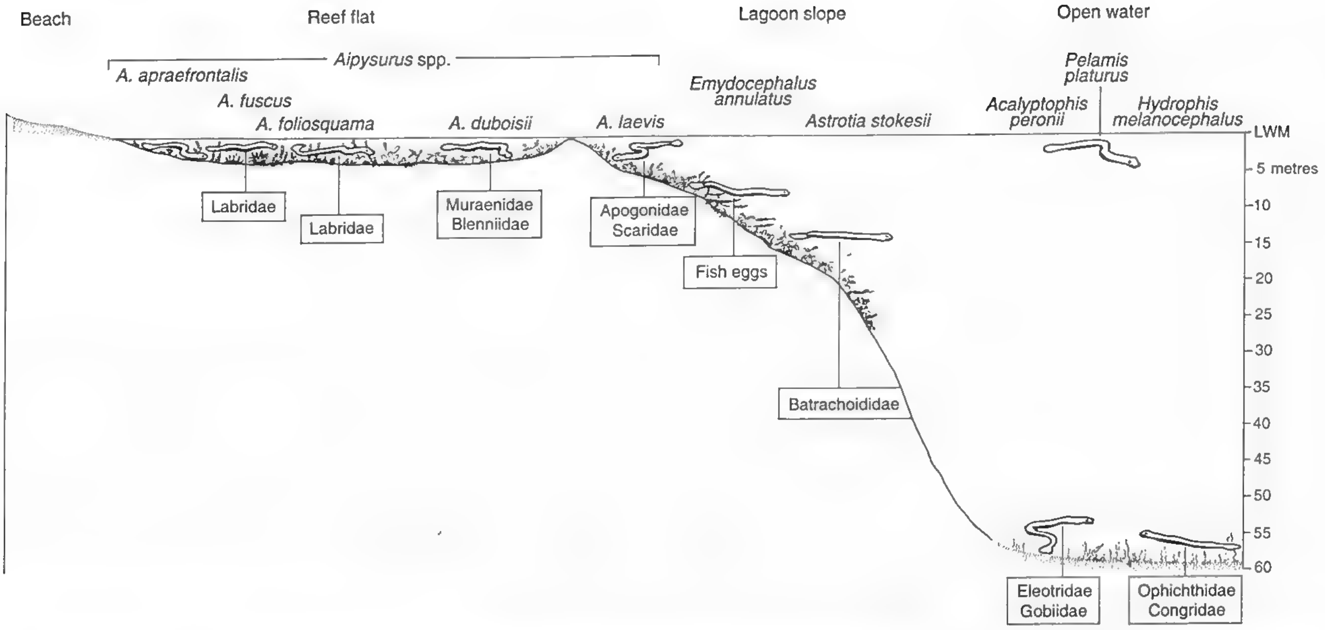

Figure 36.8 Diagram of the spatial and ecological separation of sea snakes on the leeward edge of Ashmore Reef, Australia. The preferred prey of several hydrophiid species is indicated; prey categories overlap considerably at the familial level, but not at the species level. (After McCosker 1975) [W. Mumford]

may also have been involved, or regional differences over such a large area; it is likely that more than one assemblage was included in these investigations. The problem is currently under study.

Many species of sea snake have extensive distributions and individuals may wander widely. For example, *Pelamis platurus*, which occupies slicks on the surface of the ocean, may be carried by currents and storms. It is often found far out of its breeding range and is one of the most common species cast up alive on beaches. Some species, however, have very limited home ranges. Individually marked *Aipysurus laevis* confined their activities to a section of reef edge 150 m or less in length (Burns 1984). The home ranges of different individuals overlapped broadly and there was no evidence of territorial defence.

The tiger shark (*Galeocerda cuvieri*) and sea eagles (*Haliastur indus*; *Haliaetus leucogaster*) commonly prey on sea snakes (Heatwole 1975a). Other species of sharks and birds as well as some predatory teleosts and mammals also may occasionally take them (MacLeish 1972; Heatwole, Heatwole & Johnson 1974; Heatwole 1975a; Heatwole & Finnie 1980). Attempted predation upon sea snakes may be frequent as suggested by a high incidence of missing tails or bite-like injuries (up to 24%) and of scars on the back presumably inflicted by bird talons (up to 7%) (Heatwole 1975a).

Pelamis platurus seems to suffer less from predators than do other sea snakes and its conspicuous black and yellow pattern has been interpreted as an advertisment of its venomous nature (Kropach 1975; Ineich 1988). Attacks on this species, but without evident ingestion, by gamefish (Paulson 1967) and seabirds (Wetmore 1965; Reynolds & Pickwell 1984) have been reported. Only two instances of predation (by a pufferfish and a seal) have been authenticated under natural conditions (Heatwole & Finnie 1980; Pickwell, Bezy & Fitch 1983). Rubinoff & Kropach (1970) showed that hungry predatory fish from areas in which *P. platurus* occurred avoided live or dead *Pelamis* and even pieces of skinned meat. By contrast, naive fishes allopatric with *P. platurus* sometimes ingested them and occasionally died from having been bitten. *Pelamis platurus* also is noxious in other ways and detection of these qualities may be chemoreceptory rather than visual. Weldon (1988) found that snappers (*Lutjanus* spp.) tended to reject pieces of *P. platurus* after snout contact with them, and when they were eaten often they were regurgitated. The skin had a stronger emetic effect than pieces of skinned meat, and snake skin extracts rendered pieces of fish meat less palatable.

Commensals of sea snakes include diatoms, foraminiferans, hydrozoans, serpulid polychaetes, bivalve molluscs, higher algae, bryozoans and barnacles (Zann, Cuffey & Kropach 1975); the last three are the most commonly encountered. Two species of barnacles, *Platylepas ophiophilus* and *Octolasmis grayii*, are exclusive to sea snakes. The former has morphological adaptations that allow it to penetrate the host's tissues and adhere more effectively (Zann 1975) whereas the latter merely adheres to the skin's surface (Jeffries & Voris 1979). Barnacles have been recorded from most species of sea snake for which adequate samples were available and infestations were often high, sometimes reaching 50 to 75%. Barnacles tend to clump together and are more prevalent toward the tail. Frequent skin-shedding by sea snakes periodically rids them of most commensals (Zann *et al.* 1975). Because of its pelagic habit, *Pelamis platurus* does not have access to solid substrata for anchoring the skin during ecdysis, and it coils and knots itself as a means of loosening and freeing the skin (Pickwell 1971).

Ectoparasitic ticks and mites, such as those reported from laticaudids (see Chapter 37), are not known from hydrophiids, probably because of their more completely marine life history. Nematodes and platyhelminths are recorded from the digestive tract (Kropach 1975). Digenean trematodes of the family Hemiuridae include *Plicatrium visayanensis* from the stomach and small intestine of *Hydrophis ornatus* (Bush & Holmes 1984), *Sterrhurus carpentariae* from the stomach of *Lapemis hardwickii* (Bush & Holmes 1979) and lung flukes of the genera *Hydrophitrema* and *Pulmovermis* from various species (Vercammen-Grandjean & Heyneman 1964; Ko, Lance & Duggan 1975).

Feeding Behaviour

Like terrestrial snakes, sea snakes swallow large prey whole and can consume fish of a diameter at least up to twice that of their own necks (Voris & Moffett 1981). They capture prey in several ways. *Pelamis platurus* floats at the surface and small fish seeking shelter under it are struck and eaten. Vibrations produced by the motion of the fish induce the snake to slowly turn the head toward the source, sometimes with open mouth, followed by a rapid sideways lunge. Backward swimming occurs in response to presence of fish or to light tactile response and is often a component of the feeding sequence (Kropach 1975).

Some sea snakes rely on capturing confined prey. They examine crevices among coral or burrows in the sand (Heatwole *et al.*

1978), all the while flicking out the tongue (Fig. 36.7). When the tongue touches a fish and relays odours from it to the chemosensory Jacobson's organ in the roof of the mouth, the snake lunges and bites. The captured fish is held until its struggles abate under the effect of the injected venom. It is then released and the snake moves entirely around its circumference, flicking out its tongue against the edges. This appears to be a means of ascertaining whether the prey is of a size that can be swallowed.

Another means of prey capture is exemplified by the piscivorous *Enhydrina schistosa* which inhabits muddy water of low visibility. It cruises near the bottom and when it bumps into fish or comes close to them, it strikes laterally to effect the capture. It maintains its hold until the fish stops struggling, then works around to the head end and swallows it head first. During swallowing, the snake turns its head away from the direction of swimming and faces its tail (Voris *et al.* 1978).

It appears that vision is of little importance in any of these methods of prey capture. Indeed, sea snakes probably cannot identify a fish as a prey item by sight. If a captured fish is lost from the jaws of a crevice feeder, but lying nearby in full sight, the snake does not recognise it and initiates a random search pattern while sticking out the tongue. If the fish is accidentally contacted by the tongue, it is immediately seized and feeding continues. Similarly, *Pelamis* cannot retrieve lost prey (Kropach 1975).

The three species of fish-egg-eating hydrophiids, *Emydocephalus annulatus*, *Emydocephalus ijimae* and *Aipysurus eydouxii* (Voris 1966; Gopalakrishnakone & Kochva 1990) have a unique feeding method. Contraction of the specialised *m. geniomucosalis*, which links the oral mucosa to the lower jaw, probably allows them to suck in fish eggs along with substantial quantities of sand (McCarthy 1987a, 1987b).

Economic Significance

In 1982 the Commonwealth Government permitted the export of a limited number of skins of sea snakes taken as a by-catch of commercial prawn fishing in tropical Australia. Under the provisions of the Wildlife Protection (Regulation of Exports and Imports) Act 1982 (proclaimed in 1984), this export trade could only be continued as part of a management program under the Act; this trade continues until the present (1993). In an unpublished report to the Conservation Commission of the Northern Territory, Ward (1993) cited the sea snake by-catch of northern Australian prawn trawlers during 1989-90 as exceeding 200 000 specimens; the mean catch rate of sea snakes in his study was similar to the 0.26 snakes/hour recorded by Heatwole & Burns (1987).

As part of the sea snake management program, the Commonwealth Government has provided funds to various agencies to place sea snake 'observers' on commercial fishing vessels; this had led to the accumulation of a large, but mostly unpublished, body of data on sea snake distribution and local and regional taxonomic composition. However, despite these surveys, the knowledge of the broad distribution patterns of Australian hydrophiid sea snakes has changed little from that documented by various authors in Dunson (1975a).

In some parts of Asia, sea snakes are used as food by humans and domestic animals, and the skins are a source of leather; important fisheries occur in the Philippines and Japan. In Australia, sea snakes are not an item of human diet but there is a growing sea snake leather industry (both illegal and legal) (see Heatwole 1987). The sea snake (*pagi* or *ger*) is the subject of one of the many string games devised by the Torres Strait Islanders (Haddon 1912).

The main practical interest in sea snakes in Australia arises from their threat to human health and life. The potential danger of a snake depends on several factors. They include the likelihood of encounter, the potency and amount of venom delivered, the aggressiveness of the snake and the length of the fangs (a measure of how deeply the venom can be injected). Sutherland (1983) and Heatwole (1987) have reviewed these topics. Here, they are summarised briefly.

The venom of Australian sea snakes (except for those that eat fish eggs) is extremely toxic, by an order of magnitude greater than that of most dangerous viperids, but about the same or slightly lower than that of the most toxic terrestrial elapids. Its direct myotoxic effect is a clinical characteristic of serious hydrophiid envenomation of humans and laboratory animals (Fohlman & Eaker 1977), in which muscle fibres are attacked and break down. Muscle damage from myotoxins causes the release of myoglobin and creatine phosphate into the blood and eventually into the urine. Excess myoglobin could block kidney tubules and cause kidney damage (Zimmerman & Heatwole 1987). In addition to such a potential secondary effect, whole venom of *Aipysurus laevis* and six fractions derived from it all have a direct myotoxic effect (Zimmerman, Heatwole, Andreopoulos & Yong in press c).

Venom yields are lower than for many dangerous terrestrial snakes, and fangs are shorter (an exception is *Astrotia stokesii* which has long fangs and can deliver a massive dose of venom). Taking all these factors into consideration, most of the Australian sea snakes should be considered as potentially lethal.

The most aggressive and dangerous species of sea snakes inhabit muddy estuaries. In South-East Asia those species inflict many serious and sometimes fatal bites on people operating hand-seines, barefooted in shallow, turbid waters (Reid 1956, 1975; Murthy & Rao 1977). In Australia, most sea snake bites are sustained by crews of prawn trawlers. Serious envenomations seldom result because by the time the sea snake is brought to the surface it has exhausted its venom against fish or restraining ropes of the net and can give only a 'blank' bite. The species most often encountered directly by the general public are those that live in the clear water of coral reefs. Fortunately, those species usually become aggressive only if disturbed or mistreated and are seldom a danger to a sensible diver or swimmer. Unprovoked attacks are extremely rare but do occur occasionally (Heatwole 1975e, 1978b; Zimmerman 1988a, 1988b). Even when provoked into biting, often no venom is delivered (Heatwole 1990).

Given the potential danger of sea snakes and the more frequent contact between them and humans as a result of the developing leather industry and increasing tourism to waters inhabited by snakes, it is likely that sea snakes will become of greater medical importance in the future. There are antivenoms that protect against sea snake envenomation; that of the terrestrial Australian tiger snake (Elapidae) is one of the more effective ones readily available (Baxter & Gallichio 1976). One should be wary of folk remedies as many of the supposed 'cures' merely reflect recovery from blank bites, not from real envenomations (d'Aulaire & d'Aulaire 1980). For a more detailed treatment of the medical aspects of sea snake bite see Sutherland (1983).

BIOGEOGRAPHY & PHYLOGENY

Distribution

Approximately 50 species of hydrophiid sea snakes are known. With the exception of *Pelamis platurus*, which ranges across the Indian and Pacific Oceans from the east coast of Africa to the west coast of the Americas, the remaining species are found from the Persian Gulf to South-East Asia, New Guinea, Australia, and the islands of the south-western Pacific as far east as Fiji. They are abundant and species-rich throughout the shallow seas and inshore waters of tropical Australia. Of the 31 species recorded from Australian waters, 15 (48%) are endemic, 12 (39%) are shared with South-East Asia, while four (13%) are shared with the western Pacific.

Hydrophiid sea snakes have been recorded also from the colder waters of the southern oceans: from northern Tasmania, Victoria and South Australia (Cogger 1975). These latter records are presumed to be of individuals caught up in the strong summer Eastern Australian Current which sweeps down the eastern coast from the warm waters of the Great Barrier Reef. These individuals are unable to return to their feeding and breeding grounds, and ultimately find themselves in waters which are lethally cold. This summer influx of snakes is accompanied by a parallel influx of larval tropical fish species (Paxton pers. comm.).

Only one species, *Pelamis platurus*, appears to be a regular winter visitor to the seas off the south-east and south-west coasts of Australia. These intrusions were long regarded as waifs. For example, Dunson & Ehlert (1971) suggested that the lower lethal limit for this species lies between 14.5° and 17°C, However, Cogger (1975) showed that this species is not only a regular inhabitant of the cooler winter waters off New South Wales (mean winter surface temperature 16°C), but that reproduction also occurs in these waters at this time. Because the mean size of *Pelamis platurus* in cooler eastern Australian waters is significantly larger than that recorded from eastern Pacific populations, the eastern Australian population may be genetically distinct.

Apart from the ubiquitous *Pelamis platurus*, two broad distribution patterns stand out. The first is a large suite of species which range from the east coast across the top of Australia (the Gulf of Carpentaria and the Arafura Sea) to the north-west shelf and the tropical coast of Western Australia. These include three species of *Aipysurus* (*laevis*, *eydouxii* and *duboisii*), *Acalyptopthis peronii*, *Astrotia stokesii*, *Disteira major* and *D. kingii*, *Emydocephalus annulatus*, *Enhydrina schistosa*, three species of *Hydrophis* (*elegans*, *mcdowelli* and *ornatus*) and *Lapemis hardwickii*.

However, differences in dominant colour phases between eastern and western populations suggest that in some instances gene flow between populations of the same species on either side of Torres Strait may be low. Indeed, both *Emydocephalus annulatus* and *Hydrophis coggeri* appear to have a geographic discontinuity of approximately 1500 km between their populations on either side of Torres Strait.

There is a second, smaller group of species apparently confined to the waters west of Torres Strait: three species of *Aipysurus* (*apraefrontalis*, *foliosquama* and *fusca*), *Ephalophis greyi*, *Parahydrophis mertoni* and *Hydrelaps darwiniensis*.

For most other species recorded from Australian waters, records are few, or so isolated, that the extent of their ranges within Australian waters remains speculative.

Affinities

The first rigorous phenetic classification of the Hydrophiidae was proposed by Smith (1926) based on morphological and cranial characters. Smith had included all marine snakes (including those in the genus *Laticauda*) within a single family, the Hydrophiidae. These were characterised by the presence of proteroglyphous ('fixed front fang') dentition, dorsal, valvular nostrils, posteriorly compressed bodies, short tongues in which typically only the cleft portion is protrusible, strongly developed caudal hypophyses and neural spines, and paddle-shaped tails. Within this family, Smith recognised two distinct subfamilies: the Laticaudinae with relatively broad belly scales, forward-projecting maxilla, broad parietal bones and a separate median prolongation of the rostral shield (*Laticauda* spp., *Aipysurus* spp. and *Emydocephalus* spp.) and the Hydrophiinae, to include all other marine snakes, with much reduced belly scales, a more posteriorly-located maxilla, narrow parietal bones and a fused median prolongation of the rostral shield.

In a major review of the world's sea snake fauna, using numerical taxonomy and cladistic principles, Voris (1977) concluded that there are three major monophyletic stocks of independent origin: Smith's Hydrophiinae and two separate groups within Smith's Laticaudinae: *Laticauda* spp. and *Emydocephalus* spp./*Aipysurus* spp.

Earlier, McDowell (1967, 1969a, 1969b, 1972a) had begun a series of detailed studies on the comparative anatomy, cranial osteology and external morphology of sea snakes. He concluded that three distinct monophyletic groups of hydrophiids can be recognised: the *Hydrelaps* group (*Hydrelaps*), the *Aipysurus* group (*Ephalophis, Aipysurus* and *Emydocephalus*) and the *Hydrophis* group (remaining hydrophiid genera). Seven genera (including five from Australia) can be recognised in the *Hydrophis* group: *Hydrophis*, *Acalyptophis*, *Kerilia*, *Thalassophis*, *Pelamis*, *Disteira* and *Lapemis*. Within the *Hydrophis* group three subgroups (which McDowell accorded subgeneric status) can be recognised: *Hydrophis*, *Leioselasma* and *Aturia*. Some workers have treated these subgenera as full genera (for example, Kharin 1984).

Burger & Natsuno (1974) subsequently combined McDowell's *Ephalophis* and *Hydrelaps* subgroups into a new subfamily: the Ephalophiinae.

McDowell also examined the phylogenetic relationships between various groups of sea snakes, and between sea snakes and other proteroglyphous snakes. He concluded that laticaudid sea snakes represent a radiation separate from and independent of that of hydrophiid sea snakes, and that hydrophiid sea snakes are most closely allied to, and indeed are confamilial with, the Australasian radiation of terrestrial elapid snakes, all of which should be placed together in the family Hydrophiidae.

McDowell's conclusions were first interpolated into a new higher classification of snakes by Smith, Smith & Sawin (1977), who placed the laticaudids in a separate Tribe (Laticaudini) within the subfamily Elapinae of the family Elapidae. Other sea snakes were placed in four separate tribes (Ephalophini, Hydrelapini, Aipysurini and Hydrophiini) within the subfamily Hydrophiinae of the family Hydrophiidae. All Australasian terrestrial proterogplyphs were also included in this family.

Burger & Natsuno (1974) had argued earlier that the apparent independent origin of laticaudids from other marine snakes was best reflected in their assignment to separate families under the umbrella of a superfamily Elapoidea. This approach has generally been followed by subsequent authors who, while acknowledging the close phylogenetic relationships between all existing proteroglyphous snakes and the strong evidence for common ancestry, have tended to continue to recognise all three groups as distinct families: Elapidae, Hydrophiidae and Laticaudidae (for example, Cogger 1983) or as subfamilies (McCarthy 1986). The reason for this is not simply inherent conservatism; rather, the classification proposed by McDowell is based on weighting of certain characters (for example, heart position, arching of maxilla) for phylogenetic analysis. The relationships between these three groups remain speculative.

37. FAMILY LATICAUDIDAE

Harold Heatwole & Michael L. Guinea

DEFINITION AND GENERAL DESCRIPTION

The nasal scales of laticaudids are separated by one or two internasal scales. This feature, in conjunction with wide gastrosteges running the full width of the venter, like those of land snakes, separates this group from the Hydrophiidae. Oviparity is the sole proven means of reproduction. Sea kraits are amphibious and move freely on land.

The snakes of the family Laticaudidae constitute a discrete taxonomic group which represents either an independent lineage originating from terrestrial elapids, or an early separation from the hydrophiid sea snake lineage (Voris 1977).

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

The laterally positioned nostrils, broad ventral scales and a cylindrical body form are laticaudid characters that are considered primitive for sea snakes. The body scales are smooth, imbricate and arranged in 19 to 25 rows at mid length. The tail is laterally compressed, an advanced feature shared with hydrophiids. Usually laticaudids have conspicuous light and dark bands, and superficially resemble kraits, a feature giving rise to their common name, sea kraits. Banding is probably an advertisement of their noxious qualities, and some eels that can hardly be distinguished from *Laticauda colubrina* unless they are in hand are believed to be Batesian mimics (Pernetta 1977).

Locomotion

Aided by their wide ventral scales, sea kraits move on land in a manner similar to terrestrial snakes. They are competent climbers amongst rocks and vegetation (Mao & Chen 1980). In water, rhythmic lateral undulations of the body and flattened tail propel the animal forward. Laticaudids are usually sedentary on land, though rain stimulates them to be active (Guinea 1987).

Feeding and Digestive System

Sea kraits have potent venom and hollow fangs positioned at the front of the mouth. Prey is located underwater by foraging in

Table 37.1 Comparison of physiology, lung morphology and diving ability of the Acrochordidae, Laticaudidae, Hydrophiidae, Colubridae (Homalopsinae), Elapidae and Boidae. Apart from extrarenal excretion, sea snakes appear to have few specialised physiological adaptations to their marine environment. (Data sources: metabolic rate, cutaneous respiration, relative heart weight and relative lung volume, Vinegar, Hutchinson & Dowling 1970; Heatwole & Seymour 1975; Heatwole & Seymour 1978: blood volume (% mass), Lillywhite, Smits & Feder 1988: blood volume (haematocrit %), Seymour 1976; Pough 1979; Heatwole & Dunson 1987): extrarenal excretion, Minnich 1979: cutaneous diffusion, Dunson 1984)

	Acrochordidae	Laticaudidae	Hydrophiidae	Colubridae Homalopsinae	Elapidae	Boidae
Metabolic rate	Low	High	High	High	High	Low
VO_2 (ml 100 $g^{-1}h^{-1}$)	0.2–0.4	–	0–1.1	–	–	0.5–4.0
Cutaneous respiration	High	Low	High	Low	Low	Low
(ml O_2 100 $g^{-1}h^{-1}$)	0.07–0.2	0.74–0.89	1.5–1.94	0.4–2.25	–	0.06
% of O_2 requirements	7–13%	–	12–33%	–	–	3%
Blood volume	High	Low	Low	Low	Low	Low
% mass	12.5–13.3	5.9–6.5	5.5–9.9	3.9–13.3	–	–
Haematocrit %	41–57	24–34	26–35	32.2	28	25–29
Relative heart weight %	0.26	0.52	0.11–0.79	–	0.43	–
Lung morpholgy	Lobular	Vascular & sacular	Vascular & sacular	Sacular	Sacular	Sacular, & paired in primitive forms
Relative Volume (ml g^{-1} body weight)	0.22–0.39	0.32	0.1–0.89	–	–	–
Diving ability	Shallow	> 60 m	> 100 m	Shallow	Shallow	Shallow
Extrarenal excretion	Sublingual gland	Sublingual gland	Sublingual gland	Premaxillary gland	None	None
Rate (µEq 100 $g^{-1}h^{-1}$) Na, K, Cl	–, –, 39	33.9, 2.7, 36.7	218, 9.2, 169	–	–	–
Cutaneous diffusion	High	Low	High	Low	Low	Low

crevices while protruding the tongue. Detected prey is envenomated and then swallowed, usually head first. Digestion may take several weeks (Saint Girons 1964).

Despite their effective venom apparatus, sea kraits are docile and reluctant to bite defensively, even when roughly handled, although bites to humans have been recorded (Punay 1975). Lethal doses (LD_{50}) for laboratory mice are: *Laticauda colubrina* 0.42 mg kg^{-1}; *L. laticaudata* 0.18 to 0.30 mg kg^{-1}; *L. semifasciata* 0.28 to 0.50 mg kg^{-1} (Tamiya 1975). The toxicology, immunology, biochemistry and physical properties of sea krait venom are relatively well known through the publications of Tamiya & Arai (1966), Uwatoko, Nomura, Kojima & Obo (1966a), Uwatoko, Nomura, Kojima & Obo (1966b), Tu & Salafranca (1974), Low (1979), Kim & Tamiya (1982), Guinea, Tamiya & Cogger (1983), Tamiya, Sato, Kim, Teruuchi, Takasaki *et al* (1983), Singh & Guinea (1984), Takasaki, Kuramochi, Shimazu & Tamiya (1988), Obara, Fuse, Tsuchiya, Nonomura, Ménez & Tamiya (1989), Rowan, Harvey, Takasaki & Tamiya (1989) and Fuse, Tsuchiya, Nonmura, Ménez & Tamiya (1990).

Respiration, Circulatory System and Diving

Sea kraits are seen most often on land or foraging in shallow water near the islands they use for refuge (Gail & Rageau 1958), and consequently have a reputation as less capable divers than many hydrophiids. However, *L. colubrina* was observed at a depth of 45 m and when disturbed the snake swam into deeper water, estimated to be greater than 60 m (Mebs, pers. comm.). Usually, the species dives voluntarily for 15–25 minutes and has been recorded submerged for longer than 50 minutes (Heatwole 1975b; 1981a). Its maximum capacity for breathhold is unknown. When actively foraging in shallow water (less than 13 m deep), *L. colubrina* may surface every few minutes (Cogger, Heatwole, Ishikawa, McCoy, Tamiya & Teruuchi 1987).

The single tubular lung of sea kraits comprises three distinct sections (Heatwole & Seymour 1975b). The anterior tracheal section is a modified trachea and retains remnants of the tracheal cartilages. This part and the lung proper, or bronchial section, are heavily vascularised and collectively form the vascular lung which functions as the major gas exchange organ. The third and most posterior section is the saccular lung, which is not vascularised, plays no part in gas exchange and has only a minimal role in buoyancy (Heatwole 1981a). In water, the breathing cycle of *L. colubrina* consists of a number of quick breaths at the surface followed by a long period of apnea while submerged, much like the rhythm exhibited by hydrophiids. However, unlike hydrophiids, sea kraits can shift from this 'aquatic rhythm' to a 'land rhythm' of more regularly spaced breaths, similar to that of terrestrial snakes (Heatwole 1981a).

In many hydrophiids the capacity for prolonged submergence is enhanced significantly by cutaneous respiration. Sea kraits have less than half the capacity of hydrophiids to take up oxygen through the skin (Table 37.1; Heatwole & Seymour 1978). Sea kraits do not exhibit true diving bradycardia (Heatwole 1977), nor is their blood especially adapted for oxygen storage (Seymour 1976; Heatwole & Seymour 1976). Indeed, they resemble terrestrial snakes more than hydrophiids in the temperature sensitivity of the oxygen carrying capacity of their blood (Table 37.1; Pough & Lillywhite 1984).

Blood flow to the lung, and hence pulmonary uptake of oxygen and nitrogen by the blood, can be regulated through intrapulmonary and intraventricular shunting of the systemic cardiac output. Compression causes non-uniform lung collapse, an increase in partial pressure of oxygen in the lung and arteries, and enhances shunting. Protection from the bends is afforded by maintenance of arterial nitrogen levels below those of the lung through increased shunting and by loss of nitrogen through the skin (Seymour 1978, 1989). *Laticauda colubrina* has a lower capacity for shunting and for cutaneous gaseous exchange than an hydrophiid and consequently is less well adapted to deep diving (Table 37.1). In deep water it could actually lose oxygen to the sea (Seymour 1987).

Osmoregulation

Excess salt is removed from the body of sea kraits by a sublingual salt-excreting gland that discharges into the tongue sheath. The skin is resistant to inward passage of salt (Dunson 1984). Laticaudids drink freshwater when it is available, which assists osmoregulation (Guinea 1987, 1991).

Reproduction

All species of laticaudids that have been studied are oviparous (Saint Girons 1964; Pernetta 1977; Guinea 1981; Bacolod 1983; Toriba & Nakamoto 1987). Reports of viviparity in *Laticauda colubrina* (in Singapore, Smith 1930) and in *L. crockeri* have not been substantiated (Cogger *et al.* 1987). Clutch sizes vary with species: two to 10 eggs in *L. colubrina* (Pernetta 1977; Guinea 1981); one to five eggs in *L. laticaudata*; three to 10 eggs in *L. semifasciata* (Bacolod 1983). In this last species, clutch size increases with size of the female and the relative clutch mass (RCM) is 21.1% of the mother's weight. Hatchling males are significantly larger (43.1 g) than females (40.0 g) and the sex ratio among hatchlings is skewed in favour of males (61%) (Toriba & Nakamoto 1987).

NATURAL HISTORY

Life History

Reproductive seasonality is geographically variable. In the Philippines, *L. colubrina* breeds aseasonally (Gorman, Licht & McCollum 1981; Bacolod 1983). The same species has a twice-yearly breeding cycle in Sabah (Steubing 1988) and a single breeding season in Fiji, in the warm summer months (Guinea 1981, 1987). The eggs are deposited in rock crevices and caves (Herre & Rabor 1949; Bacolod 1983). Incubation periods vary from about 123 days for *L. colubrina* (Guinea 1987) to 140 days for *L. semifasciata* (Nakamoto & Toriba 1986).

Ecology

Laticauda colubrina forages on coral reefs (Fig. 37.1) and rests and seeks shelter on adjacent land, often on very small islands or cays. Movement to and from the sea coincides with nocturnal high tides (Heatwole 1987). All species of sea kraits are piscivorous. *Laticauda colubrina* and *L. laticaudata* feed almost exclusively on moray and conger eels (Muraenidae and Muraenesocidae) (Pernetta 1977; Voris & Voris 1983; Moriguchi 1988); known departures from this diet are so rare that when they occur they occasion comment. *Laticauda semifasciata* eats various bony fish species (Voris 1972). A gudgeon, *Eleotris*, forms the sole diet of *L. crockeri* in Lake Te-Nggano, Rennell Island, Solomon Islands (Cogger *et al.* 1987).

Predators on sea snakes include sea eagles and some predatory fishes, especially tiger sharks (Heatwole 1975a), and these may prey on sea kraits as well. Guinea (1987) reported crabs preying on sea kraits.

Laticauda colubrina is host to the ectoparasitic ticks, *Amblyomma nitidum* and *Aponomma* sp. (Zann, Cuffey & Kropach 1975) and parasitic mites have been found in the respiratory tract of *L. laticaudata* (Gail & Rageau 1958). Parasites recorded for *Laticauda semifasciata* include flagellate protozoans, digenetic trematodes, nematodes, trombiculid mites and unidentified larval helminths (Telford 1967). Barnacles frequently encrust the skin of sea kraits (Gail & Rageau 1958).

Behaviour

The body temperature of *L. colubrina* approximates that of their immediate environment, although the full range of fluctuation in environmental temperature is not experienced because snakes select cool microhabitats. In New Caledonia, body temperatures of

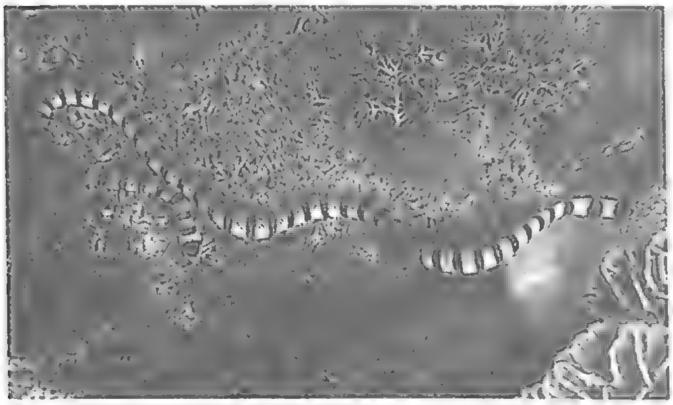

Figure 37.1 *Laticauda colubrina* foraging on a coral reef at a depth of 10 m at Pig Island, near Madang, Papua New Guinea. [Photo by D. Mebs]

snakes on land range from 27° to 28°C in the cooler part of the year and 28° to 30.5°C in snakes in shade or near shelter in warmer seasons; the mean is 27.8°C (Saint Girons 1964). Those in the Philippines are similar (mean 28.4°C; range 26.7° to 30.1°C; Heatwole 1981b). Temperatures of more exposed snakes in hotter periods reach temperatures of 30° to 33° C (mean 31.2° C). At night body temperatures dropped to 12° to 18° C, depending on the season. Snakes foraging in the water had temperatures of 17° to 19°C and 20° to 21°C, depending on the season.

Terrestrial aggregations of sea kraits are common in localities throughout their distribution. Estimates of the numbers of *Laticauda colubrina* using specific islands range from 600 and 721 on small islands in Sabah (Steubing 1988; Lading, Steubing & Voris 1991) to 1400 on Sausau Island, Fiji (Guinea 1987) and 1700 on Signal Island, New Caledonia (Saint Girons 1964).

Economic Significance

Laticaudids are used for stock and human food in parts of Asia and they are important in the leather industry. In the Philippines in the early 1970s, 4000 to 5000 kg of dried sea snake meat per month was ground for pig and poultry food, and 180 000 to 200 000 skins per year were exported to Japan (Punay 1975). *Laticauda semifasciata* and *L. laticaudata* were two of the principal species involved. In addition, local trade in *Laticauda* leather reached 5000 pieces per month. A sea snake industry operates in the Ryukyu Islands. No data are available on the annual catch, but receipt of about 1000 individuals of *L. semifasciata* on a single day was observed once (Heatwole 1987). In Australia, laticaudids are too rare for commercial exploitation. Potential danger to sea kraits comes from overexploitation by the leather industry, introduced predators (Guinea 1981), destruction of reefs by humans (Steubing 1988) and wanton slaughter (Saint Girons 1964).

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Sea kraits are restricted to tropical waters of the western Pacific and eastern Indian Oceans (Fig. 37.2; Heatwole 1978a). The broadest distribution is shared by *Laticauda colubrina* and *L. laticaudata* which are broadly sympatric from India to southern Japan and to the eastern coast of Australia. *Laticauda semifasciata* ranges from southern Japan to Indonesia, with one subspecies, *L. s. schistorhynchus* restricted to Niue (Cook Islands), Tonga and Samoa. *L. crockeri* is known only from Lake Te-Nggano, Rennell Island, Solomon Islands (Cogger *et al.* 1987). Only *L. colubrina* and *L. laticaudata* have been recorded from Australian territorial waters, and then only as isolated individuals, not as breeding populations (Cogger, Cameron & Cogger 1983). Though this may reflect the low collecting effort in parts of northern Australia (Cogger 1975b), present information suggests that sea kraits occur in Australia only as waifs brought by oceanic currents from Melanesia. Their absence from the Australian coastline west of Torres Strait has been attributed to a cold water barrier in the Timor Sea during lowered sea levels in the Pleistocene (Cogger 1975b), or alternatively, to competitive exclusion by the hydrophiid *Aipysurus* (McCarthy 1986).

Affinities with other Groups

Burger & Natsuno (1974) accorded sea kraits full familial rank as the Laticaudidae, an arrangement supported by amino acid sequences of neurotoxins (Tamiya 1985). We follow Cogger *et al.* (1983) in accepting that assignment, pending further studies. For a more detailed discussion of the relationships of sea snakes and sea kraits, see Chapter 36.

Historically, sea kraits have been grouped most often in the subfamily Laticaudinae, as part of either the family Hydrophiidae (Smith 1926) or Elapidae (Dowling 1967; McDowell 1972a). Smith's concept of the subfamily was broader than currently accepted, and included, in addition to sea kraits, the hydrophiines *Aipysurus* and *Emydocephalus*. Some herpetologists assigned sea kraits to rankings lower than subfamilial level. Smith, Smith & Sawin (1977) considered them only as a tribe within the Elapidae. Because of the similarities in haemoglobin fingerprinting and serology linking sea kraits and other sea snakes, Mao & Chen (1980) included *Laticauda* within the Hydrophiidae and dispensed with the subfamilial designation, Laticaudinae.

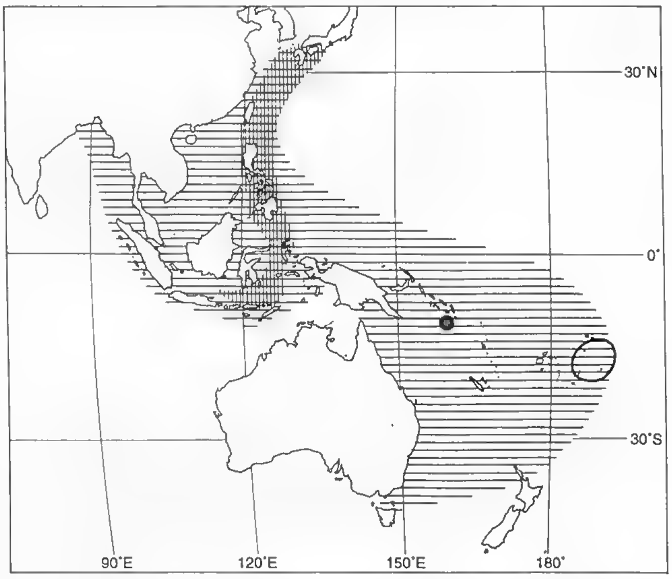

Figure 37.2 Distribution of sea kraits. Horizontal shading, *Laticauda colubrina*, *L. laticaudata*; vertical shading, *L. semifasciata*; open circle, *L. schistorhynchus*; closed circle, *L. crockeri*. (After McCarthy 1986) [W. Mumford]

Affinities within the Taxon

Kharin (1984) proposed splitting the sea kraits into two genera, *Laticauda* and *Pseudolaticauda*. This division is not supported by morphological (McCarthy 1986; Cogger *et al.* 1987) or toxicological (Slowinski 1989) studies and accordingly we retain all of the sea kraits in the single genus, *Laticauda*.

The species form three distinct complexes based on head colouration, presence or absence of an azygous prefrontal shield, division or not of the rostral shield, and numbers of scale rows around the body (Cogger *et al.* 1987). The *Laticauda colubrina* complex contains *L. colubrina* and *L. frontalis*, the *Laticauda laticaudata* complex comprises *L. laticaudata* (two subspecies of doubtful validity; McCarthy 1986) and *L. crockeri* (Cogger *et al.* 1987), and the *Laticauda semifasciata* complex includes two subspecies of the nominate species (Guinea *et al.* 1983).

38. FAMILY ACROCHORDIDAE

Richard Shine & Darryl Houston

DEFINITION AND GENERAL DESCRIPTION

The Acrochordidae consists of three living species, placed by most authors within the single genus, *Acrochordus*, and commonly known as file snakes. In Australia, *A. granulatus* is found in marine and estuarine areas of the Indo-Pacific and *A. arafurae* is confined to freshwater habitats. These snakes are highly modified for aquatic life, lacking the enlarged ventral scales typical of terrestrial snakes. Their scales are small, rugose and granular. The skin is loose and baggy, the trunk stout, and the eyes small and positioned dorsally as in many other aquatic snakes.

HISTORY OF DISCOVERY

Hornstedt in 1787 described the genus *Acrochordus* (from the Greek *akrochordon*, meaning wart) for the Asian species *A. javanicus*. Many workers have since followed Cuvier's recognition in 1817 of a separate genus, *Chersydrus*, for the marine species *A. granulatus*. The Australian freshwater species *Acrochordus arafurae* was not recognised as distinct until the major review of McDowell (1979). Hence, much of the early literature refers to Australian *A. arafurae* as *A. javanicus*, and the particularly inappropriate common name of 'Javan File Snake' is still widely applied.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Australian acrochordids range in maximum body size from one metre for *A. granulatus* to two metres for *A. arafurae*. The head is short and blunt, without enlarged head shields (Fig. 38.1). Colour patterns are more distinct in neonates, fading gradually with age. Adults are mottled shades of brown dorsally, tending towards lateral striping in *A. arafurae* (Pl. 7.6), and more distinct grey-and-white banding in *A. granulatus*.

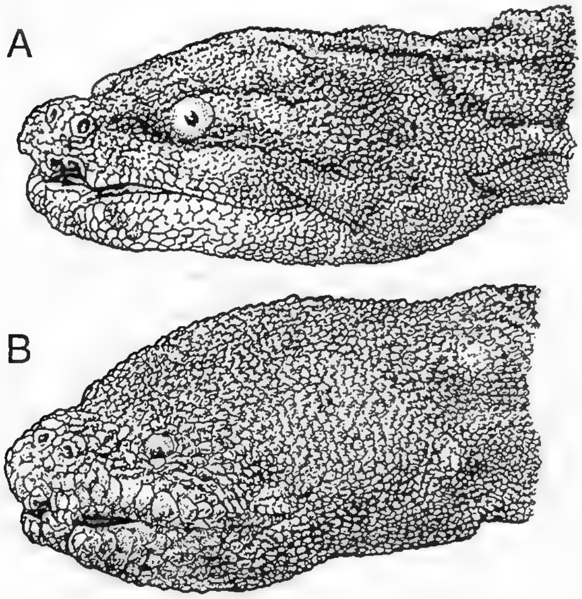

Figure 38.1 Heads of the two Australian species of *Acrochordus*. **A**, *A. granulatus*; **B**, *A. arafurae*. (After McDowell 1979) [J. Courtenay]

Body Wall

The body bears small non-overlapping rugose scales and is unique among snakes in having sensory, bristle-bearing tubercles on the interstitial skin, and sensory organs on the scales themselves (Schmidt 1918; McDowell 1979). The outer keratin layer of the epidermis is shed regularly. Aspects of the dorsal musculature of *A. granulatus* are described by Auffenberg (1966).

Skeletal System

McDowell (1979, 1987) described the osteology in detail. Numerous distinctive features include the constant presence of paracotylar foramina on the vertebrae, the lack of well-defined tubera costae on the ribs, and the division of the articular surface of the rib into a hemispherical dorsal portion and a wider, saddle-shaped ventral portion. The ear region is also unusual, primarily through retention of embryonic features.

Locomotion

Acrochordids are almost entirely aquatic, although both captive and wild individuals of *A. arafurae* have been seen moving short distances overland (Shine & Harlow pers. obs.). Underwater, filesnakes move about both by crawling on the bottom and by swimming in open water. The loose skin flattens out in free-swimming acrochordids to increase the lateral surface available for aquatic propulsion, and the laterally compressed tail of *A. granulatus* aids in swimming (Dowling 1960; Shine pers. obs.).

Feeding and Digestive System

Filesnakes are entirely piscivorous and the skull is highly modified, with elongate quadrates and an unusual quadrate-columellar articulation that facilitates swallowing large fishes (Savitzky 1983). Relative cranial proportions differ considerably between males and females in *A. arafurae*, apparently reflecting the profound dietary differences between the sexes (Shine 1986c; Camilleri & Shine 1990; Houston & Shine 1993). The anatomy of the acrochordid digestive system is unusual among snakes in several respects, including the close proximity of the gall bladder to the liver, and the remarkable degree of convolution of the intestine (Fig. 38.2; Bergman 1958).

Circulatory System and Respiration

The relatively posterior placement of the heart (close to midbody), may be an aquatic specialisation, because some proteroglyphous seasnakes show a similar condition (McDowell 1979). *Acrochordus* has the most extensively vascular respiratory system of any known snake (Table 37.1). The roof of the trachea bears two rows of vascular sacs (Brongersma 1952). The right lung bears vascular parenchyma for its total length, and extends to quite near the cloaca (Bergman 1958). Significant cutaneous respiration also occurs (Table 37.1). Metabolic rates are unusually low whereas blood volumes (and hence blood oxygen stores) are much higher than for other reptiles (Table 37.1). Typically, acrochordids remain underwater for long periods before moving to the surface to take several breaths in succession, thus replenishing their oxygen stores to support another long period of submersion (Glass & Johansen 1976; Feder 1980; Seymour, Dobson & Baldwin 1981).

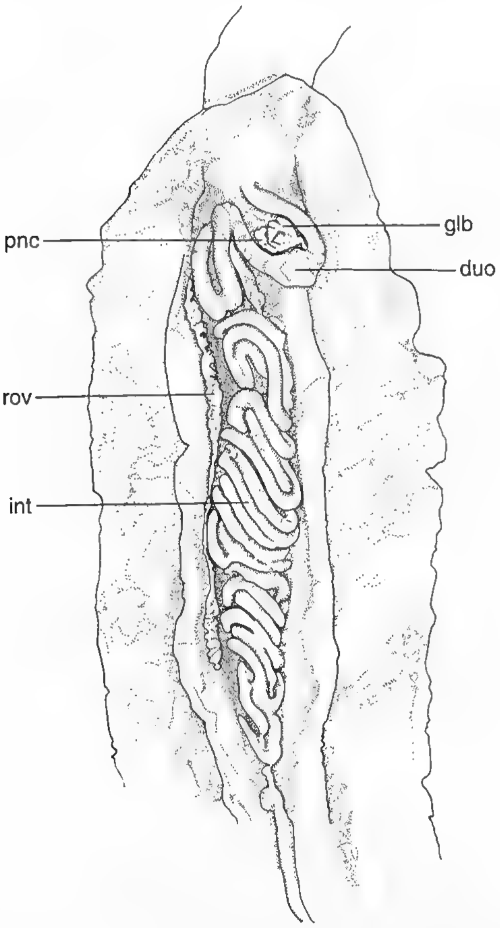

Figure 38.2 Transverse loops of the intestine of *A. javanicus* are immediately apparent on dissection. Bergman (1958) likened their appearance to those of a quadruped more than any other snake he had studied. **duo**, duodenum; **glb**, gall bladder; **int**, small intestine; **pnc**, pancreas; **rov**, right ovary. (After Bergman 1958) [J. Courtenay]

Acrochordus arafurae maintains high and relatively stable body temperatures, averaging around 26° to 30°C (Shine & Lambeck 1985).

Excretion

The kidneys are paired and lie posteriorly in the body cavity (Bergmann 1958). Sublingual salt glands have been described in the marine species *A. granulatus* (Dunson & Dunson 1973) (Table 37.1).

Sense Organs and Nervous System

The eyes are small and positioned further anteriorly and more dorsally than are those of most other snakes. The valved nostrils are also in an anterior dorsal position, presumably an adaptation to aquatic life. The scales and interstitial skin are richly supplied with projections that appear to be sensory in structure (Schmidt 1918; McDowell 1979), and probably function in prey recognition. Usually, captive *A. arafurae* will not strike or constrict a fish until they actually come into contact (Shine & Houston pers. obs.). The tongue is extruded to detect substances in the water and the low frequency and long duration of extrusion is apparently unique among snakes (Gove 1979). Tongue-flick frequencies in captive snakes are greatly increased when potential prey items are added to the tank (Shine pers. obs.).

Reproduction

The gonads are paired, and have been described by Bergman (1958). Paired hemipenes lie within the base of the tail when inverted, and are everted from the cloaca for intromission. Hemipenial morphology differs considerably among the three *Acrochordus* species, and is described and illustrated by McDowell (1979). Detailed information on organ sizes and placement is provided by Bergman (1958).

Filesnakes are viviparous, with highly seasonal reproduction. Litter sizes range from 11 to 25 in *A. arafurae* (Shine 1986a) and around one to eight in *A. granulatus* (Bergmann 1958; Voris & Glodek 1980; Gorman, Licht & McCollum 1981). One isolated captive female *A. arafurae* produced a viable embryo after seven years, suggesting either parthenogenesis or prolonged sperm storage (Magnusson 1979a).

NATURAL HISTORY

Life History

Field studies on *A. arafurae* in Kakadu National Park in the Northern Territory suggest that this species is a specialist with low rates of energy throughput and unusually low rates of feeding, growing and reproducing. Maturity is delayed compared to most other snakes, and is attained at more than five years in both sexes (Houston & Shine unpub. obs.). However, most adult-size females do not reproduce in most years; the proportion of reproductive animals increases with body size (Shine 1986a). Feeding occurs mainly during the wet-season and feeding rates vary annually in relation to variation in the duration of flooding. There is high year-to-year variation in body condition and reproductive frequency. Hence, the overall population is dominated by cohorts from occasional years of particularly successful reproduction. The marine *A. granulatus* also shows low feeding frequencies, prolonged gestation and less-than-annual reproduction in adult females (Bergmann 1958; Gorman *et al.* 1981).

Ecology

In Kakadu, filesnakes live in widely separated billabongs for most of the year, but can travel freely over wide areas during wet-season flooding. The snakes feed primarily at night in shallow water, especially on sleeping fishes. Adult female *A. arafurae* are much larger than males (mean snout-vent length 135 cm, 1.4 kg vs. 105 cm, 0.67 kg), have relatively larger heads, and eat much larger prey (Shine 1986c). Females also tend to be found in deeper water than males (Shine 1986c). Population densities can be extremely high, with several thousand adult filesnakes in some floodplain billabongs (Houston 1991). Arafura filesnakes are eaten by a variety of birds, mainly the sea eagles (*Haliaeetus leucogaster*) and the stork (*Ephippiorhynchus asiaticus*), reptiles, fishes and humans (Shine 1986a, 1986b).

Surprisingly, the marine *A. granulatus* shows very little sexual dimorphism either in snout-vent length or relative head size (Shine 1991b). This species is widely distributed through marine, estuarine and freshwater habitats, especially mangrove areas, and feeds mainly on gobioid fishes located by active foraging in small crevices on the sea bottom (Dunson & Minton 1978; Voris & Glodek 1980).

Behaviour

Acrochordids are typically reluctant to bite when handled, even when injured. Arafura filesnakes are active foragers, travelling slowly along the edge of the billabong at night searching for fishes (Shine 1986a). Mean daily displacement in radiotracked snakes was 68 m during the dry-season, and 166 m during the wet-season (Shine & Lambeck 1985). Fishes are seized either with the mouth or the coils, and rapidly immobilised by constriction (Dowling 1960). During the mating season, intertwined groups of one female and one to eight males may be found in shallow water among treeroots.

Economic Significance

Arafura filesnakes are popular traditional food items for aboriginal people in northern Australia. The snakes are collected by groping under logs and among weedbeds when water levels are low. Gravid females are most easily caught because of their size, and are highly prized by the hunters (Shine 1986b). Filesnakes also enter baited drum-nets and, more reliably, unbaited fyke-nets (Shine 1986a, 1986b).

Freshwater filesnakes are legally protected but marine populations may not be covered by the legislation. Natural habitats of *A. arafurae* are under threat in some areas because of introduced species, ranging from water weeds (*Salvinia molesta*) to water buffalo (*Bubalus bubalus*), and from pollution resulting from human activities. Marine filesnakes are also harvested, but primarily on a commercial basis for their skins (which make high-quality leather) and mainly in Asia rather than Australia.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Acrochordids are found from India eastward through tropical Asia to the Philippines, south through the Greater and Lesser Sunda Islands to New Guinea, northern Australia, the Bismarck Archipelago, and the Solomons. *Acrochordus arafurae* is restricted to drainages of Australia and New Guinea entering the Arafura Sea.

Affinities

Despite the array of primitive features and unique specialisations, derived character states of the vomerine apparatus and facial carotid artery in acrochordids suggest that these snakes are an early offshoot from the main colubroid ('advanced snake') lineage (Groombridge 1979, 1984). The symmetrical paired common carotid arteries also suggest that they are primitive colubroids (McDowell 1979). Their closest relatives may be the extinct families Nigerophiidae, Palaeopheidae and Anomalopheidae (McDowell 1987).

The three living species are all very distinctive. McDowell (1979) suggests that the two freshwater taxa may be derived from an earlier *granulatus*-like marine form.

Fossil Record

A single species, *A. dehmi*, has been described from the upper Miocene and lower Pliocene of Pakistan (Hoffstetter 1964).

39. GENERAL DESCRIPTION AND DEFINITION OF THE ORDER CROCODYLIA

Harold G. Cogger

Crocodilians, and the birds with which they share a common ancestor, represent the only extant members of the diapsid subclass Archosauromorpha. They represent an ancient conservative lineage which first evolved in the Triassic, about 215 million years ago. This group is characterised by the presence of a cranial pneumatic system in the snout, in the form of the antorbital fenestrae (Carroll 1988a).

Among living reptiles, the crocodilians are so distinctive in external appearance and behaviour that they cannot be confused by even the most inexperienced observer with representatives of any other reptilian groups (Pl. 9). All are large, semi-aquatic predators. They are usually protected by thick scaly skins under which are numerous large and small osteoderms. The tail is a long, powerful organ of locomotion and the skull is elongate and heavily built.

In modern crocodilians the palatine and pterygoid bones have extended laterally to form a full secondary palate, separating the mouth from the air passages above. This structural feature is accompanied by a large, fleshy transverse valve at the base of the tongue which can seal off the open mouth from the respiratory passage; it allows a crocodilian to open its mouth underwater to feed, and prevents water from entering the air passages. Assisting this process are the valved external nostrils which can seal the air passages when the animal is under water. These nostrils are situated on a mound at the end of the snout, allowing a crocodilian to breathe with only the tip of the snout above the surface of the water. Similarly, the eyes are elevated above the flat surface of the head, so that watch can be kept for prey or predators while remaining almost entirely submerged.

While the structure of the soft anatomy of extinct crocodilians is virtually unknown, extant ones have a fully four-chambered heart in which oxygen-rich arterial and oxygen-depleted venous blood remain separate. However, they also have an aperture between the right and left ventricles (the foramen of Panizza) which allows them to shunt blood to that part of the body where it will be warmed or cooled, according to the body's need to raise or lower its core temperature. They also have a complete muscular septum dividing the visceral from the pectoral cavity, which is thought to increase respiratory efficiency by helping to ventilate the lungs, like the diaphragm of mammals.

All living crocodilians are quadrupedal, but as the limbs are able to lift the heavy body off the ground for only brief periods, crocodilians can generally move quickly on land only in short bursts. In water, they are propelled mostly by the oar-like actions of the muscular tail, and the limbs lie alongside the body, thereby reducing drag. When floating, the limbs are held out from the body and used as stabilisers. The relatively small forelimbs have five digits, while the larger hindlimbs have only four. In all modern crocodiles the teeth are peg-like and lie in deep sockets (thecodont condition). The teeth wear, and are lost and regularly replaced throughout life by newly-erupting teeth in the sockets. Some form of parental care of the nests, eggs and young appears to be the norm in modern crocodilians.

Currently six suborders are recognised. Five are entirely restricted to fossil forms and only one, the suborder Eusuchia, contains both fossil and extant forms (Steel 1973). Within this suborder extant species are assigned to one of three families: the Crocodylidae (crocodiles), the Alligatoridae (alligators and caimans) and the Gavialidae (gharials). Of these, the crocodylids are pan-tropical, being found in all of the world's tropical regions with large permanent lakes and rivers. With the exception of a single species in China, alligatorids are confined to the Americas. Gavialids are restricted to the Indian subcontinent; one species, the false gharial (*Tomistoma schlegeli*) of the Malay Peninsula, has been transferred recently from the Crocodylidae to this family on the basis of biochemical evidence (Gatesy & Amato 1992).

These three families are distinguished mainly on the shape of the skull and the arrangements of skeletal elements at the front of the skull. These, in turn, mainly reflect the shape of the head in the species of the three families.

Crocodilids have an elongated head in which the snout is relatively long and slender, tapering from the broader hind region of the skull. Alligatorids have a blunter, less tapering snout, while that of gavialids is very long and slender, more or less round in section, and strongly demarcated from the hind region of the skull.

Australia has two native crocodilians, both of which belong to the genus *Crocodylus* of the family Crocodylidae. Characteristic of this genus is the notch or perforation in the maxilla to receive the first mandibular tooth (Pl. 9.3, 9.6), and the lack of contact between the prefrontal bone and the maxilla, and between the fronto-parietal suture and the supratemporal fenestra. Typically there are five premaxillary teeth, 16 to 19 maxillary, and 14 to 15 mandibular, teeth on each side. The fifth maxillary tooth on each side is enlarged and caniniform.

40. MORPHOLOGY & PHYSIOLOGY OF THE CROCODYLIA

Gordon Grigg & Carl Gans

EXTERNAL CHARACTERISTICS

The 22 species of extant crocodilians (Order Crocodylia) are remarkably similar. Various morphological details have been used to subdivide them into three families, the Alligatoridae (the caimans, *Caiman*, *Palaeosuchus*, *Melanosuchus*, and alligators *Alligator*), the Crocodylidae ('true'crocodiles, *Crocodylus* and dwarf crocodile *Osteolaemus*) and the Gavialidae (the Gharial *Gavialis* and False Gharial *Tomistoma*) whose affinities are uncertain within and without the group. Australia has two species of crocodiles, the saltwater or estuarine crocodile, *Crocodylus porosus* and the freshwater crocodile, *C. johnstoni*. Readable and well-illustrated reviews of the biology of world crocodilians may be found in Webb & Manolis (1989) and Ross (1989).

The remarkably homogeneous extant species are the remnants of a large radiation which peaked in the Mesozoic. Their hard parts are impressively similar to those of fossil forms of the Triassic (see Steel 1973). The three extant lineages were distinct by the Upper Cretaceous. With the birds, they are the only surviving archosaurs, the group which included the dinosaurs. Relationships between the modern crocodilians have been examined extensively (Cohen & Gans 1970; Densmore & Owen 1989; Densmore & White 1991).

These large amphibious and carnivorous reptiles inhabit tropical and subtropical lakes, rivers and coasts. They lay their eggs in nests constructed on land. Their morphology and physiology have been shaped by similar lifestyles, allowing many generalisations about the group of crocodilians as a whole. Research work, concentrating on the few more easily available species, has emphasized homogeneity within the group rather than differences among its members.

Body Form and Size

Crocodilians are sturdy lizard-shaped reptiles, with a well-armoured head and trunk and with horny skin and scales, reinforced with bony plates (Pl. 9). In modern Crocodylia, at least, the head is generally flattened and the snout elongated. The nasal capsules lie near the tip of the snout, and nostrils which can close in the external nares tend to be raised above the tip of the snout; thus submerged crocodilians are inconspicuous when drifting toward terrestrial prey. Members of the Alligatoridae tend to have broad snouts (Fig. 40.1A, B), whereas those of the Crocodylidae range from broad to long and slender (Fig. 40.1C, D). In gavialids the snout is extremely slender (Fig. 40.1E, F).

Crocodilians have laterally compressed tails, webbed hind feet, and the nostrils, eyes and ears are placed high along the head and snout, all consonant with aquatic habits (Pl. 9.3, 9.7). Skull and jaws are solid and together with the strong peg-like teeth can maintain an effective hold on prey. The palatal flap, a rigid plate of tissue at the rear of the oral cavity, closes the posterior buccal space (oesophagus and glottis) against the entry of water. A well-developed hard palate permits ventilation from nostril to glottis, bypassing the mouth (Fig. 40.2). The nostrils can be closed tightly during submergence.

Adult crocodilians are large and species show an enormous size range. The smallest are species of *Palaeosuchus* and *Osteolaemus* which grow to an adult size of 1 to 1.5 m. Males of *Crocodylus porosus* more than 7 m in length and weighing perhaps 2000 kg, are the largest of the extant reptiles. Crocodilians show a

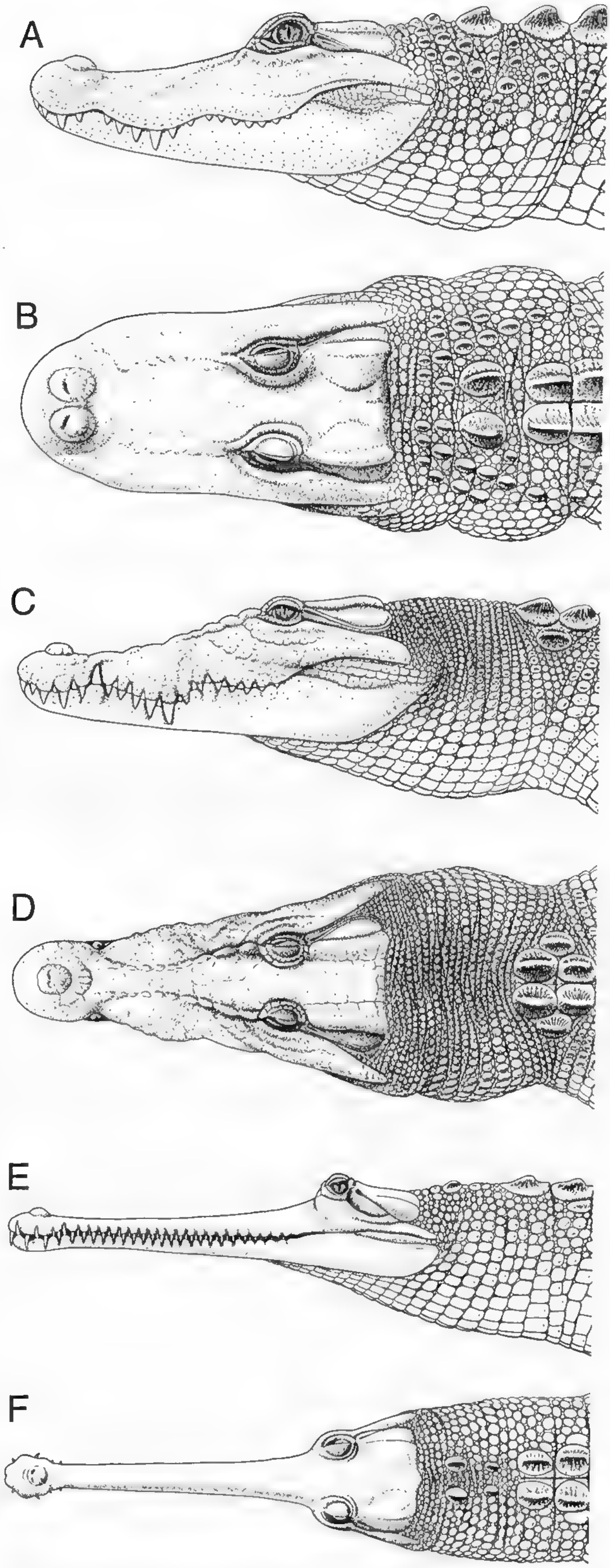

Figure 40.1 Head shapes and dentition in Crocodylia. **A**, **C**, **E**, lateral views; **B**, **D**, **F**, dorsal views; **A**, **B**, Alligatoridae; **C**, **D**, Crocodylidae; **E**, **F**, Gavialidae. [D. Kirshner]

pronounced sexual dimorphism. Males grow larger and often more rapidly than females, even though they attain sexual maturity at an equivalent age (Pl. 9.1). Apart from size, there is no external indication of sex. The alimentary, urinary and reproductive systems open to the exterior via the midventral longitudinal slit of the cloaca.

Skin and Scalation

The skin is covered with keratinised scales, or scutes, many of which are reinforced with bony plates, or osteoderms. Interspecific differences in scales can be used for identification (Brazaitis 1987). Osteoderms are most prevalent in the dorsal and nuchal scutes which commonly bear conspicuous ridges, and in the belly scales of some species. The nuchal, dorsal and some of the rectangular and keeled scutes are covered by hard, wear-resistant beta-keratin. Since they are vascularised, scutes may act as heat absorbers or radiators (see Thermoregulation). The fields of scutes are embedded in the intermediate skin under a covering of alpha-keratin which provides an important barrier to water and electrolyte exchange. This facilitates the homeostasis of body fluids in a wide range of salinities (see Salt and Water Regulation). Flexible skin covers the neck and the flanks, whereas the abdomen and sides of the tail are sheathed in large, flat, squarish scutes arranged neatly in rows.

Crocodilian scales bear a pore that is generally thought to be sensory, analogous to the lateral line of fishes. Higher densities of small scales around the head, particularly on the upper and lower jaws (Pl. 9.3, 9.6), concentrate this supposed mechanosensory apparatus. Alternatively, the pores could be a source of a detergent-like or oily substance (perhaps a modification of betakeratin) since mud seems to flush off them easily in the wild.

Often the prominent paired gular and paracloacal integumentary glands are everted at capture. The gular glands lie in ventral folds of skin at the angles of the jaw and the paracloacal glands are embedded in the lateral walls of the cloaca. Their holocrine secretions are primarily lipid. The histology of the gular glands has been described in *Alligator mississippiensis* and *C. porosus* (Weldon & Sampson 1988; Wright & Moffat 1985). Secretions analysed from both pairs of glands in most crocodilian species contain sterols, free fatty acids, triglycerides, steryl esters and aliphatic alcohols and, commonly, hydrocarbons (Weldon, Scott & Tanner 1990; Weldon & Tanner 1991). The proportions differ between sexes, and among glands and individuals for the gular and paracloacal glands, suggesting different functions. Secretions, presumably from the paracloacal glands, could be detected in the air after a headslap in *A. mississippiensis*; an oily sheen, then appeared on the water surface (Vliet 1989). LeBuff (1957) suggested that alligators spray secretions from the gular glands while bellowing, but the volume of material would seem to be insufficient for that. Wright & Moffat (1985) speculated on a glandular role in predator deterrence. Immature alligators respond to exudates of both glands by increased rates of gular pumping (Johansen & Wellington 1982; see Sense Organs), suggesting that a pheromonal role in intraspecific communication is quite likely. Pooley (pers. comm.) noted that female *C. niloticus* rub their chin glands over males before nesting, and during courtship each investigates the other's head and tail base and rubs its gular area over the other's head (Kofron 1991). Clearly pheromonal chemistry deserves more study.

MUSCULAR SYSTEM

The crocodilian muscle masses seem to reflect the general tetrapod pattern (Frey 1988a, 1988b). Until recently, they have been described mainly on the basis of juveniles, in spite of the fact that their proportions change allometrically. Also, the few studies of functional analysis reflect particular species. The obvious differences in muscular types or relative masses among species have yet to be documented.

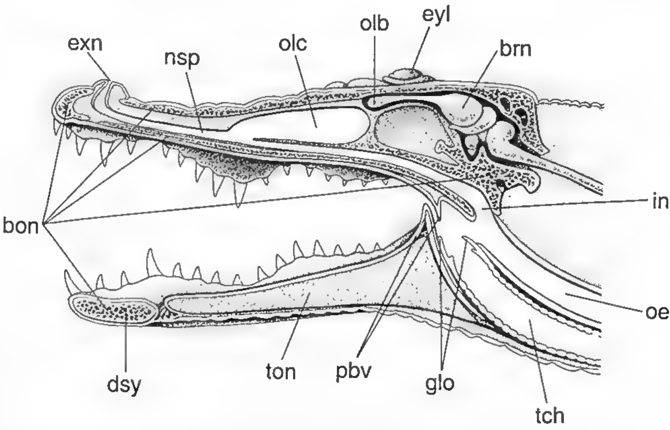

Figure 40.2 Sagittal section of the head of *Crocodylus porosus*. **bon**, bones of the skull; **brn**, brain; **dsy**, dentary symphysis; **exn**, external nares; **eyl**, eyelid; **glo**, glottis; **ina**, internal nares; **nsp**, nasal passages; **oes**, oesophagus; **olb**, olfactory bulb; **olc**, olfactory chamber (location of conchae); **pbv**, palato-buccal valve; **tch**, trachea; **ton**, tongue. [D. Kirshner]

The crocodilian muscles reflect the general short fibre phenomenon (Gans & Gaunt 1992). Jaw closing muscles appear to be much more massive than the openers and the jaws of even of medium-sized specimens can be held shut comparatively easily, especially when coupled with the leverage attainable by grasping the snout. Much of aquatic propulsion depends on the axial musculature. However, terrestrial locomotion is effected by the muscles of limbs and the associated girdles. Some ventilation is powered by the intercostals, but much of inhalation reflects the contraction of the *m. diaphragmaticus*, a striated muscle that connects the liver to the pelvic girdle (Gans & Clark 1976).

SKELETAL SYSTEM

The crocodilian skeleton is typical of that of tetrapods in general and of archosaurs in particular, with the skull and pelvis particularly specialised (Romer 1956). Also of interest are the structure of the head vertebrae (atlas and axis), the osteoderms, and the gastralia, or stomach ribs, which protect the ventral surface. Steel (1973), Iordansky (1973) and Langston (1973) provide useful reviews of the structure of both modern and extinct crocodilian skulls.

As archosaurs, crocodilians are diapsid, although the post-temporal fenestrae are reduced. Palatal and external mandibular fenestrae (Fig. 40.3) and ossified laterosphenoids are present. The wall of the braincase is ossified, but supratemporals and postfrontals are absent. The pterygoid and quadrate adhere tightly to the lateral wall of the braincase and the otic notch closes posteriorly. All species lack a parietal (pineal) foramen. The premaxillae are expanded postero-dorsally, isolating the external nares from the maxillae. Internal nares are prolonged posteriorly by a secondary palate formed of the palatal processes of the premaxillae, maxillae, palatines and pterygoids and the secondary choanae open within the pterygoids (Fig. 40.3).

The premaxilla, maxilla and dentary bear peg-like conical thecodont teeth (Iordansky 1973). The largest teeth of the upper jaw are premaxillary 4 in the Alligatoridae, premaxillary 5 in the Crocodylidae, and maxillary 9 and 11 and dentary 1, 4, 11 and 12 throughout this group. The vertically undulating jawline coincides with the distribution of the largest teeth, thus accentuating the pseudoheterodonty, particularly in the shorter-snouted species. In the long-snouted, fish-eating crocodilians, the teeth are more uniform in size, approaching a homodont condition, and the jawline is straight rather than undulating. In the Alligatoridae, the 4th dentary tooth fits into a pit in the upper jaw at the junction of premaxilla and maxilla, and the mandibular tooth rows lie inside the upper tooth rows at occlusion. In the Crocodylidae and Gavialidae, upper and lower teeth alternate at occlusion, and the 4th dentary tooth fits into a lateral notch at or near the junction of the pre-maxilla with the maxilla. Thus the teeth of crocodiles are far more conspicuous than those of alligators when the mouth is

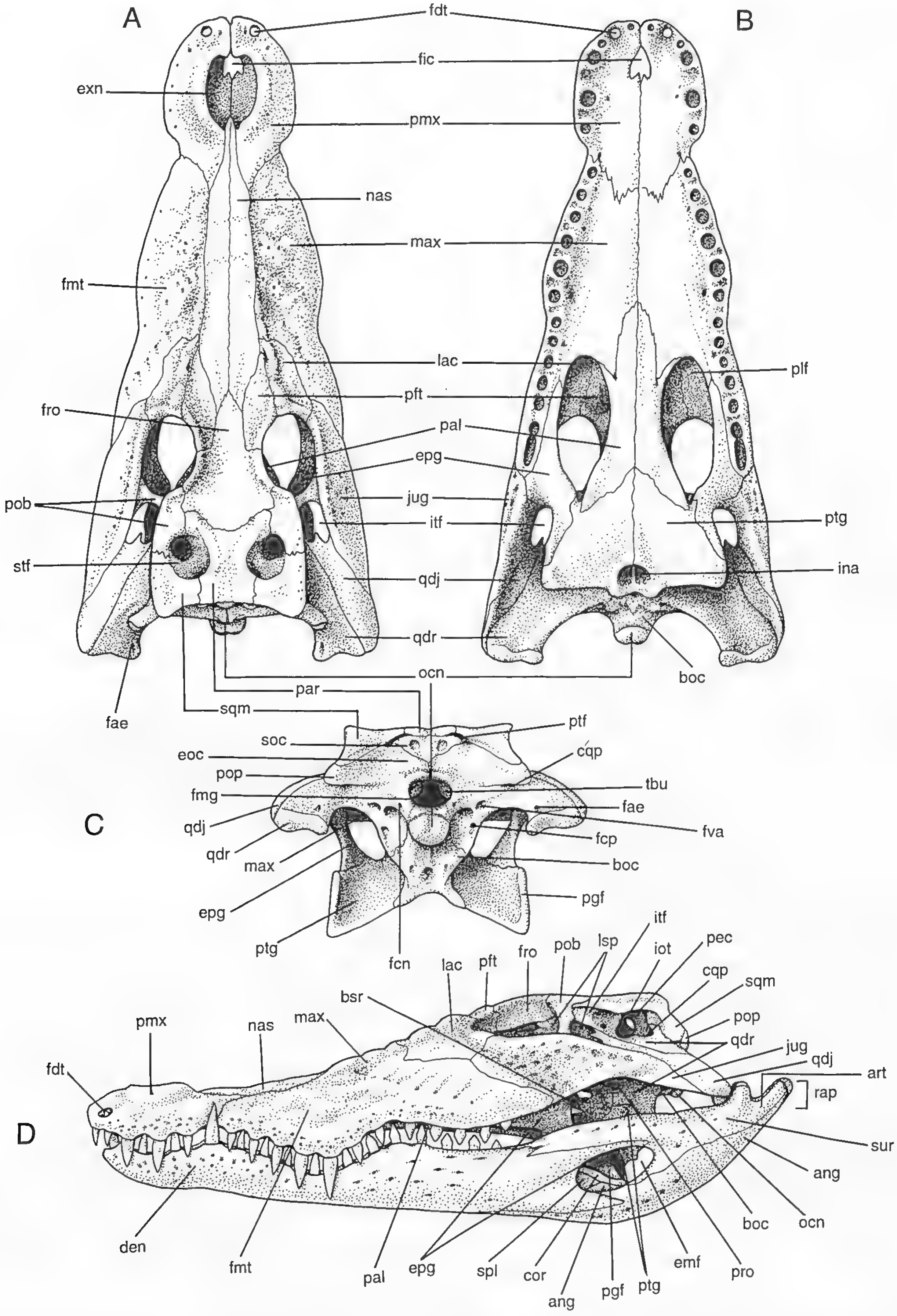

Figure 40.3 Skull of *Crocodylus porosus*. **A**, dorsal view; **B**, ventral view; **C**, posterior view; **D**, lateral view. **ang**, angular; **art**, articular; **boc**, basioccipital; **bsr**, basisphenoid rostrum; **cor**, coronoid; **cqp**, cranio-quadrate passage; **den**, dentary; **emf**, external mandibular fenestra; **eoc**, exoccipital; **epg**, ectopterygoid; **exn**, external nares; **fae**, foramen aëreum; **fcn**, foramen of cranial nerve XII; **fcp**, foramen caroticum posterius; **fdt**, foramen for first dentary tooth; **fic**, foramen incisivum; **fmg**, foramen magnum; **fmt**, swelling over alveolus of fifth maxillary tooth; **fro**, frontal; **fva**, foramen vagi; **ina**, secondary choanae (internal nares); **iot**, incisura otica; **itf**, inferior temporal fossa; **jug**, jugal; **lac**, lacrimal; **lsp**, laterosphenoid; **max**, maxilla; **nas**, nasal; **ocn**, occipital condyle; **pal**, palatine; **par**, parietal; **pec**, transverse canal between middle ear cavities; **pft**, prefrontal; **pgf**, lateral pterygoidal flange; **plf**, palatal fenestra; **pmx**, premaxilla; **pob**, postorbital; **pop**, paraoccipital process; **pro**, prootic; **ptf**, posttemporal fenestra; **ptg**, pterygoid; **qdj**, quadratojugal; **qdr**, quadrate; **rap**, retroarticular process; **soc**, supraoccipital; **spl**, splenial; **sqm**, squamosal; **stf**, superior temporal fossa; **stp**, supraoccipital; **sur**, surangular; **tbu**, tympanic bulla. [D. Kirshner]

closed. Teeth generally are replaced continuously with new ones growing from below in the same socket, but this process slows down and stops in older individuals; some of the largest individuals are likely to be edentulous.

Cranial sculpturing becomes more complex with age as a result of secondary dermal ossifications on the dorsal surface. Some species (*Ostaeolaemus* and *Palaeosuchus palpebrosus*) have palpebral osteoderms in the upper eyelids. The middle ear region is modified extensively, and the quadrate is inclined so that the hinge of the jaw is displaced far posteriorly. Cranial growth is allometric and the naris-eye dimension increases several times faster than that between eye and condyle. As the olfactory bulbs lie close to the nares, the proportions of the brain reflect those of the skull.

Many cranial bones are pneumatised, and have gas-filled cavities connected to the Eustachian tubes of the middle ear and the nasal passages. These may equalise pressure in the inner ear (Colbert 1946), or isolate the inner ear from underwater sounds when listening above water (Iordansky 1973). However, pneumatisation also reduces the cranial mass (and inertia), while maintaining its strength, which is an important consideration in both buoyancy and feeding.

The nine cervical vertebrae are keeled ventrally. The last two to five of the 15 to 16 dorsal vertebrae lack free ribs. The caudal vertebrae bear relatively long neural and haemal spines, as well as chevron bones on the anterior two-thirds. The cervical ribs are solid and the dorsal ones articulate ventrally with two partly calcified elements, the ventral-most of which reaches the sternal system. The most superficial gastralia are located between the sternal region and the pelvic girdle. The shoulder girdle is simple and plate-like, and the three components of the pelvic girdle radiate from the articular fossa.

LOCOMOTION AND BUOYANCY

Crocodilians are amphibious, but travel most easily in water which they traverse with sinuous movements of the strong, laterally compressed tail, holding the limbs at the sides. On land they have several gaits (Brinkman 1980; Kälin & Knüsel 1944; Parish 1987): walking, high walking with the body held clear of the ground, running and, in some species, a galloping gait in which limbs of the two sides move in unison, driven by dorsoventral flexion of the vertebral column (Fig. 40.4). They also undulate down steep slopes. Galloping is a conspicuous escape movement in *C. johnstoni* (Webb & Gans 1982). Although they can travel at great speed, such bursts are shortlived as they are sustained by anaerobic metabolism. Crocodiles can travel substantial distances both overland (Pooley & Gans 1976; Webb pers. comm.) and by sea (Walsh & Whitehead 1993).

They are excellent swimmers, under water or at the surface. When chasing or fleeing from other individuals, as is common in the breeding season, they may plane along the water surface, driven by the thrashing tail (Pl. 9.2). The anterior half of the chest and abdomen serve as a hydroplane, and creating significant bow wave and wake in the process. The tail can be used to accelerate the body completely out of the water or to launch a rapid lunge at prey. However, most movements made by crocodilians are silent and surreptitious, often with only the nostrils, eyes and the top of the skull platform emergent. They brace themselves against the bottom with the hind legs and tail to anchor themselves in a current and use tidal currents to provide low energy transport up and down estuaries.

Crocodilians manage their buoyancy very skilfully. They are denser than water (Kirshner 1985), and achieve neutral buoyancy by appropriate inflation of the lungs. Shallowly breathing crocodilians are able to float at the water surface for long periods, the water line constant within a couple of millimetres just below the eye (Fig. 41.3). They are able to lie immobile on the bottom between breaths for many minutes, or hours in larger individuals (see Respiration). It is unlikely that pulmonary volume can be modified by muscular contraction during a dive, but negative buoyancy increases with depth as the lungs are compressed and as oxygen is removed and replaced with a smaller volume of carbon dioxide.

Most larger crocodilians accumulate gastroliths (stomach stones), including individuals which live in areas where stones are uncommon, implying that some effort may be made to collect them. Larger crocodiles have a larger burden of stones (Cott 1961). Buoyancy hypotheses have been considered in some detail by Kirshner (1985) in relation to experiments performed on juvenile *C porosus*. The gastroliths do not increase specific gravity, because the crododiles compensate for added load by inhaling more deeply. Consideration of ontogenetic changes in body proportions tends to support the views of Cott (1961) and Brander (1925), who argue that the stones may function as a counterpoise for the weight of the head, which increases proportionally with increasing age.

Some authors have suggested that the gastroliths have digestive significance (see Chapter 41), analogous to the role of gravel in the avian gizzard in the trituration of foods. This hypothesis is, however, unconvincing and the counterpoise one remains most likely (Kirshner 1985).

FEEDING AND DIGESTION

Crocodilians are carnivorous, sit-and-wait predators, which rely on swift attack from the water to seize large terrestrial prey and immobilise it before it is swallowed. Smaller prey is commonly taken by a sideways strike of the head, which reduces the change of cranial momentum. It may then be broken up by being lifted from the water and 'whiplashed', in a similar manner to that used by monitor lizards. Large prey may be stored until it starts to disintegrate. In cooperative feeding, several individuals grasp a single prey item and dismember it by twisting in opposite directions.

The hard palate and the palatal flap at the back of the buccal cavity allow food to be held in the mouth for long periods without interrupting the respiratory flow, while prey is dismembered or drowned. Food is commonly picked up near the anterior tips of the jaws. It is repositioned and shifted toward the oesophagus, by inertial feeding (Gans 1969), in which the jaws quickly release and shift the food to a new position before it can fall far. This is obviously more effective in air than in water and, in addition to breathing, may explain why ingestion usually occurs with the head above the water. The head is then lifted clear of the water and the tail is lifted as a counterbalance if the prey object is large. To pick up food on land, a crocodilian turns the head and much of the body to the side, as the neck is comparatively inflexible (Fig. 41.2).

The crocodilian gut is comparatively short and simple and the viscera are typically reptilian (Chiasson 1962). General reviews of digestion and the digestive system in reptiles are given by Dandrifosse (1974), Parsons & Cameron (1977), and Guard (1980). Chunks of food are swallowed whole and pass to the stomach via a long oesophagus. The stomach lies posterior to the heart, which is positioned about midway between the front and rear limbs. The cardiac sphincter occurs at the junction of the oesophagus with the cardiac sac at the left anterior corner of the stomach. The cardiac sac is divided into left and right halves by a thick collar of muscle and spongy tissue, which may operate as a gizzard. The pyloric region is much smaller, and opens to the duodenum via a pyloric sphincter (Chiasson 1962). It is likely that the cardiac (or fundic) stomach has a glandular epithelium which secretes HCl and pepsinogen, whereas the pyloric portion secretes mucus. As crocodilians do not secrete chitinases (Jeuniaux 1963), chitinous and keratinous remains, snail opercula and fur accumulate in crocodilian gut contents. Such indigestible remnants are likely to be cast out via the mouth, as in many avian species. Though data from the wild are lacking, ejection of hair and fur balls by captive occurs routinely.

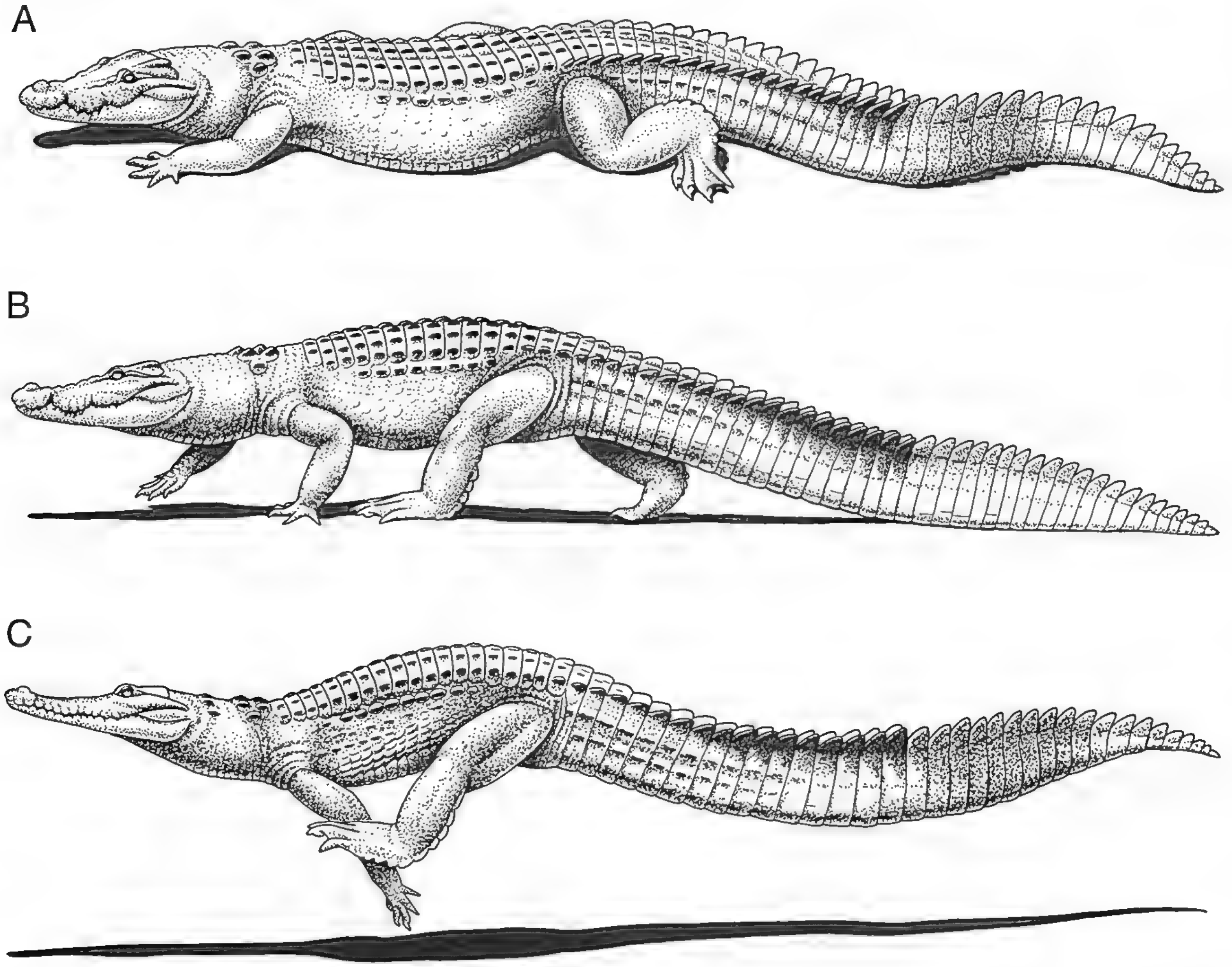

Figure 40.4 Gaits of crocodiles on land. A, *Crocodilus porosus* walking; B, *C. porosus* high walking; C, *C. johnstoni* galloping. [D. Kirshner]

Crocodilians digest flesh and bones fully, including that from fresh carcasses, and cache only very large prey for its initial dismemberment. Concerning control mechanisms, gastrin/cholecystekinin-like hormones are secreted by the pyloric mucosa, and emphasise the similarity of Crocodylia to other vertebrates. Further studies are needed of the nature of digestive enzymes and the control of digestion.

THERMAL RELATIONS

Crocodilians are ectotherms. Their body temperature reflects their behaviour in relation to the thermal heterogeneity of the habitat (see Chapter 41), modified to some extent by physiological mechanisms. Reptilian thermoregulation has been reviewed comprehensively by Huey (1982), Bartholomew (1982) and Avery (1982). The thermal relations of crocodilians are affected markedly by their large size and by the long time they spend in water. Except for large individuals (Grigg 1977), body temperatures will therefore be at or near ambient water temperature much of the time, commonly 25° to 28°C for *C. porosus* in northern Australian estuaries (Messel *et al.* 1979–85). During the day, crocodilians often leave the water to bask (Pl. 9.4). Rates of temperature increase are governed by thermal time constants, which are strongly mass-related (Grigg, Drane & Courtice 1979), and thus heating is quite slow in large individuals. Radiotelemetered and directly observed values from animals on a thermal gradient or in a naturalistic captive environment show that temperature in active individuals ranges from about 25° to 35°C, and mainly between 30° and 33°C. These values are comparatively low for reptiles. Indeed, upper lethal temperatures seem to be in the vicinity of 35°C (Grigg pers. obs.). As crocodilians live in many places where ambient air temperatures are higher than this, they need to avoid high temperatures frequently by seeking shade or by returning to the water. *Crocodylus porosus* sometimes coat themselves with a thick layer of mud, which presumably assists in reducing insolation.

Thermoregulatory behaviour seems to be more pronounced in alligators and caimans, which inhabit thermally variable environments, than in crocodiles (Lang 1987). Basking, shade-seeking, and shifts into and out of water are the most important thermoregulatory behaviours; size is implicated also, particularly whenever thermoregulation is augmented by physiological mechanisms. Large individuals have some measure of thermal stability because of their high thermal inertia during heating and cooling (Grigg 1977; Grigg, Taplin, Harlow & Wright 1980); no studies in the wild have been reported. Also, large reptiles in general may heat rapidly but cool more slowly (thermal hysteresis; Fraser & Grigg 1984) as the result of lower thermal conductance during heating. Thermal hysteresis has been documented in the Alligatoridae (Smith 1975a, 1976c, 1976d, Smith, Standora & Robertson 1984) and Crocodylidae (Grigg & Alchin 1976; Grigg *et al.* 1980; Loveridge 1984). The change in thermal conductance is affected by control over dermal blood flow (Grigg & Alchin 1976), particularly flow to the scutes of the limbs (Turner & Tracy 1983) which are particularly well supplied with blood vessels. The importance of thermal hysteresis in the wild animals remains to be determined.

Crocodilians sometime select specific body temperatures with a degree of precision. Thus larger hatchlings of both Alligatoridae and Crocodylidae in a thermal gradient select higher temperatures (+1.5° to 4.0°C) after feeding and lower ones during fasting (reviewed by Lang 1987). Increased temperatures may reduce digestion time. Selection of lower temperatures may conserve energy in larger individuals because of the effect of temperature on metabolic rate. Grigg (1978) and Smith (1975b) have reported quite high Q_{10} values in crocodilians (2.7 to 3.1), suggesting markedly enhanced energy conservation at low body temperatures. Another example of selection of high temperatures is described Lang (1987) as 'behavioural fever', in which juvenile American alligators increased their temperatures by 2° to 5°C following infection with the pathogenic bacterium, *Aeromonas hydrophila*. The thermophily has been interpreted as a mechanism for resisting the infection, in a manner analogous to the endothermic fever developed in infected birds and mammals.

There are some exceptions to the preceding generalisations about crocodilian thermoregulation. Some caimans, such as both species of *Palaeosuchus*, live in jungle streams where the closed canopy suggests they have minimal, if any, basking behaviour. They may construct their nests near termite mounds, the warmth of which may facilitate incubation of the eggs (Magnusson, Lima & Sampaio (1985); see also Reproduction). Similarly, in winter the body temperature of American alligators may drop to 5°C in very cold water. Some have been observed under an ice-layer, but they maintain an open breathing hole (Brisbin, Standora & Vargo 1982). *Crocodylus johnstoni* in northern Australia and *C. niloticus* in southern Africa also become dormant in the cooler, dry season (Walsh 1989; Pooley 1982), and retreat into caverns excavated or enlarged in river banks.

RESPIRATION AND CIRCULATORY SYSTEM

Lungs and Ventilation

The paired lungs are well developed and well perfused, and lie in the thorax, served by a trachea which originates anteriorly in a glottis which can be closed. The latter lies on the floor of the posterior pharyngeal cavity and is supported by the cartilaginous hyoid plate. Interestingly, in large *C. porosus* and perhaps in other species, the trachea forms a large loop in the upper thorax, reminiscent of a water-trap, but its function is unknown. The anatomy and functioning of the respiratory system have been described by Gans & Clark (1976). During ventilation the glottis is lifted into close proximity to the internal nares, and the gases then pass above the secondary palate to and from the exterior via the external nares (Fig. 40.2). The palatal flap at the rear of the buccal cavity prevents the entry of water into the posterior pharynx, even when the open mouth holds prey. During swallowing, the glottis is closed and depressed, and the palatal flap opened.

In crocodilians, the liver is connected to the body wall by an annulate connective tissue sheet which divides the pleural and visceral cavities (Fig. 40.5). Inspiration is effected by contraction of portions of the intercostal muscles which distend the rib cage, and of the *m. diaphragmaticus* which retracts the liver caudally. Expiration is by contraction of the superficial intercostal muscles, and of the transverse abdominal muscles which move the liver forward, thereby decreasing the pleural volume.

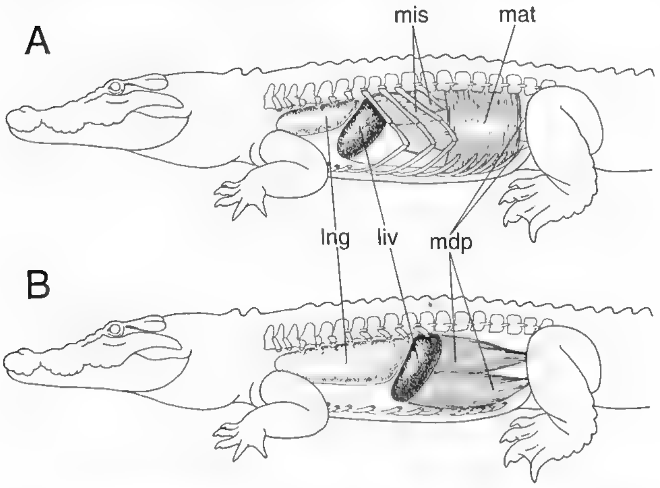

Figure 40.5 Respiration in *Crocodilus porosus*. **A**, expiration; **B**, inspiration. **lng**, lungs; **liv**, liver; **mat**, *m. abdominalis transversus*; **mdp**, *m. diaphragmaticus*; **mis**, *m. intercostalis superficialis*. [D. Kirshner]

Apart from their importance as an oxygen store and a carbon dioxide sink, crocodilian lungs are important in controlling buoyancy. Indeed, the volume of the lungs in a swimming or diving individual is determined by buoyancy requirements, not oxygen store demands (Kirshner 1985). Wright & Kirshner (1987) report that whereas the relationship of oxygen requirements with body mass has an exponent of approximately 0.75, buoyancy requirements scale with body mass at 0.91, almost in direct proportion. This implies an increased maximum duration of aerobic dives in larger individuals. Thus, at 25°C a resting 1000 kg animal would be able to undertake aerobic submergences of approximately 110 minutes, compared to 20 minutes for a 1 kg animal.

Heart and Circulation

Functionally the crocodilian heart appears to be the most sophisticated of all vertebrate hearts. Unlike other reptiles, crocodilians have a complete four-chambered heart with two atria and two ventricles. Structure and pressure balance are similar to those of birds and mammals, with a high pressure (60 to 100 mm Hg) systemic circuit and a low pressure (15 to 20 mm Hg) pulmonary circuit. However, as detailed below, the system also incorporates a number of unusual features which endow strong pulmonary bypass capabilities.

The major anatomical and functional specialisations (Fig. 40.6) have been the focus of much interest and speculation for more than 150 years (Panizza 1833b). Firstly, the left systemic arch persists as a small vessel which leaves from the right ventricle, alongside the pulmonary arch! It runs dorso-laterally above the lungs to join the dorsal aorta (right systemic arch) via a small connecting vessel. However, anatomy suggests that most of its flow would be directed towards the coeliac artery rather than the dorsal aorta (Fig. 40.6). Secondly, left and right systemic arches communicate where they cross, via a small foramen of Panizza in their common wall. Functional aspects of this unusual anatomy have been studied by many workers in many species (White 1970; Webb 1979; Greenfield & Morrow 1961; Sabatier 1873; Pettersen, Axelsson & Nilsson 1992; Grigg & Johansen 1987; Axelsson, Fritsche, Holmgren, Grove & Nilsson 1991).

The persistence of the left systemic arch and its connection from the right ventricle to the coeliac artery and the dorsal aorta affords a pulmonary bypass shunt (Grigg 1989, 1992). Normally, blood enters the left aorta from the right aorta via the foramen of Panizza, and the valves at the base of the left aorta remain closed to the right ventricle because its pressure remains lower than that in the left aorta. Hence, the left aorta normally carries well-oxygenated blood which reflects its origin from the right aorta. However, towards the end of aerobic breath-hold dives, and probably in anaerobic dives as well, the blood pressure rises in the right ventricle under the influence of pulmonary circuit vasoconstriction. At this stage, some low oxygen blood, otherwise destined for the lungs, is directed into the left aorta and then towards the gut; it does not mix with any of the oxygenated blood until downstream of the dorsal confluence, and thus preserves a well-oxygenated supply for the head and brain. The circumstances under which this extraordinary pulmonary bypass is used under natural conditions still require study, perhaps by radiotelemetry of the flow from the major vessels.

Grigg (1989, 1992) has speculated that the shunt pathway may even allow a complete shutdown of the pulmonary circuit, perhaps during anaerobic respiration, and the whole body is then supported by perfusion driven by the single right ventricle. Indeed, Pettersen *et al.* (1992) experimentally blocked both pulmonary arteries and achieved this result, with reversed flow through the foramen of

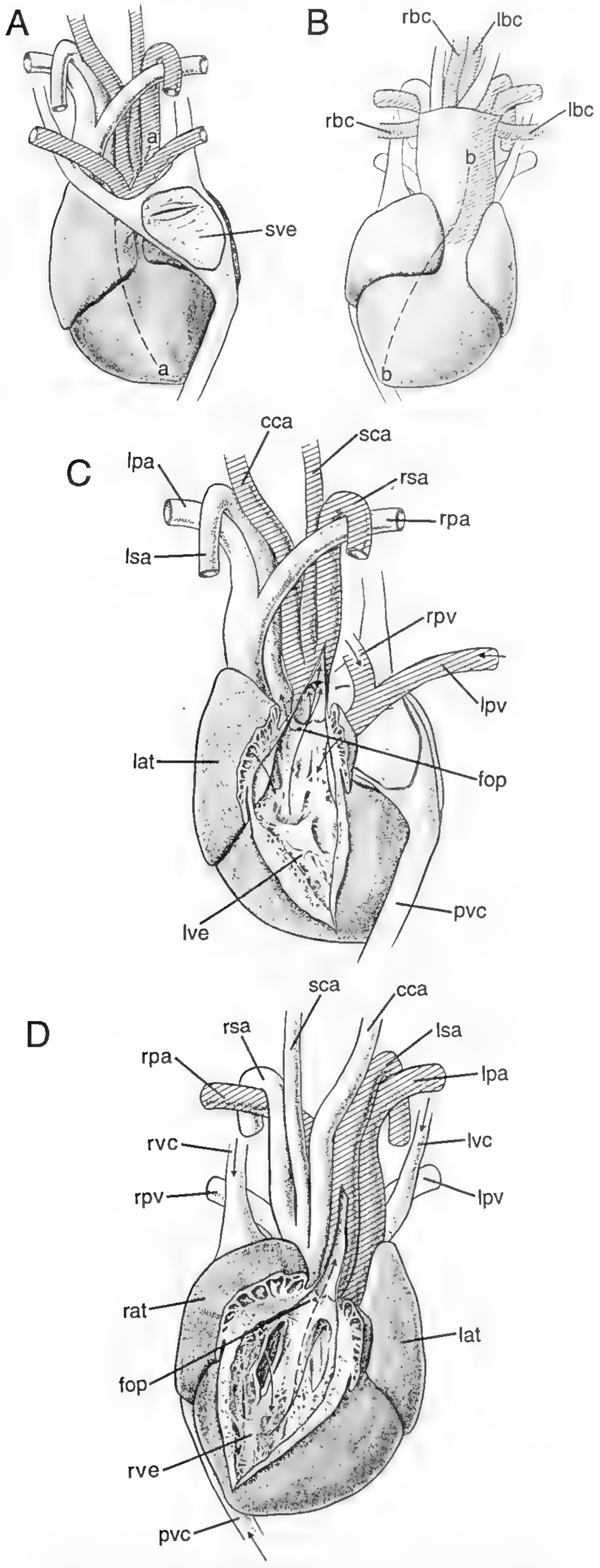

Figure 40.6 Morphology of the heart of *Crocodilus porosus*, shown in dorsal view (**A**, **C**), and ventral view (**B**, **D**). In **B** and **D**, the heart is opened along lines a-a and b-b shown in **A** and **C** respectively. **B**, arrows indicate blood flow during normal breathing, from left atrium to left ventricle to right systemic arch, and through the foramen to the left systemic arch; **D**, solid arrows indicate blood flow during normal breathing, from right atrium via the right ventricle to the pulmonary arch. The dashed arrow shows the direction of flow via the pulmonary bypass shunt. **cca**, common carotid artery; **fop**, foramen of Panizza; **lat**, left atrium; **lbc**, left bronchus; **lpa**, left pulmonary vein; **lpv**, left pulmonary vein; **lsa**, left systemic arch; **lvc**, left anterior vena cava; **lve**, left ventricle; **pvc**, post vena cava; **rat**, right atrium; **rbc**, right bronchus; **rpa**, right pulmonary vein; **rpv**, right pulmonary vein; **rsa**, right systemic arch; **rvc**, right anterior vena cava; **rve**, right ventricle; **sca**, subclavian artery; **sve**, sinus venosus. (After Grigg 1989) [J. Jeffery]

Panizza, although whether this occurs under natural circumstances is unknown.

Aside from the heart and associated blood vessels, the blood system is essentially similar to that in other reptiles. A renal portal system is present.

The extensive lymphatic system is the most complex and modified among the reptiles (Ottaviani & Tazzi 1977). It differs from those of other reptiles in the absence of the great sinuses and has finer and more plexiform trunks which are generally similar to those of mammals. As the flow of lymph is driven largely by hydrostatic pressure, the similarity may reflect its association with a blood vascular system which operates at higher pressures than those of most reptiles.

Gas Transport

Oxygen is transported by haemoglobin contained in oval nucleated erythrocytes. The mean haematocrit of a sample of 96 wild individuals of *C. porosus* was 24.8% (range 19.1 to 31.3%; Gruca & Grigg 1980), but this declined in captivity, presumably as a correlate of reduced activity. Grigg & Cairncross (1980) described oxygen equilibrium curves for *C. porosus* over a range of temperatures and carbon dioxide tensions (Fig. 40.7A, B). They reported a general descriptive equation:

$$\log_{10} P_{50} = 0.4163 + 0.0200\, T\ {}^{o}C + 0.3763\ \log_{10}\ P_{CO_2}$$

Of particular interest, however, is the strong sensitivity of oxygen affinity to carbon dioxide (Bauer & Jelkman 1977) and a comparatively low 'fixed acid' Bohr effect. Grigg & Gruca (1979) have interpreted this as an adaptation to diving which relies on anaerobic rather than aerobic metabolism. Rapid blow-off of carbon dioxide at the end of a dive results in a rapid left-shift of the curve and facilitates reloading of the blood with oxygen. Metabolism of accumulated lactic acid, on the other hand, takes much longer and any effect on the oxygen equilibrium curve would be slow. This interpretation was supported by Seymour, Bennett & Bradford (1985). Studying solutions of crocodilian haemoglobin, Bauer & Jelkman (1977) also reported low sensitivity to changes in pH, and, most significantly, the lack of 2,3-DPG or other red cell organic phosphates (RCOP). In most vertebrates RCOPs act as ligands, which bind to haemoglobin within the red cells and reduce the very high affinity of unliganded pigment into the physiological range. Grigg & Gruca (1979) confirmed this lack in *C. porosus* and *C. johnstoni*. Noting that dialysis of human haemoglobin to remove bound RCOP also enhances the sensitivity of oxygen affinity of the haemoglobin to carbon dioxide and reduces the 'fixed-acid' Bohr effect (Duhm 1976). Grigg & Gruca proposed that the loss of RCOP, which seems to be a general occurrence in crocodilians post-hatching, may provide the mechanism for the adaptive, low 'fixed acid' Bohr effect described above. Interestingly, *C. porosus* has two RCOPs during embryonic life, and two distinct haemoglobins (Grigg, Wells & Beard 1993). In early embryos, haemoglobin is present and sensitive to ATP which is present in high levels. Later, embryonic haemoglobin is replaced by the adult type, ATP is replaced by 2,3-DPG, but in small quantities (Fig. 40.8A, B) and, intriguingly, oxygen affinity of the adult haemoglobin type is unaffected by either ATP or 2,3-DPG. It is, of course, strongly affected by carbon dioxide.

As might be expected from a high dependence on anaerobically-supported activity, crocodilian blood has a high capacity for carrying and buffering carbon dioxide (Grigg & Cairncross 1980; Seymour *et al.* 1985).

Gas Exchange and Metabolism during Diving

Cutaneous gas exchange is negligible in *C. porosus* (Wright 1986) and should be in other species also, as *C. porosus* is among the species with least dermal ossification. Biphasic ventilation of the

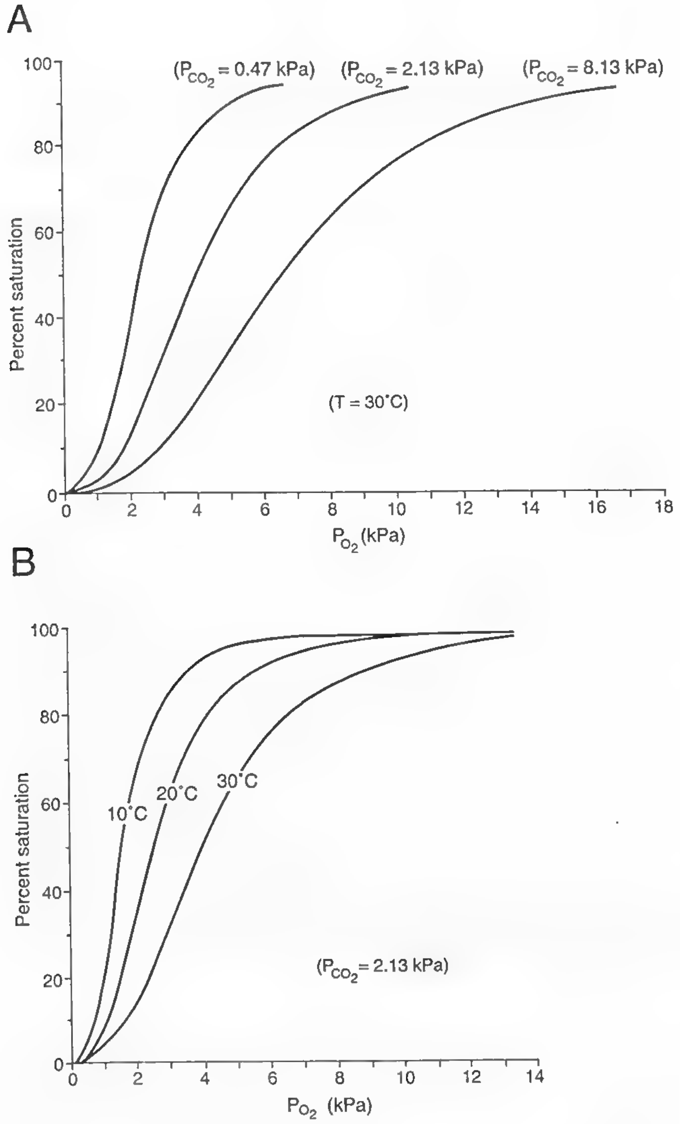

Figure 40.7 Respiratory relationships in *Crocodylus porosus*. **A**, the effect of increased P_{CO_2} on blood oxygen levels; **B**, the effect of temperature on blood oxygen levels. (After Grigg & Cairncross) [W. Mumford]

lungs is periodic, interrupted by apneas during which pulmonary pressures (of submerged animals) are slightly above ambient. At least in captivity, crocodilians frequently rest for hours submerged in shallow water and periodically lift the snout to the surface to ventilate the lungs. During such behaviour, juvenile *C. porosus* may be supported entirely aerobically in 10 to 12 minute voluntary dives (Wright 1985). Lung P_{O_2} falls from approximately 120 to 140 mm Hg, while P_{CO_2} rises from approximately 20 to 40 mm Hg. Meanwhile, arterial oxygen saturation falls from 95% to approximately 30%, but blood lactate remains throughout at resting levels of about 1 mMol l^{-1}. At any disturbance, however, bradycardia is initiated and blood lactates rise three or four fold very rapidly, indicating the implementation of anaerobic metabolism. If dives are prolonged by force, blood lactates rise to 20 mMol l^{-1} after 40 to 50 minutes. In larger individuals, the time period of these events is much slower, as discussed above.

The acidbase status of *C. porosus* has been examined at rest and after exhaustive exercise (Seymour *et al.* 1985). Whereas normal plasma pH is approximately 7.43, it falls to 7.0 after 5 minutes of exercise; lactate rises to 20 to 30 mMol l^{-1}. Struggles associated with capture cause pH values to drop as low as 6.4, but recovery occurs by respiratory compensation as carbon dioxide is excreted, followed by metabolic reduction of lactate. Full recovery may take 1 to 2 days. The frequent death of large crocodilians after a prolonged struggle at the time of capture most likely reflects a pronounced lactic acidosis.

SALT, WATER BALANCE AND EXCRETION

Ionic balance has been reviewed recently by Taplin (1988) and Mazzotti & Dunson (1989). Species of the Alligatoridae and Crocodylidae are good ionic and osmotic regulators. They maintain plasma osmotic pressures of approximately 300 mOsm l^{-1} and the ionic composition is similar between species. The skin provides a significant barrier to the movement of both water and ions. With a smaller surface area/mass ratio, larger individuals can tolerate exposure to osmotic stress for longer than smaller ones when osmotic values depart from normal. Maintenance of internal homeostasis is frequently managed against a threat of flood or drought in fresh and salt water respectively.

Whereas most crocodilians are found in fresh water, some Crocodylidae (notably *C. porosus* and *C. acutus*) occur routinely in hyperosmotic estuarine habitats while many others are exposed at least to brackish environments (Taplin 1988). Hatchlings of *C. porosus* are able to survive and grow without access to fresh water (Grigg *et al.* 1980; Taplin 1984). Hatchlings of *C. acutus* also enter hyperosmotic water from nest sites around the Florida Keys, but they are thought to make use of floating lenses of fresh water from rainstorms (Mazzotti & Dunson 1984, 1989; Mazzotti, Bohnsack, McMahon & Wilson 1986). It is unknown whether they could survive without drinking fresh water.

No studies suggest that any of the Alligatoridae can live indefinitely in hyperosmotic conditions. However, the American alligator *A. mississippiensis* sometimes ventures temporarily into salt water, and *Caiman latirostris* occurs in estuaries in southern Brazil.

The mechanisms which support crocodilian ionic and osmotic homeostasis are essentially the same as those in other reptiles (Minnich 1979, 1982; Dunson 1976; Dantzler 1976). Mesonephric kidneys are the organs of ionic and osmotic regulation and of nitrogen excretion, supported by the cloaca, and lingual salt glands in the

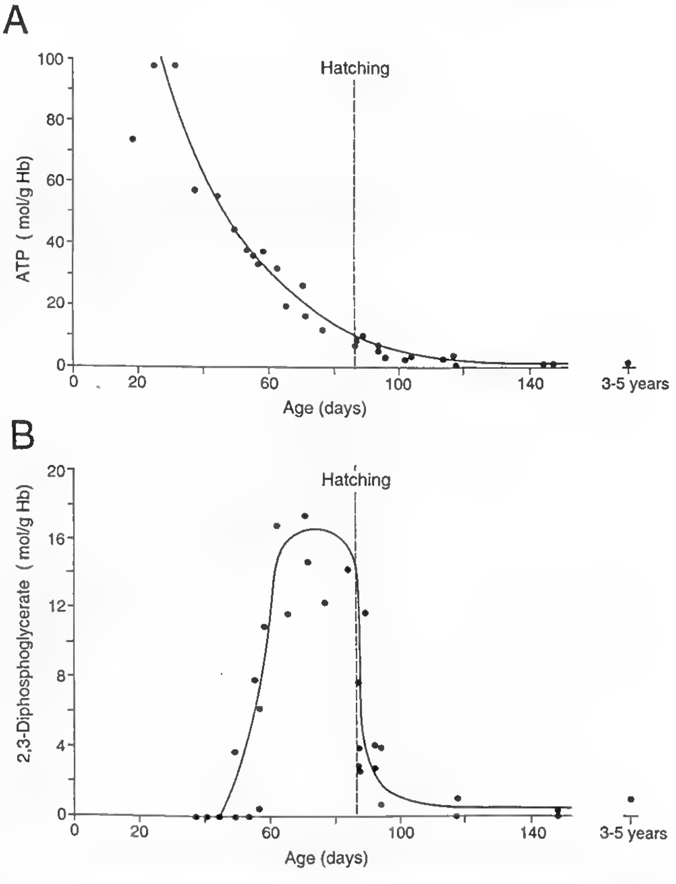

Figure 40.8 Ontogenetic changes in red cell organic phosphates before and after hatching in *Crocodylus porosus*. **A**, ATP levels; **B**, 2,3-DPG levels. [W. Mumford]

Crocodylidae but not Alligatoridae. All crocodilians lack a bladder. In fresh water, the cloacal urine is copious, clear and dilute, and excess nitrogen is lost as ammonium ions, excreted as ammonium bicarbonate (Coulson & Hernandez 1959, 1983).

Under hyperosmotic conditions, the urine of *C. porosus* is opaque white/cream and often reduced in volume. Nitrogen is excreted as insoluble uric acid, which achieves a water saving, as in birds (Grigg 1981; Grigg, Taplin, Green & Harlow 1986). The liquid fraction is low in sodium and never hyperosmotic to the plasma, but in salt water the cloacal urine contains small quantities of urea, plus significant excess potassium and divalent cations (Grigg 1981).

More information is needed about the composition of the ureteral urine in both the Alligatoridae and Crocodylidae. At least in crocodiles, the urine is presumably subject to water reabsorption by sodium pumping, probably after temporary reflux to the distal colon, in the manner of birds (Skadhauge 1977). This would account for the low levels of sodium in the cloacal urine of individuals of *C. porosus* in salt water, referred to above. The excess sodium is excreted via salt glands.

Lingual salt glands appear to be present in all crocodylids. Some 23 to 93 discrete lobulated glands open by conspicuous pores onto the surface of the tongue (Fig. 40.9A; Taplin & Grigg 1981; Taplin, Grigg, Harlow, Ellis, & Dunson 1982; Taplin, Grigg & Beard 1985; Taplin 1988). The ultrastructure of these glands (Fig. 40.9B, C) is very similar to the (non-homologous) glands of marine turtles. Salt glands have not, however, been found in any member of the Alligatoridae (Taplin 1988; Grigg & Beard unpub. obs.) and a study of captive *A. mississippiensis* suggests that it cannot maintain homeostasis in hyperosmotic water (Lauren 1985). The situation in both *Gavialis* and *Tomistoma* is unclear. The buccal morphology of *Tomistoma* suggests the presence of similar lingual glands, whereas *Gavialis* has glands that are distributed differently. Data on secretory capabilities are lacking. Taplin *et al.* (1985) have postulated a marine phase in the evolution of the Crocodylidae, but not for the Alligatoridae, an idea developed subsequently in a historical zoogeographic context (Taplin & Grigg 1989).

Typical concentrations of salt gland secretions, using the methacholine stimulation method, approach or exceed that of sea water (SW = 1000 mOsm l^{-1}, compared with plasma at approximately 300 mOsm l^{-1}), with sodium and chloride the dominant ions (see review by Taplin 1988). Rates of flow differ among species. Rates of sodium secretion range from less than 10 (*C. johnstoni*) to more than 40 uMol $100g^{-0.7}hr^{-1}$ (*C. porosus* and *C. acutus*). Questions have been raised about the relevance of measuring secretory performance of glands stimulated artificially by methacholine chloride (Mazzotti & Dunson 1984; Mazzotti *et al.* 1986) and, by implication, about the functional significance of the glands. However, isotopic measurements of sodium effluxes in *C. porosus* living in natural hyperosmotic habitats show that the field efflux is less than the maximum measured in the laboratory (Grigg *et al.* 1986), and apparently the salt glands are sufficiently competent to maintain homeostasis under these conditions. Hatchling *C. porosus*, indeed, are known to survive and grow in hypersaline creeks at salt concentrations nearly twice that of sea water, where fresh water is unavailable during the dry season (Taplin 1984). In comparison to a control group kept in fresh water, captive hatchling *C. porosus* maintained for months in 570 mOsm salt water showed increased vascularisation of the lingual glands (Franklin & Grigg in press).

There is evidence of some physiological adaptation in *Crocodylus johnstoni*, which does occur in brackish waters, though uncommonly (Messel *et al.* 1979–1985). Individuals captured in the Limmen Bight River, Northern Territory, in hyperosmotic salinities sometimes in excess of 600 mOsm l^{-1}, exhibited plasma homeostasis, with values comparable to individuals from a nearby fresh water population (Taplin, Grigg & Beard 1993). Salt gland performance is lower than that of *C. porosus*, in both concentration and rate. Whether or not *C. johnstoni* can tolerate hyperosmotic conditions indefinitely, and to what maximum concentration, remains unknown.

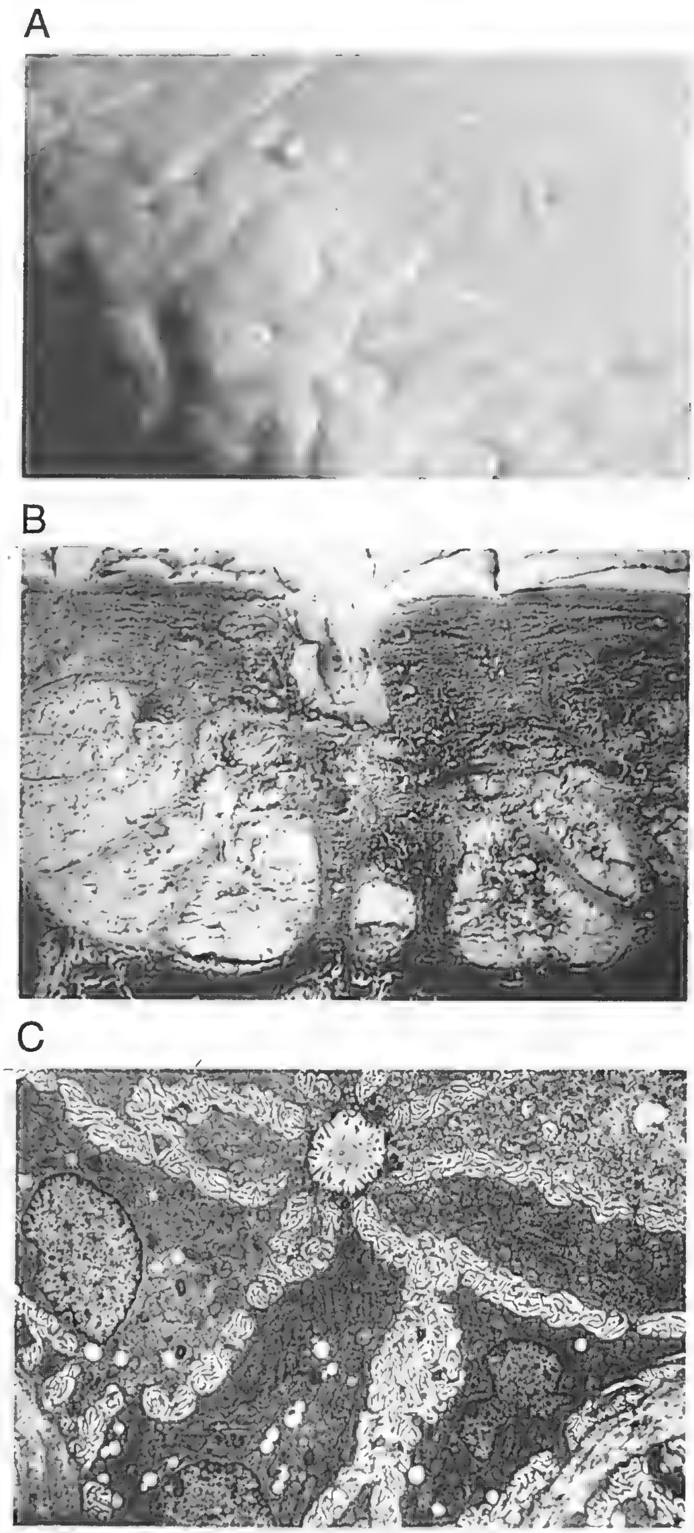

Figure 40.9 Salt glands of *Crocodylus porosus*. **A**, secreted droplets welling from pores on the surface of the tongue; **B**, scanning electron micrograph of a thick section of the tongue showing lobules comprising a single salt gand; ducts from the gland unite to form a pore on the surface of the tongue; **C**, transmission electron micrograph of a lobulated gland in transverse section.
[Photos by L.E. Taplin]

SENSE ORGANS AND NERVOUS SYSTEM

Before dismissing the mental capabilities of crocodilians, it is as well to remember the complexity of their predatory and reproductive behaviour (see Reproduction) and their homing capacities (Walsh & Whitehead 1993). Reptilian brains are about one tenth the mass of avian or mammalian brains at comparable body size and crocodilians appear to be no exception (Jerison 1969).

Crocodilians are well provided with sense organs, having good vision, hearing, olfaction and senses of touch. The eyes are well situated for vision in air by an almost submerged individual. While submerged, a translucent 'third eyelid', the nictitating membrane, moves across horizontally to protect the eye. When underwater vision is probably restricted to sensing light and dark. Touch receptors and ears are probably the main operational sense organs underwater.

The structure of the crocodilian eye was reviewed by Underwood (1970). The eye may be closed by depression of the upper eyelid, which is protected by a bony scute. Binocular vision is implied, as the cornea subtends an angle of 128°, with 25° of overlap in the forward fields in *C. porosus* (Pettigrew & Grigg 1990). Of importance in night vision is the tapetum lucidum, a layer of retinal cells containing guanine crystals, which reflects incoming light, and serves as an image intensifying system. The reflective tapetum allows crocodilians to be located easily at night, the eyes reflecting the beam of a spotlight or flashlight. The iris is a vertical slit by day, and opens to a wide circle at night.

The ear was discussed by Baird (1970). Crocodilians vocalise when in distress and during aggressive behaviour, and are said to have excellent auditory capabilities. The tympanic membranes are concealed and protected by flat rectangular flaps that may be raised and lowered by muscles (Pl. 9.7). Presumably they are closed during diving, though reception of underwater sounds is an important aspect of social communication (see Reproduction). The middle ear, surrounded by bone, is more complex than in other reptiles and shows similarities to the ears of birds.

Olfaction originates from receptors within the nasal cavities (Parsons 1970). The nasal cavities are the most complex among the reptiles and are essentially similar within the Crocodylia. The nasopharyngeal ducts are elaborated dorsally in a series of sinuses, sacs and blind ducts. Adult crocodilians lack Jacobson's organs. The olfactory bulbs of the forebrain are well-developed, consistent with the importance of olfaction.

Experiments on *A. mississippiensis* (Weldon *et al.* 1990) have shown that alligators use chemical cues to locate food both on land and under water. Gular pumping increases in the presence of meat odours and probably serves to improve the efficiency with which air is sampled by olfaction. Taste is probably involved as well in the contact identification of food, as taste buds occur on the tongue (Bath 1906) and posterior palate (Ferguson 1981).

REPRODUCTION

A detailed natural history of reproduction is outside the scope of this chapter. It has been reviewed recently in excellent, well-illustrated books about crocodilians in general (Ross 1989) and *C. porosus* and *C. johnstoni* in particular (Webb & Manolis 1989). Another valuable reference is Webb, Manolis & Whitehead (1987), and much of the detail referred to below has come from these sources, plus personal experience.

Briefly, crocodilians have a complex social hierarchy which is established by aggression and by elaborate social signalling (Vliet 1989). Large males are dominant and territorial and are thought to fertilise most of the females in a particular area. Most observations have been made on small numbers of captive species, and their relevance to wild populations can only be inferred. Studies on *A. mississippiensis*, *C. niloticus* and *C. porosus*, coupled with elements of similar behaviour recorded in other species, suggest that all crocodilians are probably broadly similar in their reproductive biology.

Mating behaviour of *C. porosus* observed in captivity in north Queensland provides an example which seems to be typical of crocodilians in general. Mating occurs in the water. Females usually approach the male and an elaborate, sometimes prolonged courtship ensues. The individuals swim together, often in circles, make body contact frequently and rub their head over the other body (see comments on gular and paracloacal glands). The female may flee a short distance, and draw the male into a chase before circling is resumed. Typically females show headlifting, submissive postures. Copulation occurs when the male curls his tail under the female, lying to the side. In shallow water, both individuals may be seen lying on their sides.

All Alligatoridae, half of the Crocodylidae and *Tomistoma* nest in mounds. The remaining species use holes. *Crocodylus acutus* nests sometimes in a hole and sometimes in a mound. Mound nesters lay their eggs in a nest constructed from grass or other vegetation, litter, and sand or soil in various proportions, depending upon what is available at the site. The mound is constructed using material dug up with the hind legs, or from vegetation torn off with the teeth (Fig. 41.4).

Crocodylus johnstoni lays an average of 13 eggs (range four to 21; weight 65 to 75 g) in August, during the north Australian dry season. Eggs are laid about six weeks after mating into a hole which is dug with the hind feet into the sandy substrates of a river bank. Though incubation time is temperature dependent, under average field conditions *C. johnstoni* hatch after about eleven weeks. *Crocodylus porosus* is a mound nester and, unlike *C. johnstoni*, breeds in the wet season. After courtship at the end of the dry season, nests are built at the onset of 'the wet'. If the wet season begins early, the nesting season may be quite prolonged and tapers off towards March and April. *Crocodylus porosus* lays 50 to 60 eggs, which are heavier than those of *C. johnstoni*, weighing about 100 g (range 70 to 140). The number and size of the eggs reflects the age and size of the mother. At normal field temperatures, incubation takes about 80 to 90 days. Clutch characteristics of specific populations of *C. porosus* and *C. johnstoni* are discussed in Chapter 41.

Parental care and the temperature dependence of the sex of the young are two features of crocodilian reproduction of particular interest. Persistent and often ancient anecdotal reports about maternal care were confirmed by observations on captive *C. niloticus* (Pooley & Gans 1976) and have since been extended to other species, including *C. johnstoni* and *C. porosus*. Females commonly guard their nests, though the effectiveness of this behaviour as a predator deterrent is doubtful. At the end of incubation, hatchlings emerging from the eggs in the nest cavity emit characteristic, staccato, rasping vocalisations. These sounds encourage the female to excavate the nest and to collect emergent hatchlings in the jaws and carry them to the water (Fig. 41.3). Several trips may be required to transport a whole clutch. Eggs not yet hatched may be taken in the mouth and manipulated to release the young. Pods of hatchlings seem to be defended by the mother (and the father) for some time after these have entered the water, but more data are needed about this behaviour and its effectiveness.

As is typical for many turtles and some lizards, the sex of crocodilian hatchlings is determined by the incubation temperature, rather than genetically. Reviews of aspects of temperature sex determination (TSD) may be found in Webb *et al.* (1987), Webb & Cooper-Preston (1992) and Deeming & Ferguson (1992). Crocodiles and alligators are slightly different. At constant incubation temperatures, *A. mississippiensis* and *Caiman crocodilus* eggs produce males above 32°C and females below 31°C, with mixed sex ratios in between. Crocodiles eggs also produce females when incubated below 31°C, and a mixture of sexes is produced between 31° and 32°C. Embryos incubated between 32° and 33°C hatch as males, and females dominate in the mixture of sexes above 33°C. Experiments with constant incubation temperatures are misleading as sex is likely to be determined during brief intervals.

The influence that a very small difference in temperature may provoke is of great interest, as is the phenomenon itself in evolutionary and ecological terms. Nest site selection, which determines incubation temperature, therefore has a marked influence not only on the duration to hatching and the survivorship of the eggs, but on their sex as well. Most natural nests produce a mixture of males and females, but some produce only a single sex.

The temperature regime of both holes and mounds is buffered compared to diurnal fluctuations; metabolism of the eggs themselves contributes to elevated temperatures, and decomposition of vegetation may be an important heat source of heat in mound nests. Whatever the mechanisms, measurements in the nest cavities generally show temperatures above but close to 30°C, with little diurnal variation. Periods of heavy rainfall may provide an exception, as shown by Magnusson (1979) in a nest of *C. porosus*. Eight days were required to regain the warmth lost after several days of cyclonic rain, during which the nest cavity temperature declined from 32°C to 25°C.

Much more needs to be learned of the morphology and physiology which supports crocodilian reproduction. Illustrations of the male and female reproductive (and urinary) systems are available in Chiasson (1962). The single, rigid penis is pulled out and forward by muscles. A middorsal, open groove receives sperm through juxtaposition with the vasa deferentia, which open dorso-laterally through the cloacal wall. The testes are paired and adjacent to the kidneys. They undergo a conspicuous annual cycle in size and activity (see below). The clitoris of females is much smaller than the penis, but lies in the same position.

The oviducts open anteriorly to receive ova from the paired ovaries, adjacent to the kidneys. Longitudinal differentiation and specialisation of the oviducts has been described in detail (Palmer & Guillette 1992), and appears to be more similar to birds than to other reptiles, again emphasising the archosaurian connection. Unlike other reptiles, the eggshell membranes and the calcareous shell are formed in different regions of the oviduct, as they are in birds. Thus, the whole clutch is treated sequentially, egg by egg, in different parts of the oviduct. Fertilisation presumably occurs in the anterior end of the oviduct. Albumen proteins are secreted in the oviducal tube, shell membranes are secreted in the anterior uterus, and the calcareous shell is deposited by the posterior uterus. Each of the two oviducts opens into the cloaca via a vagina with a narrow lumen which spirals through the muscular cloacal walls (Palmer & Guillette 1992). How these walls relate functionally to the role of a vagina as a receptacle for a penis, is unclear and the appropriateness of the term is uncertain.

The coordination of the anatomical, physiological and behavioural events involved in reproduction and subsequent care of the developing embryo is achieved by endocrine regulation, under the influence of environmental factors. Thus, photoperiod, temperature, rainfall, nutritional status and social factors all influence the level of circulating reproductive hormones. This has received closest attention in *A. mississippiensis* (Lance 1987; Lance 1989) and *C. niloticus* (Kofron 1990). The reproductive cycle of *A. mississippiensis* commences in March (early spring) as air and water temperatures increase. In males, testis mass, plasma testosterone (> 50 ng ml^{-1}) and spermatogenesis peak around April. Mature spermatozoa appear from midMay when mating occurs. Testosterone and testis size decline rapidly after spermiation and the testes are fully regressed in July and August. There is a small peak in testosterone in September, with no visible changes in testicular histology. In females, plasma oestradiol peaks in mid April (> 600 pg ml^{-1}), and ovarian follicles increase from 5 to 45 mm in diameter in May, at ovulation. Testosterone is high also in preovulatory females (approximately 1.5 ng ml^{-1}), but its function is unknown. Plasma progesterone shows a peri-ovulatory surge to 16 ng ml^{-1}, with a rapid decline during the two to three weeks between ovulation and oviposition. During incubation, while the female remains at the nest, ovarian steroids are undetectable. These patterns are broadly similar to those in other tetrapods, but Lance (1989) has drawn attention to the need for more work on the pituitary gonadotropins and other aspects of the endocrine regulation of reproduction in crocodilians. The large size and difficulty of handling sexually mature individuals, and their limited availability, assure that both heroic and herculean efforts will be needed to answer many of the questions which remain on the physiology of crocodilian reproduction.

41. NATURAL HISTORY OF THE CROCODYLIA

Harvey Cooper-Preston & Robert W. G. Jenkins

Although the following is a discussion of the natural history of crocodilians in general, the Australian crocodiles, *Crocodylus porosus* and *C. johnstoni*, are used to illustrate examples whenever possible. A good introductory work based on Australian crocodiles is that of Webb & Manolis (1989).

LIFE HISTORY

Reproductive Strategies

The age and size at sexual maturity in crocodilians is variable, even among different populations of the same species (Cott 1961; Graham 1968; Staton & Dixon 1977; Gorzula 1978; Hutton 1984; Joanen & McNease 1987; Cooper-Preston 1992). Females of *Crocodylus johnstoni* mature at approximately 0.75 m snout-vent length and 12 years old in river systems such as the McKinlay River, Northern Territory (Webb, Buckworth & Manolis 1983a). In contrast, females as small as 0.55 m snout-vent length are mature in the upper Liverpool River in Arnhem Land where growth rates are low, at an estimated age of 20 years (Webb 1979b; Cooper-Preston 1992). Differences in age and size at sexual maturity probably reflect both genetic and environmental factors (Joanen & McNease 1981; Ferguson 1985) and may be adaptations to environments with differing food resources. Reproduction can be maximised by attaining a large size before maturity in suitable habitats. However, marginal areas can be populated by compromising growth for a reduced, yet sustainable, reproductive effort.

In part both social and environmental factors, along with the number of potential breeding females, determine the nesting effort during a given year in a particular population (Hines & Abercrombie 1987; Joanen & McNease 1987). It appears that the proportion of sexually mature *C. johnstoni* that nest annually varies greatly, but in certain populations the nesting effort is consistently lower than that in other populations (Smith & Webb 1985; Cooper-Preston 1992).

Young and very old females may not contribute much to recruitment. High rates of infertility in eggs and small clutch sizes have been attributed to small or young females of *C. johnstoni* (Dunn 1981; Smith 1987; Webb unpub. data) and *C. porosus* (Webb unpub. data).

Crocodilians are polygynous and a lack of males rarely, if ever, limits reproduction in *C. johnstoni* (Webb Webb, Buckworth & Manolis 1983a) and probably in other crocodilians. Although no studies have been conducted on *C. porosus* in the wild, in captivity only the larger males in multiple animal enclosures breed with the available females (Mengden pers. comm.).

Clutch Characteristics and Hatching

Average clutch size, mass and egg dimensions vary inter- and intraspecifically. The size, age and diet of the female affect clutch size. In *C. johnstoni*, the average clutch size varies from four to six eggs along the upper Liverpool River (Banks pers. comm.) to 12 to 13 eggs on the McKinlay River (Webb *et al.* 1983a; Smith 1987). The average clutch size for *C. porosus* is 53 in the Northern Territory (Webb & Manolis 1989) and 59 in Papua New Guinea (Cox 1985). Mean clutch mass is similar, suggesting that the Northern Territory and Papua New Guinean females are of similar average size (Cox 1985; Webb & Manolis 1989), since clutch mass appears to be the best clutch characteristic for predicting individual female size in crocodilians (Smith 1987; Webb unpub. data). Grigg & Gans (Chapter 40) record a range of clutch sizes from four to 21 for *C. johnstoni* and 50 to 60 in *C. porosus*. The average egg dimensions for *C. porosus* in the Northern Territory are 80 mm by 50 mm (Webb & Manolis 1989) and those of *C. johnstoni* are approximately 66 mm by 42 mm (Webb *et al.* 1983a).

Egg mortality may result from predation, inundation, desiccation, and excavation by other females. The extent varies between years and populations. In *C. johnstoni*, up to 60 to 70% of the eggs at the McKinlay River are lost each year, mostly as a result of predation by varanids (Webb *et al.* 1983a). Mortality appears to be much lower in areas such as the Katherine River region, perhaps because of the lower nesting effort and therefore the absence of communal nesting banks. Flooding is the major cause of egg mortality in *C. porosus*, and up to 90% of nests in the Northern Territory may be inundated in some areas (Webb & Manolis 1989).

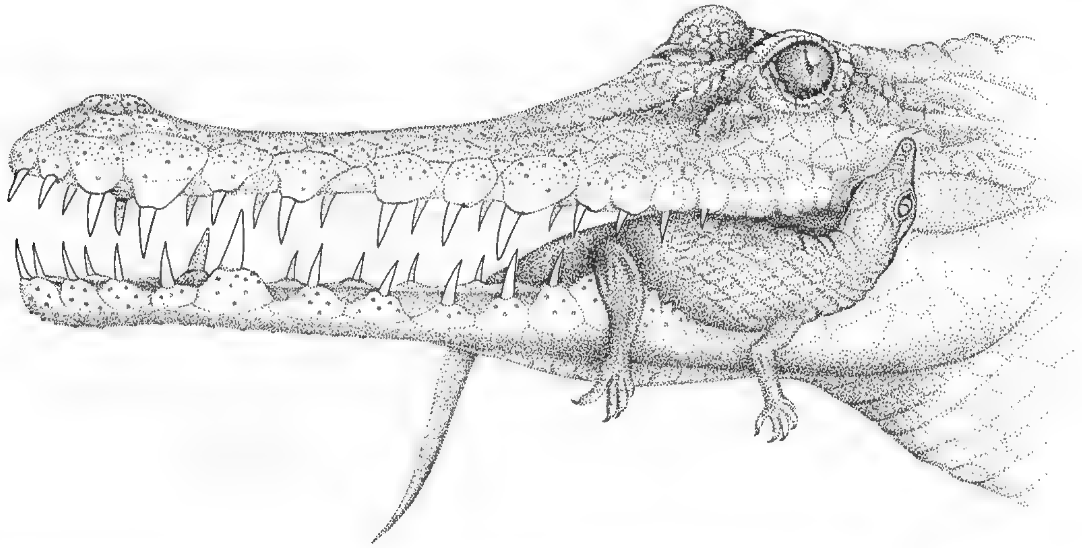

Figure 41.1 After excavating the nest, a female *Crocodylus johnstoni* picks up hatchlings and carries them to the water. (After ABC 1988) [T. Wright]

Incubation periods range from 40 to 120 days for crocodilians (Ferguson 1985). The incubation periods for *C. johnstoni* and *C. porosus* are from 63 to 98 days (Webb *et al.* 1983a) and 70 to 98 days (Webb, Sack, Buckworth & Manolis 1983b), respectively. The period varies with nest temperature because of its effect on embryonic developmental rates (Webb & Smith 1984).

Hatchling size is determined principally by egg size (Webb & Manolis 1989), but is also affected by incubation temperature (Hutton 1987b; Manolis pers. comm.). *Crocodylus johnstoni* hatchlings are approximately 240 mm long and weigh 42 g and those of *C. porosus* are 290 mm long and 72 g in weight (Webb & Manolis 1989; Cooper-Preston 1992).

In many, if not all crocodilians, the female excavates the nest upon hearing the calls of the hatchlings and assists them to the water (see also Chapter 40). Experiments with *C. johnstoni* have shown that the hatchlings will die in the nest if not assisted by a female (Fig. 41.1; Limpus pers. comm.). This is probably true for all hole-nesters. Experimental manipulation of *C. johnstoni* nests showed that females other than the mother will also open nests in response to hatchling calls (Smith 1987). In *Caiman crocodilus fuscus* both parents assist in releasing the hatchlings (Alvarez del Toro 1974).

Primary Sex Ratio

The sex of crocodilians is determined during the first third of embryonic development by incubation temperature which acts either directly or indirectly by influencing the embryonic developmental rate and release of hormones (Ferguson & Joanen 1982, 1983; Webb & Smith 1984; Ferguson 1985; Hutton 1987b; Lang 1987; Smith 1987; Webb, Beal, Manolis & Dempsey 1987; Yamakoshi, Magnusson & Hero 1987; Lang, Andrews & Whitaker 1989; Webb & Cooper-Preston 1989; Deeming 1990; Magnusson, Lima, Hero, Sanaiotti & Yamakoshi 1990). Temperature-dependent sex determination tends to produce males in the conditions most conducive to high chances of survival and good post-hatching growth (Webb & Cooper-Preston 1989). Under constant laboratory temperatures, female *C. johnstoni* are produced at all temperatures (28° to 34°C) and males only between 31° to 33°C (Webb & Smith 1984). The highest percentage of males produced in laboratory trials was 31% (Webb, Beal, Manolis & Dempsey 1987). However, the results of experiments using constant incubation temperature should be viewed cautiously (see Chapter 40).

Field nests have produced 100% males after an incubation period of 72 to 74 days, corresponding to incubation time at 32° to 33°C in the laboratory (Webb & Smith 1984). In *C. porosus*, males are also produced between 31° to 33°C. The proportion of males can be higher than in *C. johnstoni*, however, and at 32°C, up to 91% of the hatchlings are males (Webb *et al.* 1987). Clutches producing only females at high incubation temperature have not been documented for *C. porosus* because of high percentages of death and abnormality above about 34°C (Webb pers. comm.). Other crocodilians also tend to produce females at low temperatures and males at high temperatures (Ferguson & Joanen 1982, 1983; Hutton 1984, 1987b; Lang 1987; Magnusson da Silva & Lima 1990). Not surprisingly, primary sex ratios vary among populations of the same species and from season to season within a population. However, a female-biased sex ratio is the norm for several species, including *C. johnstoni* (Webb *et al.* 1983a; Cooper-Preston 1992).

Longevity

Although it is well-known that crocodilians live for a long time, the maximum age and the age at senility can only be guessed. *Crocodylus porosus* are known to live for over 70 years and may even reach 100 years, whereas *C. johnstoni* are not as long-lived, and animals of 50 years are considered old (Webb & Manolis 1988a, 1988b).

ECOLOGY

Environmental Relations

Crocodilians are ectothermic, and exploit the external environment to regulate their body temperature by such thermophilic and thermophobic behaviours as basking, movement in and out of water, and mouth gaping. Physiological mechanisms of temperature control are described in Chapter 40.

Temperate species are more thermophilic than tropical ones (Mazzotti 1989). The American alligator, *Alligator mississippiensis*, typically spends the morning basking, moves into shallow water in the afternoon but keeps its back exposed, and retreats into deeper water as the air temperature drops at night (Mazzotti 1989). However, the estuarine crocodile, *Crocodylus porosus*, avoids heat by remaining in the water during the day and comes up on the banks at night, often burying itself in the mud of tidal areas (Lang 1987). Basking in both *C. porosus* and *C. johnstoni* is most evident during the winter months of June and July, especially in the mornings. A basking *C. porosus* aligns itself with the sun for maximum heat exchange; as its body temperature rises it faces the sun with mouth agape thereby reducing the impact of heat on the brain (Webb & Manolis 1989).

Mouth gaping increases the area for evaporative cooling which affects internal temperature. Many species gape and, although Spotila, Terpin & Dodson (1977) confirmed some

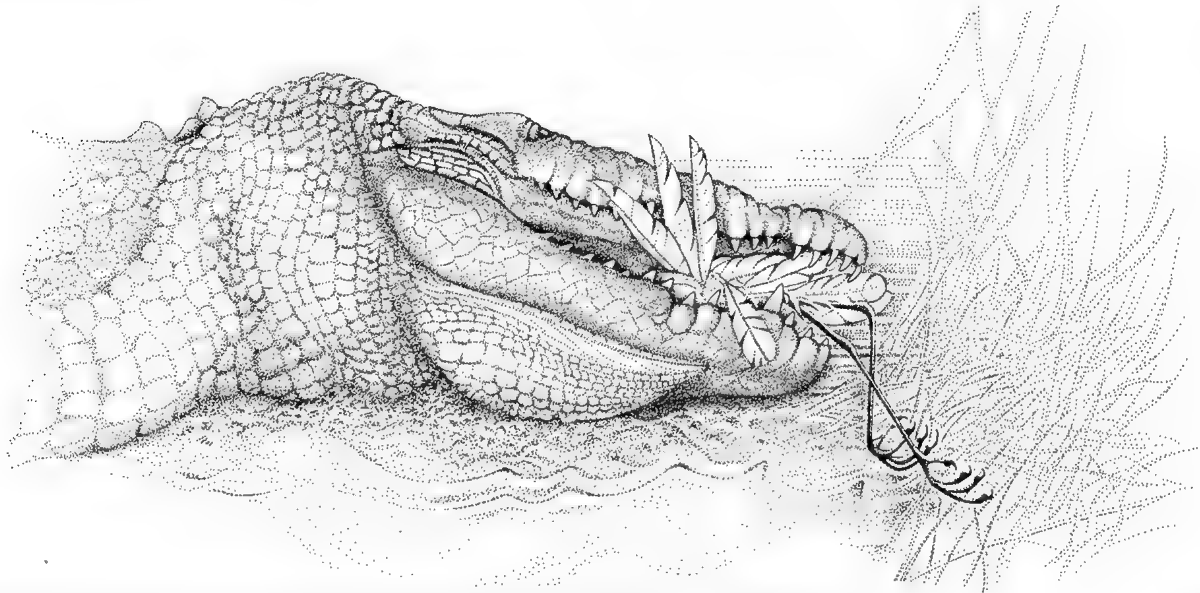

Figure 41.2 Typically *Crocodylus porosus* turns its head to one side when taking prey from land. (After photo by G. Grigg) [T. Wright]

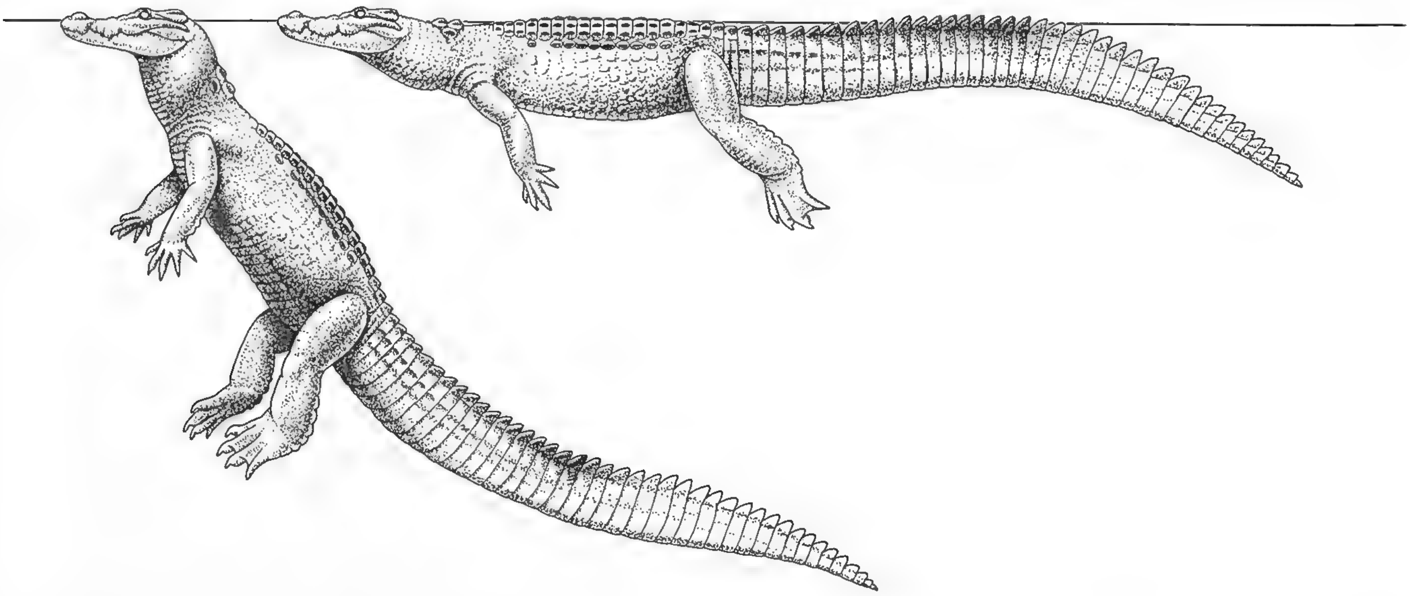

Figure 41.3 Fine-tuned bouyancy control enables *Crocodylus porosus* to approach very close to prey without detection. Although denser than water they inflate the lungs appropriately to achieve neutral buoyancy. Crocodilians using shallow breathing can float at the water surface for long periods, and maintain the eye constantly within a couple of millimetres above the water the level. [D. Kirshner]

thermoregulatory role, the habit remains puzzling. Since the water loss is related to body temperature, thermoregulatory behaviour also affects osmoregulation (Mazzotti 1989).

Preferred body temperature is influenced by many factors, including climate and social conditions, size, age, feeding activity, health, and incubation temperature of the embryo (Lang 1987). Preferred body temperatures are the same in adults and older hatchlings, and thermophily in newly hatched crocodilians aids in the quick digestion of yolk (Lang 1987). Thermophily also increases the rate of digestion after eating, and is more prevalent in alligators than in tropical crocodilians (Mazzotti 1989). Lang (1987) found that *A. mississippiensis* will create a 'behavioural' fever that combats infection (see Chapter 40). This may be true also of other species of crocodilian.

Seasonal variation in climate may cause dramatic changes in gross behaviour in some species. No crocodilian is known to hibernate; however *Alligator mississippiensis* will position itself in shallow water with only its nostrils exposed during severe cold spells (Mazzoti 1989). *Crocodylus johnstoni* has been known to aestivate at the end of the dry season (September to November) in underground refugia along a dry creek bed in the Northern Territory (Christian pers. comm.). This behaviour may be widespread.

Crocodilians respond behaviourally to changes in environmental salinity. They do not drink saline water and move to fresh water after feeding in saline water (Mazzotti 1989; Grigg 1993).

Diet

Crocodilians tend to be opportunistic feeders. Their diet reflects both the local availability and vulnerability of prey species and size-related shifts in dietary preferences (Graham 1968; McNease & Joanen 1981; Webb, Manolis & Buckworth 1982). Many crocodilians feed primarily at the water's edge, including *Crocodylus johnstoni* (Webb, Manolis & Buckworth 1982; Cooper-Preston 1992) and *C. porosus* (Fig. 41.2; Taylor 1979). The slender-snouted *Gavialis gangeticus* and *C. johnstoni* are adapted to feeding on mobile prey such as fishes, which form a high porportion of the diet of these predators (Pooley & Gans 1976; Webb *et al.* 1982; Whitaker & Basu 1983). A slender snout can snap sideways more effectively because it meets less water resistance. In contrast, *Caiman latirostris* uses its broad snout to scoop molluscs from the river bottom (Diefenbach 1979).

Diets change with increasing size and with age (Cott 1961; Fogarty & Albury 1967; Dodson 1975; McNease & Joanen 1981; Webb *et al.* 1982; Magnusson, da Silva & Lima 1987). Insects constitute the major food items of juveniles, and adults take larger prey (Corbet 1959, 1960; Cott 1961; Dodson 1975; Staton & Dixon 1975; Gorzula 1978; Seijas & Ramos 1980; McNease & Joanen 1981; Hutton 1984; Magnusson *et al.* 1987). In some larger species of crocodilians, such as *C. porosus* (Taylor 1979), *Alligator mississippiensis* (Giles & Childs 1949; Dodson 1975; McNease & Joanen 1977), and *C. niloticus* (Cott 1961; Blomberg 1977), the diet includes an increasing proportion of terrestrial prey as body size increases. *Crocodylus johnstoni* feeds on smaller prey than other crocodilians of comparable body size, and tends to eat insects throughout its life, although the proportion in the diet diminishes (Webb *et al.* 1982; Magnusson *et al.* 1987).

Visual cues, chemoreception and tactile stimuli are important in detecting prey both in and out of the water (Whitaker & Basu 1983; Weldon, Swenson, Olson & Brinkmeier 1990; Cooper-Preston 1992); sensory pits along the side of the jaws may detect movement of prey (see Chapter 40; Webb & Manolis 1989).

Feeding behaviour is specialised in many species. *Caiman crocodilus* feeds mainly on floating semi-aquatic prey such as insects and frogs and avoids actively swimming prey (Gorzula 1978). *Paleosuchus trigonatus* is often found away from the water and consumes more terrestrial vertebrates than any other Amazonian crocodilian (Magnusson *et al.* 1987). Some species will extend the snout out of the water to catch insects in flight. Juvenile *Caiman latirostris* use this approach to feed on flying carabids (Diefenbach 1988), as do small *Crocodylus niloticus* when feeding on dragonflies at dusk in Uganda (Corbet 1959). *Crocodylus porosus* will leap partially out of the water for food. Like other crocodilians they adopt sit-and-wait tactics, and rely on swift attack from the water to seize and immobilise terrestrial prey before it is swallowed. Whilst stalking prey, crocodiles move silently and surreptitiously, often with only the nostrils, eyes and the top of the skull platform visible at the surface (Fig. 41.3; see Chapter 40).

Seasonal differences in diet reflect food availability and activity patterns of crocodiles and their prey (Gorzula 1978; Webb *et al.* 1982; Diefenbach 1988). Evidence of seasonal changes in the quantity of food eaten has been reported for some species of alligators and caimans (Fogarty & Albury 1967; Dodson 1975; McNease & Joanen 1981; Gorzula 1978; Diefenbach 1988) and in some populations of crocodiles (Hutton 1984, 1987a). Taylor (1979). Webb, Hollis & Manolis (1991) found no seasonal variation in the amount of food in stomachs of *C. porosus*, although the type of food changed from predominantly crustaceans in the dry season to a high proportion of insects in the wet season.

Stones, or gastroliths, are often found in crocodile stomachs and their presence has stimulated lively discussions on their function. Some authors have proposed that stones are ingested incidentally, and serve no function, or that they maintain stomach size and stimulate gastric juices. Others suggest that stones have an important role in buoyancy (see Chapter 40), or that a digestive function for the stones is the most plausible hypothesis (Bakker 1986; Cooper-Preston 1992).

Home Range and Movement

Home range may be defined as the area where an animal spends the majority of its time. Home ranges include centres where certain activities are concentrated such as basking or feeding (McNease & Joanen 1974). Few data are available for Australian crocodiles. However, home ranges of *Alligator mississippiensis* and *Crocodylus niloticus* differ between age groups and vary seasonally (Joanen & McNease 1972a, 1972b; Hutton 1984).

Movements among crocodilians are usually seasonal or size-specific. In some areas, male and female *C. niloticus* migrate to breeding grounds where courtship and nesting occurs (Magnusson, Vliet, Pooley & Whitaker 1989). During the breeding season females of *A. mississippiensis* leave protected marsh areas for open waters inhabited by males, and retreat back to the marshes to lay their eggs (Joanen & McNease 1980).

Annual inundation during the wet season is a major factor in dispersal of *Crocodylus porosus* in Australia (Webb & Messel 1978; Jenkins pers. comm.). During mark-recapture work on *C. porosus* in the Liverpool River area most movement was via the main streams with more males travelling downstream than females (Webb & Messel 1978). Flooding is a major factor in the dispersal of *C. johnstoni* (Webb, Buckworth & Manolis 1983c; Cooper-Preston 1992).

BEHAVIOUR

Nesting

Nesting in crocodilians takes place over either a protracted period, as in *C. porosus*, or a short 'pulse' of several weeks, as in *C. johnstoni.* The time of nesting depends on factors such as air and water temperatures, rainfall, water level and photoperiod (Joanen & McNease 1979). *Crocodylus porosus* nests during the wet season in northern Australia (November to April) and egg laying usually peaks during January (Webb & Manolis 1989). The nesting season of *C. johnstoni* is restricted to several weeks from the end of August through to the beginning of September (see also Chapter 40).

Crocodilians construct either a mound nest, mostly of vegetation (Fig. 41.4), or dig a hole nest in sand or other friable substrate (see Chapter 40). Only *Crocodylus acutus* is known to construct both types of nests (Mazzotti, Kushlan & Dunbar-Cooper 1988). *Crocodylus johnstoni* nests communally, as other hole-nesters do, except where breeding numbers are low in relation to potential nesting sites (Cooper-Preston 1992). Larger females tend to nest earlier than smaller animals (Smith 1987; Webb pers. comm.). Site selection is random (Smith 1987; Cooper-Preston 1992). In contrast, female *C. porosus* select nesting sites on the basis of access to permanent water, a refuge, suitable vegetation and a basking area (Webb, Sack, Buckworth & Manolis 1983b). Factors influencing the time of nesting are difficult to identify, because of the extended nesting period (November to May); rainfall and water level may play an important role, whereas air and water temperatures are unlikely to affect timing (Webb unpub. data).

The extent of nest defence against predators and humans is variable, and ranges from non-existent in most *C. johnstoni* to direct attacks on intruders by female *C. porosus.* Caimans are more likely to defend their nests early in incubation when nests are easier to detect (Magnusson, Vliet, Pooley & Whitaker 1989). Nesting is the only period when *Gavialis gangeticus* shows any aggression towards humans (Magnusson *et al.* 1989).

Social Behaviour

Crocodilians exhibit quite complex social behaviours associated with individual recognition, group living and courtship. Such behaviours may be stereotyped or flexible and can incorporate vocal, acoustic, visual, tactile and chemosensory communication. Certain general behaviour patterns are found throughout the order, while components of patterns are usually specific to species or even populations.

Communication begins in the egg with tapping sounds about two weeks before hatching, which may help to synchronise hatching (Lang 1989). Hatchlings vocalise (at pipping), and alert the female who usually opens the nest and assists the young to the water. Contact calls keep the pod together and distress calls usually elicit a response from the mother and often from other adults and

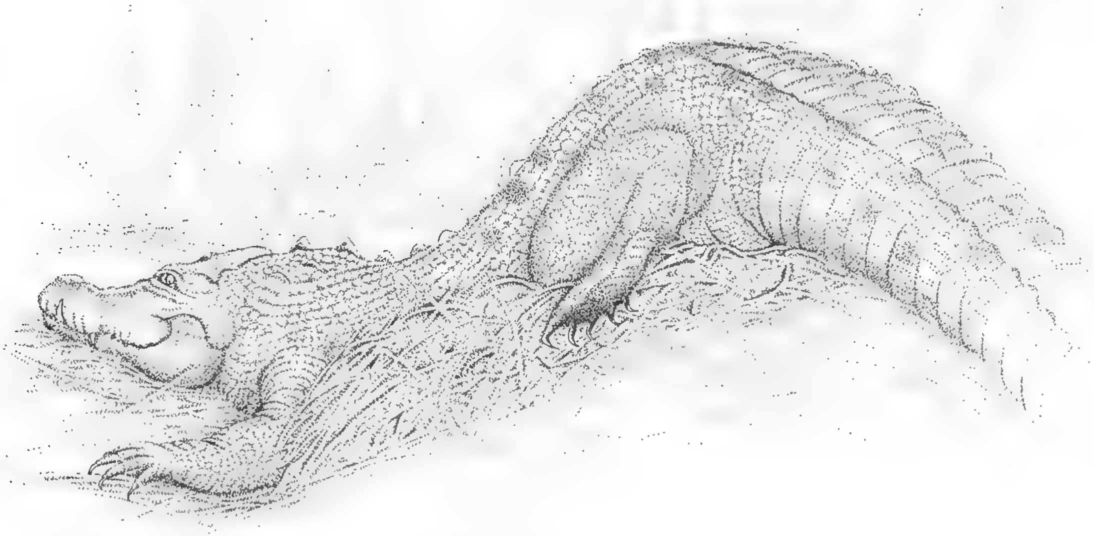

Figure 41.4 In *Crocodylus porosus* the female constructs her nest from vegetation raked together with her hind feet to form a mound in which the eggs are laid.
[T. Wright]

juveniles. *Crocodylus porosus* often growl when under threat and during courtship, especially in captivity (Webb & Manolis 1989). *Crocodylus johnstoni* may respond to a threat with a low-pitched growl or grunt (Webb & Manolis 1989).

Vocalisation among adults tends to be species- and population-specific; *Alligator mississippiensis* is the most vocal crocodilian (Lang 1989). Species living in marshes and swamps tend to be more vocal than those in open water and rivers (Lang 1989), presumably because visual cues are less effective in heavily vegetated areas.

Other acoustic behaviour also varies between species. All but *Gavialis gangeticus* perform a variation of the headslap which signals an individual's presence. The head is lifted out of the water with mouth opened and then slapped against the water, creating a loud clap as the jaws come together, and a splash as the head hits the water. This may be followed by bubble blowing, roaring and thrashing of the tail. Some species, including *C. johnstoni*, vibrate their trunk muscles, creating bubbles and low frequency waves around the body (Lang 1989; Webb & Manolis 1989). This is a threat display in *C. johnstoni* (Webb & Manolis 1989), but is also used during courtship in other species (Lang 1989). Another acoustic signal consists of exhalations from the throat and nasal passage in and above water.

Visual signals used in individual recognition include body posturing with the head, back and tail high out of the water in dominant individuals (Pl. 9.2), and snout lifting for submissive crocodiles. Snout lifting is also used in courtship in many species. Tail thrashing in the water and also on land indicates aggression in crocodilians (Lang 1989).

Other forms of communication involve tactile receptors on the head and secretory glands under the chin and in the cloaca (see Chapter 40). The importance and exact function of these has yet to be determined (Lang 1989). Other reptiles use chemosensory mechanisms for identifying individuals, marking territories and indicating reproductive status.

Studies conducted in captivity suggest that territoriality and dominance hierarchies are species-specific and density-dependent (Lang 1989). The dominant male is usually large and aggressive and exposes a large proportion of his dorsal body above the water when swimming, and submissive animals tend to submerge and retreat in his presence. Physical combat is rare in most species. However, *C. porosus* can be quite violent, especially during the breeding season, and serious injury or death can result. Males bite each other, and roll and thrash about until the subordinate one swims away (Webb & Manolis 1989). Similarly, dominant females attack other females.

Courtship displays are similar in all crocodilians. The female usually initiates courtship by approaching the male in a submissive posture (Compton 1981; Lang 1989; Magnusson *et al.* 1989; Webb & Manolis 1989). The pair will rub their snouts together lifting them out of the water. Head and body rubbing is common with both male and female mounting each other in turn. Vocalisations and exhalations can be quite noisy. The animals circle, submerge and re-emerge. Copulation takes place with the male mounting the female and positioning his tail under the base of the female's. Usually the pair then submerges. Copulation may last from a few minutes in some species to 30 minutes in *Gavialis gangeticus* (Magnusson *et al.* 1989). The actual sequence of courtship may be stereotyped as in *C. acutus* or flexible as in *A. mississippiensis*. Pre-copulatory behaviours permit assessment of potential mates and may synchronise reproductive activity (Lang 1989). Apparently they do not prevent interbreeding which occurs in captivity and may also occur in the wild (Hollands pers. comm.).

ECONOMIC SIGNIFICANCE

The commercial exploitation of crocodiles has varied according to the value of their skins on the international market. Some species such as *C. porosus* and *C. niloticus* were hunted intensively for their highly prized skins. *Crocodylus porosus* was virtually eliminated from many parts of its range in mainland South-East Asia, and its numbers in Australia were severely depleted as a result of unregulated hunting. Although the skin of *C. johnstoni* is less valuable, this species was hunted after it became unprofitable to exploit the dwindling populations of the saltwater crocodile. Numbers of *C. johnstoni* had not declined to the same extent as those of *C. porosus* when governments enacted legislation to prohibit hunting.

Legislation and CITES

The responsibility for conservation and management of native wildlife in Australia lies principally with the State and Territory Governments. *Crocodylus johnstoni* first received protection in Western Australia in 1961, followed by the Northern Territory in 1964. *Crocodylus porosus* became legally protected in Western Australia in 1969 and in the Northern Territory in 1971, and Queensland's Fauna Conservation Act extended legal protection to both species in 1974. Protection of Australian crocodiles was not provided, however, until it was apparent that both species had been seriously depleted.

The failure of State and Territory Governments to apply uniform legislation simultaneously to protect crocodiles left avenues by which skins could be traded, thus undermining the efforts of States to protect the wild resource. Crocodile skins were taken illegally from Western Australia or the Northern Territory, moved into Queensland, where neither species was protected, and used within that State or exported from Australia. The Commonwealth Government moved in 1972 to ban the export of crocodiles or their products by listing both species as prohibited exports under the *Customs Act*.

The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) was established in 1973 to regulate international trade in certain species of wild animals and plants and to ensure that such trade is conducted at sustainable levels. Australia became a Party to CITES in 1976 following the introduction of the 'Customs (Endangered Species) Regulations' under the Customs Act.

The two Australian crocodile species were listed initially in Appendix II of CITES, which includes species that may become threatened with extinction unless international trade is strictly regulated. However, concern was raised later about the conservation status of *C. porosus* when the results of the studies conducted by the University of Sydney (Messel, Green, Wells, Vorlicek, Onley *et al.* 1979–1987) were taken to indicate that the northern Australian population was critically endangered. As a result the Australian population of *C. porosus* was transferred to Appendix I of CITES, in which species are considered to be threatened with imminent extinction and are banned from commercial trade. Since the 1973 Washington Conference, no crocodilian species has been removed from the Appendices.

The Convention provides for commercial trade in specimens of Appendix I species that have been derived from closed-system captive breeding operations, on the basis that such trade can be conducted with minimal impact on the wild population. This management prescription has removed pressure from the wild resource and enhanced its potential for recovery. Appendix I species, such as *C. porosus*, have become the focus of research to provide a firm basis for their management as a renewable resource.

Farming and Ranching

The Edward River Crocodile Farm, located on the west coast of Cape York Peninsula in Queensland, was the first operation to experiment with the captive production of *C. porosus* skins for export. The farm, established in 1972 by Applied Ecology Pty Ltd, was funded by the Commonwealth Department of Aboriginal Affairs, to provide an industry by which the local Aboriginal community could derive economic independence. After more than 10 years of research on the requirements for breeding *C. porosus* in captivity, the Edward River Crocodile Farm finally received approval to export skins derived from its operation in 1984.

Importantly, this farm and others enhanced the recovery of the *C. porosus* population by promoting both public awareness of crocodiles and government attention to effective management of wild crocodiles.

As a conservation strategy, ranching was established in 1981, after the decision by Parties to CITES that some species of wildlife could benefit from management for commerce. This enabled Appendix I species (or populations thereof) to be transferred to Appendix II and managed by 'ranching'. This involves cropping the 'natural surfeit' of eggs and hatchlings of the wild population for use in commercial farming operations. In effect, this surfeit comprises the portion of the annual reproductive output that would fail to survive, as a result of predation, disease or other causes. However, in order to achieve the support of Parties to CITES for ranching, proponent Parties are required to show that commercial ranching will benefit the wild population.

Management of Wild Populations

The recovery of the Australian population of *C. porosus* has been impaired by external influences. In 1981, Messel *et al.* (1979–1987) expressed concern that netting practices used in the barramundi fishery hindered the movement of crocodiles between rivers and resulted in drowning of large numbers of adult *C. porosus*. They expressed particular concern about continued commercial fishing in the tidal waterways of Kakadu National Park. In 1987 the Australian National Parks and Wildlife Service began phasing out the commercial barramundi fishery, and completed the closure of all tidal waterways in the Park to commercial net fishing in 1989.

Crocodylus porosus is dependent for nesting on the freshwater wetlands scattered throughout the northern part of Northern Territory. These wetlands were degraded seriously by the introduced Asian water buffalo, *Bubalus bubalis*, which removed vast tracts of aquatic vegetation through grazing and wallowing, and breached levee banks, allowing saline tidal water to invade and destroy freshwater environments. The capture and removal of water buffalo and cattle as part of a program to eradicate brucellosis and tuberculosis has improved wetland habitats significantly in many coastal areas in the Northern Territory.

Currently, *C. porosus* and *C. johnstoni* are protected by Commonwealth, State and Territory conservation legislation. The removal of animals from the wild, and the possession or export of either species is illegal without a permit. The legislation applies to interstate and overseas trade and to skins or other crocodile products. Commercial use of crocodiles or parts thereof is restricted to specimens that have either been bred in captivity or have been taken in accordance with an approved management program.

Populations of both Australian crocodile species apparently have responded positively to legal protection and management for sustainable commercial use. Greatest numbers of *C. porosus* occur in the tidal rivers and associated coastal freshwater wetlands of the Northern Territory. Fewer occur in Western Australia and eastern Queensland because of limited suitable habitat. It is likely that this has always been true of Western Australia where most rivers drain rocky escarpment country characteristic of the Kimberley region. In Queensland, suitable coastal wetland habitats and tidal rivers draining into the eastern seaboard have been subject to extensive modification for agriculture, tourism and human settlements.

Management of Commercial Operations

Commercial operations involving crocodiles fall under State control in the first instance. Export of products from such operations requires approval from the Commonwealth Government under the *Wildlife Protection (Regulation of Exports and Imports) Act* of 1982. Individual operations based entirely on captive breeding are required to obtain Commonwealth Government approval before exporting any product derived from the operation.

Conservation management programs, based on the sustainable use of wild populations of *C. porosus* and *C. johnstoni*, have been implemented in Western Australia and the Northern Territory. In Queensland, commercial use of crocodiles is confined at present to closed-system captive breeding farms. Three commercial operations in Western Australia and six in the Northern Territory are based on conservation management strategies that involve regular annual harvests of wild eggs and juveniles for rearing under controlled conditions. Four operations in Queensland are exporting products from animals bred in captivity.

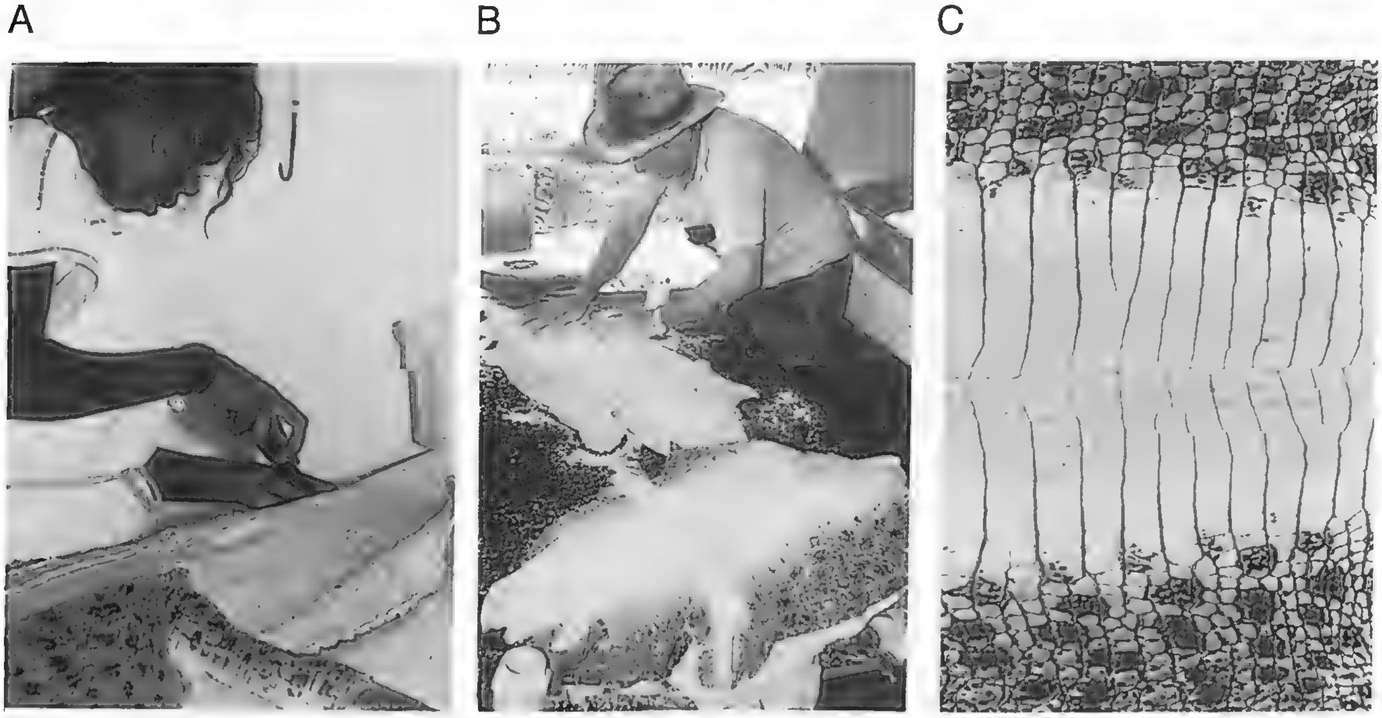

Figure 41.5 Production of crocodile skins. A, the carcass is skinned carefully from the dorsal surface to keep the ventral skin intact; B, salting of skins before they are tanned; C, the ventral skin is valued highly by producers of leather goods. (A, B, photos by G. Grigg; C, photo by G. Webb)

Crocodiles have been the subject of active research and management in the Northern Territory longer than elsewhere in Australia. Population monitoring has shown that commercial ranching is sustainable, and consequently the Northern Territory is implementing a second management program. Annual harvest quotas for *C. porosus* and *C. johnstoni* are determined by the Director of Conservation, based on the extent of nesting by each species. *Crocodylus porosus* eggs are collected from specified harvest areas, artificially incubated and distributed to participating farms under contract to the Government. *Crocodylus johnstoni* hatchlings are harvested by licensed farmers from allocated areas. The management program incorporates annual monitoring to assess the impact of commercial harvesting activities on the local and overall Northern Territory population of each species.

Management programs also include public education campaigns designed to promote general awareness of the dangers posed by crocodiles and responsible behaviour in areas frequented by crocodiles. Management agencies arrange for the removal of problem crocodiles from specified areas in the interest of public safety. These are made available to farms to be grown and skinned or to use as breeding stock, though large males cuaght as 'problem' animals are rarely successful as farm stock as they often damage enclosures and injure or kill highly valued reproductive females.

Future Directions

The continued conservation of both Australian species of crocodiles depends on retaining suitable areas of their preferred wetland habitats. The Commonwealth Government and the Governments of Queensland, Western Australia and the Northern Territory have established an extensive network of national parks and nature reserves in tropical Australia that, collectively, support viable populations of both species.

The increasing number of successful programs involving the sustainable use of crocodiles and the manner in which IUCN, CITES and other international organisations have embraced the principles of sustainable use of wildlife are clear demonstrations of the emerging importance of regulated commercial trade in conserving wild crocodiles. This strategy provides a practical and increasingly acceptable complementary approach to wildlife conservation through protected area management. In applying this strategy an economic value is conferred on the species, its habitat and other species dependent on the same habitat. Species that were formerly regarded as competitors with agriculture or as predatory pests of livestock become perceived as a valued resource, and their habitat is seen as an asset. Rather than alienating rural communities, this approach provides a foundation for changing perceptions and creates incentives to conserve crocodiles and other species outside protected areas.

Crocodiles and alligators can benefit local economies through eco-tourism. Tour operators can show these spectacular animals to clients in relative comfort and safety. Licensed safari operations targetting crocodiles for trophies and collection of live animals for zoos and wildlife parks are other management options.

Provided usage remains within the sustainable capacity of the wild resource, the enhancement of long-term conservation of wild crocodiles can accrue from these commercial activities. Clearly, the long-term conservation of crocodiles in Australia will depend on the adoption of practical policies and management strategies, which should be politically attractive, publicly acceptable and seek to achieve broadly based benefits for communities. The extent to which the general public, and local communities in particular, accept the continued presence of viable numbers of crocodiles in the wild will influence the extent of political sympathy for conservation.

42. BIOGEOGRAPHY AND PHYLOGENY OF THE CROCODYLIA

Ralph E. Molnar

The living crocodilians give no hint of the vast range of diversity of those now extinct. This contribution is intended primarily to provide some appreciation of the evolutionary history and range of diversity of pre-eusuchian crocodilians, and also to outline the history of crocodilians in Australia and the southwestern Pacific region.

Recent phylogenetic analysis has substantially altered the classification of crocodilians. The Protosuchia and Mesosuchia have been abandoned as formal taxa: the Mesosuchia has been combined with part of the Eusuchia which together constitute the Mesoeucrocodylia (Table 42.1; Benton & Clark 1988). The terminology has changed also. The animals previously called crocodilians are now termed crocodylomorphs, and the term 'crocodilian' is restricted to the common ancestor of the living taxa and its descendants (Fig. 42.1; Benton & Clark 1988). Here the term 'crocodilians' will also be used, informally, in its more traditional sense.

Crocodylomorphs arose from the plexus of primitive archosaurs known as thecodonts. They have changed less from thecodonts than any other advanced group of archosaurs (Olshevsky 1991). Because crocodilians and birds are the only surviving archosaurs, our understanding of the Archosauria owes much to the study of these groups. Both are characterised by a craniofacial pneumatic system which extends into the snout, and is indicated skeletally (at least plesiomorphically) by the antorbital fenestrae (Witmer 1987). This relationship of the pneumatic system to the antorbital fenestra fits in with the long-standing use of the antorbital fenestra as a defining character of archosaurs (Carroll 1988b), and suggests that the origin of the rostral part of the pneumatic system marked the origin of the Archosauria.

Previously, the classification of crocodilians rested largely on two characters: the position of the choanae in the palate, especially in relation to the pterygoids, and the form of the vertebral centra, especially the acquisition of procoely. Modern work has greatly increased the number of morphological characters used, particularly regarding the structure of the braincase and associated regions of the skull (for example, Norell 1989). Within the past fifteen years biochemical characters and relationships to parasites have been used in studies of the relationships of living eusuchians. These characters have traditionally been applied to living forms, however, advances in molecular palaeontology (Rowley 1991) may lead to the application of similar techniques to extinct crocodilian groups, with potentially enlightening results.

Table 42.1 Equivalent old and new terms (for example, Benton & Clark 1988) in crocodilian higher taxonomy.

Old terms	New terms
Crocodilia + Sphenosuchia	Crocodylomorpha
Crocodilia	Crocodyliformes
Mesosuchia + Eusuchia	Mesoeucrocodylia
Eusuchia (unaltered)	Eusuchia
Crocodylidae + Alligatoridae + Gavialidae	Crocodylia

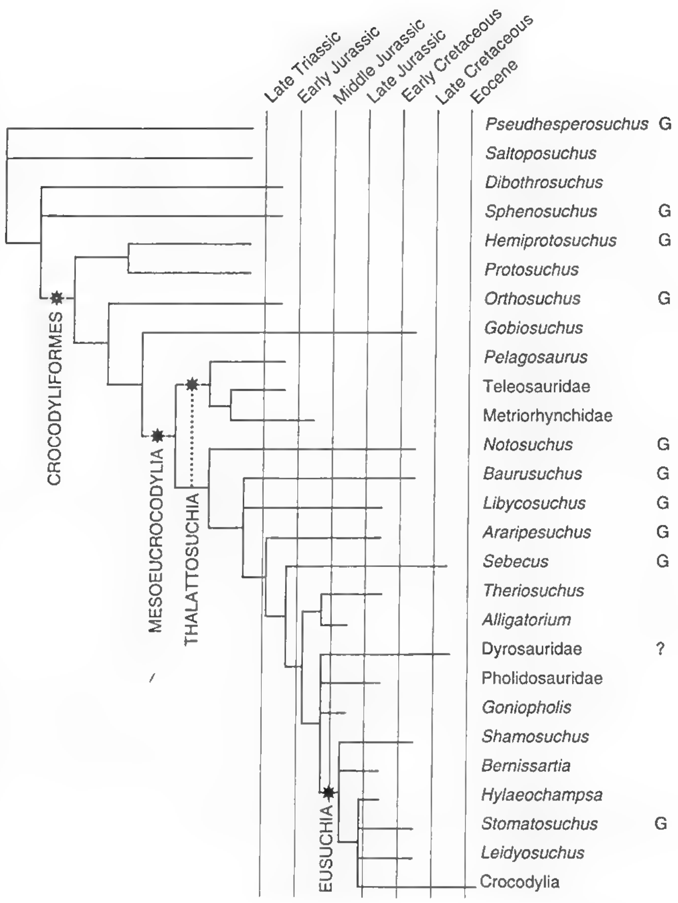

Figure 42.1 Phylogenetic relationships of selected crocodylomorphs, and their approximate time of origin. All taxa are extinct except for the Crocodylia. The major clades are identified by an asterisk. G = Gondwanan forms; ? = possible Gondwanan forms. (After Benton & Clark 1988; Willis 1993) [W. Mumford]

EVOLUTIONARY HISTORY AND ZOOGEOGRAPHY OF CROCODILIANS

Crocodilians differ from other archosaurs in having a squamosal that overhangs the quadrate laterally, contact between the prootic and the quadrate, an extensive craniofacial pneumatic system in the region of the braincase and elongate proximal carpals; they lack the postfrontal bone. The sphenosuchians are the oldest and most primitive crocodylomorphs (Fig. 42.2A). As currently used (for example, Olshevsky 1991) sphenosuchians are a paraphyletic group (*cf.* Benton & Clark 1988), lacking any uniquely defining characters. The grade contains the sister groups of the more advanced crocodylomorphs (Crocodyliformes), which includes the genera *Pseudhesperosuchus*, *Saltoposuchus*, *Dibothrosuchus* and *Sphenosuchus* (Fig. 42.1). They lived during Middle Triassic to Early Jurassic times, from 240 to 105 million years ago, and have been found in Brazil, Argentina, South Africa, China, Arizona, England and Germany; thus they were essentially cosmopolitan in Pangaea. The oldest and most primitive sphenosuchians are from South America, which suggests that crocodilians may have arisen in that part of Gondwana. Sphenosuchians appear to have been

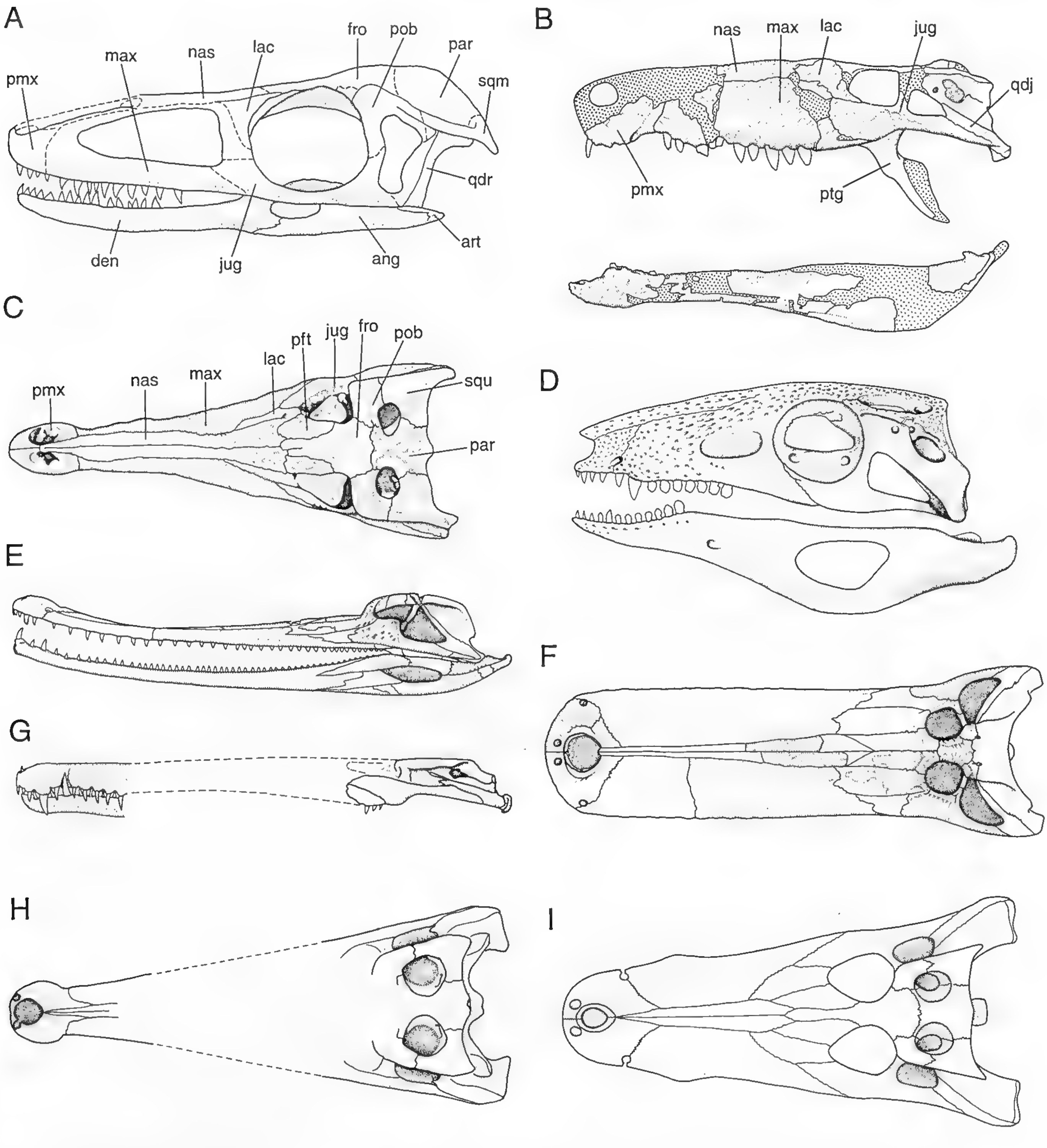

Figure 42.2 Selected skulls of extinct crocodilians. A, the sphenosuchian, *Barberenasuchus brasiliensis*, from the Middle Triassic of Brazil, is the oldest known well-preserved crocodilian, and suggests that crocodiles originated in Gondwana (lateral view); **B**, the ziphodont, *Sebecus icaeorhinus*, from the Eocene of Argentina, may have been a terrestrial carnivore (lateral view); **C**, dorsal view of *Sebecus icaeorhinus*; **D**, the tooth-row of the brevirostrine, *Uruguaysuchus aznarezi*, of the Late Cretaceous of Uruguay is almost mammal-like in its differentiation and may have been herbivorous (lateral view); **E**, lateral view of the nettosuchian, *Mourasuchus atopus*, from the Miocene of Columbia; **F**, dorsal view of *Mourasuchus atopus*; **G**, the longirostrine, *Harpacochampsa camfieldensis*, from the Miocene of the Northern Territory appears not to be closely related to other endemic Australian crocodilians (lateral view); **H**, dorsal view of *Harpacochampsa camfieldensis*; **I**. the mekosuchine, *Australosuchus clarkae*, from the Miocene of South Australia presumably resembled the stem group animals of the mekosuchines (dorsal view);. **ang**, angular; **art**, articular; **den**, dentary; **fro**, frontal; **jug**, jugal; **lac**, lacrimal; **max**, maxilla; **nas**, nasal; **par**, parietal; **pft**, prefrontal; **pmx**, premaxilla; **pob**, postorbital; **ptg**, pterygoid; **qdj**, quadratojugal; **qdr**, quadrate; **sqm**, squamosal. (After A, Mattar 1987; B,C, Kuhn 1968; D, Rusconi 1932; E, F, Langston 1965; G, H, Megirian *et al.* 1991; I, Willis & Molnar 1991b) [T. Wright]

gracile, quick-moving terrestrial predators. Together with the protosuchians, they indicate that crocodilians originated as terrestrial predators, and only some 55 million years later did crocodilians adopt the amphibious mode of life that they exploited so successfully. When they originated, the 'crocodilian niche' of amphibious ambush predator was occupied by the phytosaurs, superficially crocodile-like archosaurs. Crocodilians exploited the amphibious lifestyle only after the extinction of the phytosaurs.

The protosuchians, once thought to be the earliest crocodilians, are now considered to be paraphyletic, consisting of the monophyletic Protosuchidae (includes *Hemiprotosuchus* and *Protosuchus*) and sister groups of the mesoeucrocodylians including the genera *Gobiosuchus* and *Orthosuchus* (Fig. 42.1). The protosuchids and their allies are similar in their level of evolution. Both have choanae anterior in the palate, between the maxillae and palatines, and show no indication of a bony secondary palate. Like most pre-eusuchians, they had amphicoelous vertebral centra. Most lived during the Early Jurassic, although there is a Late Triassic genus from Argentina. Protosuchians have been found in southern South America, southwestern and northeastern United States of America, South Africa and China. As with the sphenosuchians, these records suggest a cosmopolitan Pangaean distribution, and the oldest and most plesiomorphic forms are found in North and South America.

The traditional mesosuchians are a paraphyletic group characterised by a more posterior location of the choanae between the palatines and pterygoids. The location of the choanae near the pharynx, where presumably they function as in modern crocodilians, is widely taken to reflect the adoption of amphibious habits. Mesosuchians are now included together with the Eusuchia, in the Mesoeucrocodylia (Table 42.1; Whetstone & Whybrow 1983). The Mesoeucrocodylia have a bony secondary palate formed of the maxillae and palatines, foramina for cranial nerves IX–XI well within the otoccipital and the canal for the temporo-orbital vein, and cranial nerve V walled by the quadrate, squamosal and otoccipital. The Mesozoic mesoeucrocodylians, too, were cosmopolitan in distribution, probably reflecting the equable climates of the Mesozoic (Buffetaut 1979).

Mesoeucrocodiles exhibited great diversity (Buffetaut 1982). Some, such as goniopholids, were the first crocodilians to adopt the lifestyle of amphibious ambush predator. Thalattosuchians successfully adapted to marine life, where a long snout developed, associated with massive jaw-closing muscles, flippers and a heterocercal tail. Hsisosuchians and sebecids seem to have been terrestrial predators. They acquired deep, laterally compressed snouts and trenchant, serrate teeth (known as ziphodont teeth) like those of carnivorous dinosaurs (Fig. 42.2B, C). The relatively short-snouted notosuchians (a paraphyletic group) were also apparently terrestrial. The blunt, intricately fluted cheek teeth of the uruguaysuchians (Rusconi 1932) resembled those of herbivorous dinosaurs and lizards, suggesting they were also herbivorous (Fig. 42.2D). Others, including an unnamed taxon from Malawi, had heterodont dentition, with cheek teeth like those of some contemporaneous mammals (Clark, Jacobs & Downs 1989). Notosuchians were South American and African forms which may yet be discovered in Australia.

The Gondwanan crocodilians of the Late Mesozoic seem to have evolved independently of those in Laurasia. But in early Tertiary times, Laurasian eusuchians established themselves in Africa and South America and perhaps caused the extinction of some of the more plesiomorphic southern taxa (Buffetaut 1979).

Although the phylogenetic relationships among crocodilians are reasonably clear, there are few forms that actually exemplify transitions between major groups. For example, the gap between protosuchian and thalattosuchian levels remains unbridged, nor is there any better understanding of the process by which some groups of ziphodont crocodilians (hsisosuchians, sebecids) originated. However a brevirostrine (short snouted) lineage, from which others diverged, seems to have persisted from the sphenosuchian period almost until the origin of the eusuchians (*cf.* Buffetaut 1982; Benton & Clark 1988). Some of the diverging lineages evolved snout proportions like those of modern alligators or crocodiles, such as the goniopholids, but others became longirostrine (long snouted) or ziphodont.

The eusuchians are the only traditional crocodilian group that survived the test of phylogenetic analysis. They are characterised by pterygoids which surround the choanae entirely. The Crocodylia are those eusuchians in which the anterior and posterior margins of the scapula are nearly parallel (Benton & Clark 1988). The oldest eusuchians date from the Early Cretaceous (approximately 130 million years ago), whilst the oldest crocodylians (*sensu* Benton & Clark) are difficult to date, although they may be no older than Eocene, about 50 million years (Fig. 42.1; summarised in Densmore & Owen 1989).

Morphologically, eusuchians are more uniform than earlier mesoeucrocodylians, and differ mainly in skull form, especially that of the snout. Among the living species, the differences between the broad, and moderately broad-snouted, forms (*Alligator*, *Caiman*, most species of *Crocodylus*, *Melanosuchus*, *Osteolaemus*, and *Paleosuchus*) and the narrow-snouted fish-eaters (*Gavialis*, *Tomistoma*, *Crocodylus cataphractus*, and *C. johnstoni*) are well known. The living eusuchians are divided in two families, the Alligatoridae and Crocodylidae, with the position of the gavials being uncertain (Norell 1989), as discussed later (Fig. 42.3). Extinct taxa, however, included the ziphodont pristichampsines, which were apparently terrestrial predators of Asia, Europe and North America, and convergent forms with very long and broad snouts (*Stomatosuchus* and *Mourasuchus*; Fig. 42.2E, F) (Langston 1965, 1966). Langston (1965) suggests these latter may have engulfed small floating animals, or even plants, whilst cruising slowly through the water, or perhaps scooped up bottom life. Both genera inhabited Gondwanan continents (Africa and South America respectively), and perhaps they, or similar forms, lived in Australia.

Thus extinct eusuchians and other mesoeucrocodylians exhibited a wide range of cranial forms, not represented among the surviving taxa.

GENERAL FEATURES OF CROCODILIAN EVOLUTION, ZOOGEOGRAPHY AND EXTINCTION

There are no recent comprehensive reviews of crocodilian evolution or palaeozoogeography, although some phylogenetic studies have been made (Benton & Clark 1988; Norell 1989). The several recent studies of zoogeography (cited in Taplin & Grigg 1989) concern only crocodylians, generally accepted as having a relictual distribution.

Mesoeucrocodylian lineages repeatedly adopted similar cranial forms. The piscivorous longirostrine skull evolved at least eight times (thalattosuchians, pholidosaurids, tethysuchians, *Thoracosaurus*, *Euthecodon*, gavials, *Toyotamaphimeia*, *Crocodylus cataphractus*). Ziphodont structure developed at least four times (hsisosuchians, sebecosuchians, pristichampsine crocodylids, and some mekosuchian crocodylids), possibly more (*cf.* Benton & Clark 1988). And, as mentioned previously, a broad, flat, 'duck-like' snout evolved independently in at least two lineages. These parallelisms usually occurred as a series of temporal replacements, although taxa exhibiting parallelisms did sometimes exist simultaneously in different regions, for example, among longirostrine forms (Buffetaut 1979). There is also a series of replacements among the terrestrial groups, at least in Laurasia. Sphenosuchians were replaced by protosuchids, followed by the sequential appearance of atoposaurs in Europe and hsisosuchians in China, *Gobiosuchus*, and finally pristichampsines.

Crocodilians seem not to have been greatly affected by the mysterious Cretaceous-Tertiary extinctions (Buffetaut 1979). Instead, because crocodilians are unable to reproduce at low temperatures (Magnusson, Vliet, Pooley & Whitaker 1989), extinctions have generally been accepted as having been caused by increasingly colder climates. The major crocodilian extinctions occurred later, in the Late Tertiary, and seem to have been caused by the lower temperatures of the Late Cenozoic glaciations (Buffetaut 1979). Until the Late Tertiary, crocodilians seem to have became extinct in a piecemeal fashion, related more to trophic competition than to any general environmental deterioration.

Regional endemism was evident on the southern continents after the mid-Mesozoic. Endemic genera and families inhabited both South America (peirosaurids, various notosuchian groups, dolichochampsids, sebecids, *Charactosuchus*) and Africa (libycosuchids, *Stomatosuchus*, *Aegyptosuchus*, *Euthecodon*) during the Cretaceous and Tertiary. Some of these groups were replaced by crocodylids on both continents during the Cenozoic.

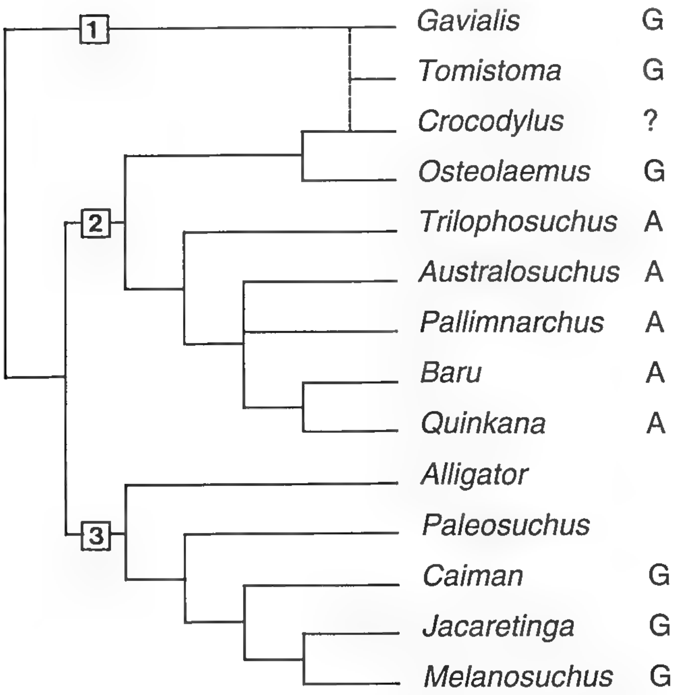

Figure 42.3 Phylogenetic relationships within the Crocodylia indicating, the uncertain family status of the Gavialidae (1), and the Crocodylidae (2) and Aligatoridae (3). G = Gondwanan forms; A = Australian endemics. (After Benton & Clark 1988; Willis 1993) [W. Mumford]

Crocodilian palaeozoogeography can be used in reconstructing ancient climates since crocodilians are limited in their ranges by environmental temperatures. However, care must be taken in such interpretations as alligators are able to survive under temporary ice cover (Brisbin 1989), and perhaps some extinct taxa were also able to do so. Thus the occurrence of crocodilian remains in the Early Cretaceous of southern Victoria (Rich & Rich 1989), need not contradict the reported near-freezing (presumably winter) ground water temperatures (Rich & Vickers-Rich 1992). The presence of crocodilians however seems to be a good indication that climates were not more rigorous than the occasional winter snowfall or freeze.

Another point of interest is the ability of eusuchians to disperse through salt water. Taplin & Grigg (1989) presented an interpretation of crocodylid evolution based on their studies of osmoregulation. The function and efficacy of the osmoregulatory organs are closely related to the ability to disperse through salt water, and hence to the role of oceans and seas as a barrier to or avenue of dispersal by crocodilians. Taplin & Grigg (1989) contended that effective osmoregulatory structures developed early in eusuchian history and so these animals were not restricted in their dispersal by oceans. However, intriguing though this interpretation is, no outgroup comparison was included in the phylogenetic analysis, so there remains some doubt that effective osmoregulatory structures were developed early in eusuchian history.

RELATIONSHIPS OF *GAVIALIS* AND *TOMISTOMA*

There is some contention amongst taxonomists regarding the relationships of the living longirostrine crocodylians, *Tomistoma* and *Gavialis* (Fig. 42.3). Palaeontologists of the last century generally considered the two genera to be closely related, but more recently Kälin (1955) and Telles Antunes (1961) both considered them to be independently derived convergent forms. This view was not accepted by all workers. For example, Langston (1965) pointed out similarities between early gavials and *Tomistoma*. More recently the application of biochemical and immunological methods suggested that *Gavialis* and *Tomistoma* are closely related (Densmore & Dessauer 1984; Hass, Hoffman, Densmore & Maxson 1992). This view has been accepted by some, such as Buffetaut (1985), but strongly contested by others. Buffetaut has argued that fossil gavials such as *Eogavialis* are very similar to *Tomistoma*, and that the differences arose late in gavial evolution and hence do not indicate a long-standing separation of the two lineages.

A dissenting view was held by Tarsitano (1985), Tarsitano *et al.* (1989) and a few other workers. Tarsitano (1985) regarded *Gavialis* as having been distinct from all other eusuchian lineages for a long time, presumably since the early Cenozoic. He noted major differences in the structure of the braincase, which in most eusuchians has been 'verticalised'. This term refers to the deepening of the basisphenoid and basioccipital such that they face posteriorly, rather than ventrally. It occurs after the first year of life and so is not seen in hatchlings. In *Gavialis*, the braincase retains its plesiomorphic condition. Major differences in the musculature of the hind limb and tail of gavials have also been reported (Frey *et al.* 1989).

Although cogently argued, this view is not generally accepted. Tarsitano's interpretation does not account for the biochemical data, and it assumes that the unusual features of gavials reflect their ancestry rather than being autapomorphies. In a paper apparently unknown in the west, Aoki (1976) argued that the absence of 'verticalisation' in the braincase of *Gavialis* is a paedomorphic character, a retention into adulthood of the condition at hatching. In addition, as Tarsitano admits, 'verticalisation' is a convergent character in archosaurs, as it occurred in several Mesozoic pre-eusuchian crocodilians and even in large theropod dinosaurs, such as *Tyrannosaurus*. So it may have evolved convergently among eusuchians and not indicate a long period of separation of the gavial lineage from those of the other eusuchians.

The problem of the relationships of *Gavialis* and *Tomistoma* is part of a larger problem of the relationships of all longirostrine crocodilians. Until recently, the relationships of the Mesozoic longirostrines have been unsettled, and even among living taxa the relationship of *Gavialis* and *Tomistoma* is not the only one in doubt. Some taxonomists (for example, Aoki 1976) consider *Crocodylus cataphractus* to belong to the monospecific genus, *Mecistops*. The longirostrine habitus has evolved independently at least eight times, and it simply is not clear which characters of these crocodilians are associated with the development of the longirostrine habitus, and which reflect ancestry.

CROCODILIANS IN THE SOUTHWESTERN PACIFIC REGION

It is useful to look at the crocodilians of the south-western Pacific region to appreciate Australian crocodilians, for these taxa share the same zoogeographic and phylogenetic patterns. In this region, the distributions of insular endemic *Crocodylus* species form a pattern 'superimposed' on the much broader range of *C. porosus.* The latter occurs throughout the region, occasionally as far as Ponape (Allen 1974), 480 km north of New Zealand (Robb 1980) (Fig. 42.4). The insular endemics are possibly derived from populations of *C. porosus* that invaded the inland waters (*cf.* Ross & Magnusson 1989). They include *C. novaeguinae* in New Guinea, *C. johnstoni* in Australia, *C. raninus* in Borneo (Ross 1990) and *C. mindorensis* on several of the southern Philippine Islands (Luzon, Mindoro, Masbate, Samar, Negros, Busuanga, Mindanao and Jolo; Ross & Magnusson 1989). There seems to be an Indonesian freshwater crocodile of unknown taxonomic affinities (Ross 1986), and possibly a second endemic in Papua New Guinea (Ross & Magnusson 1989).

Such a pattern probably persists from the past and endemic crocodilians might have lived on other southwestern Pacific islands. For example, the New Caledonian *Mekosuchus inexpectatus* became extinct less than two millennia ago. It was a plesiomorphic eusuchian with unusual derived features (Balouet & Buffetaut 1987; Balouet 1989); its ancestors probably diverged

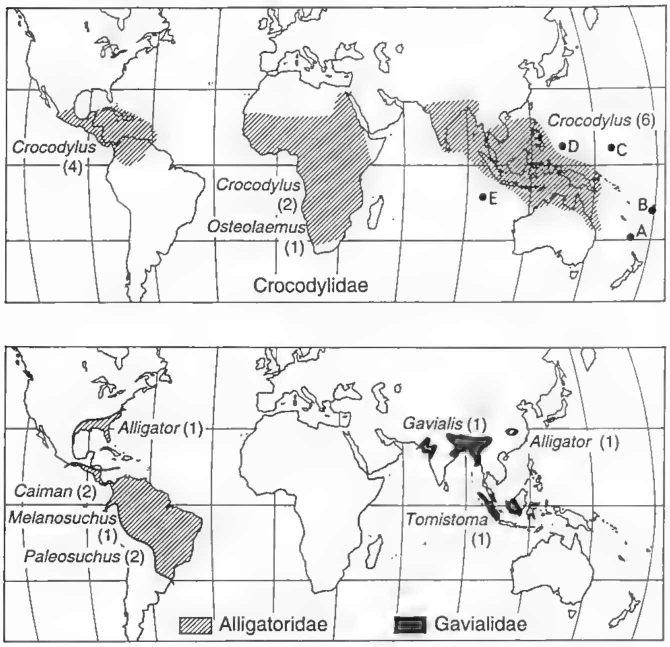

Figure 42.4 Distribution of the extant crocodilian families Crocodylidae, Alligatoridae and Gavialidae. The labelled dots represent reported sightings of individuals of *Crocodylus porosus*. A, 480 km north of North Cape, New Zealand; B, Fiji; C, Ponape; D, Palau; and E, Cocos (Keeling) (Sources: A, Robb 1980; B, D, E, Schmidt 1957; C, Allen 1974) (After Alderton 1991) [W. Mumford]

from the eusuchian line near the beginning of the Tertiary. It is believed to have fed on snails.

Pleistocene Java was home to two extinct crocodiles. *Crocodylus ossifragus*, a broad-snouted species, and *Gavialis bengawanicus*, which occurred near the eastern end of the range of the genus. This range may have extended even further east, as fragmentary remains from Murua (Woodlark) Island (*Gavialis papuensis*) include portions of a rostrum and jaws with laterally directed alveoli. Once thought to indicate a *Euthecodon*-like form (Molnar 1982), they may derive from a malformed individual of *G. bengawanicus* (Aoki 1988).

The southwestern Pacific reflects the situation of crocodilians in Australia, showing a greater past diversity now reduced to members of only the single genus *Crocodylus* (Fig. 42.4).

The most ancient known Australian crocodile is a relatively small animal, of uncertain affinities, from the Early Cretaceous deposits at Lightning Ridge, New South Wales (Etheridge 1917). Little is known of this form, if indeed only a single taxon is represented. Procoelous vertebrae are present (Molnar 1980) indicating that it was either a eusuchian or was closely related to eusuchians.

A longirostrine form, known only from a jaw, from the Queensland Eocene (Willis & Molnar 1991a) suggests that crocodilians were diverse in Australia early in the Cenozoic. Another Eocene jaw from Queensland represents a species of more typical cranial proportions. Many of the later Australian fossil crocodilian taxa are united by a series of characters which include the reduction or absence of the anterior process of the palatine, large anteriorly located palatine fenestrae, a large triangular exposure of the supraoccipital on the skull roof, well-developed alveolar processes in both jaws (Willis, Molnar & Scanlon 1993), and a marked disparity of alveolar size in the jaws (Fig. 42.2G). These features are possessed by *Mekosuchus* (Willis *et al.* 1993), suggesting an indigenous radiation of Australian and southwestern Pacific crocodilians. Willis and co-authors called this the mekosuchine radiation. Its members were diverse, and several genera are represented in some deposits (Archer, Hand & Godthelp 1991). They adopted a variety of forms. Some species, including *Pallimnarchus pollens*, had very broad, low skulls reminiscent of those of temnospondyl amphibians, others were ziphodont (*Quinkana fortirostrum*) or semi-ziphodont (*Baru darrowi*; Willis, Murray & Megirian 1990). There were small terrestrial predators (*Trilophosuchus rackhami*), and others that resembled typical crocodylids such as *Australosuchus clarkae* and *Kambara murgonensis*.

However, it is not clear that all pre-Pliocene Australian crocodilians were mesosuchines. *Crocodylus* has been reported from the Miocene Waite Formation of the Northern Territory (Woodburne 1967), but this material needs further study in the light of recent discoveries. A longirostrine crocodilian, *Harpacochampsa camfieldensis*, from the Miocene Camfield Beds in the Northern Territory (Megirian, Murray & Willis 1991) may not have been a mekosuchine (Fig. 42.2H, I).

Non-mekosuchine crocodilians were present in the late Tertiary. *Crocodylus porosus* first appears in the Allingham Formation of the Pliocene in north-eastern Queensland (Molnar 1979). Fossils of *Crocodylus johnstoni* appear in the Pleistocene of Queensland's Gulf country (Willis & Archer 1990) shortly after, in geological terms, the native mekosuchine crocodilians apparently became extinct. This extinction has been attributed to competition with the 'invaders' from Asia (Archer *et al.* 1991) leaving the present impoverished crocodilian fauna of Australia.

Throughout the southwestern Pacific region a diversity of endemic mekosuchine crocodilians has become extinct, to be replaced by a pattern of endemic species of *Crocodylus*, superimposed on the range of seagoing *C. porosus* (Fig. 42.4).

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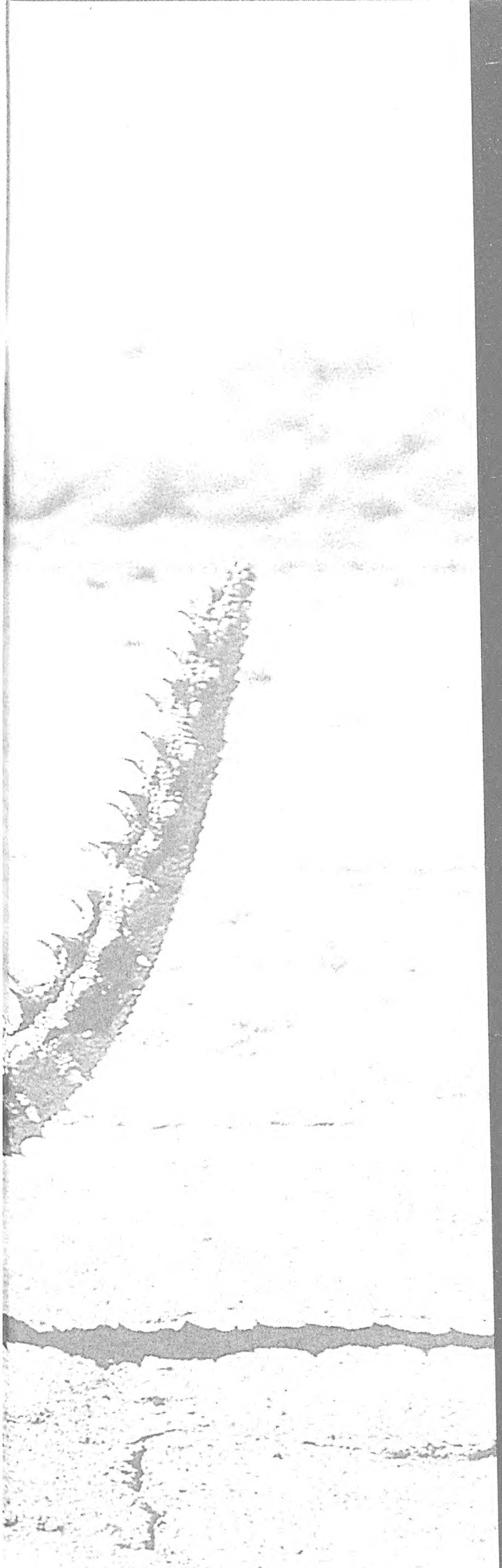
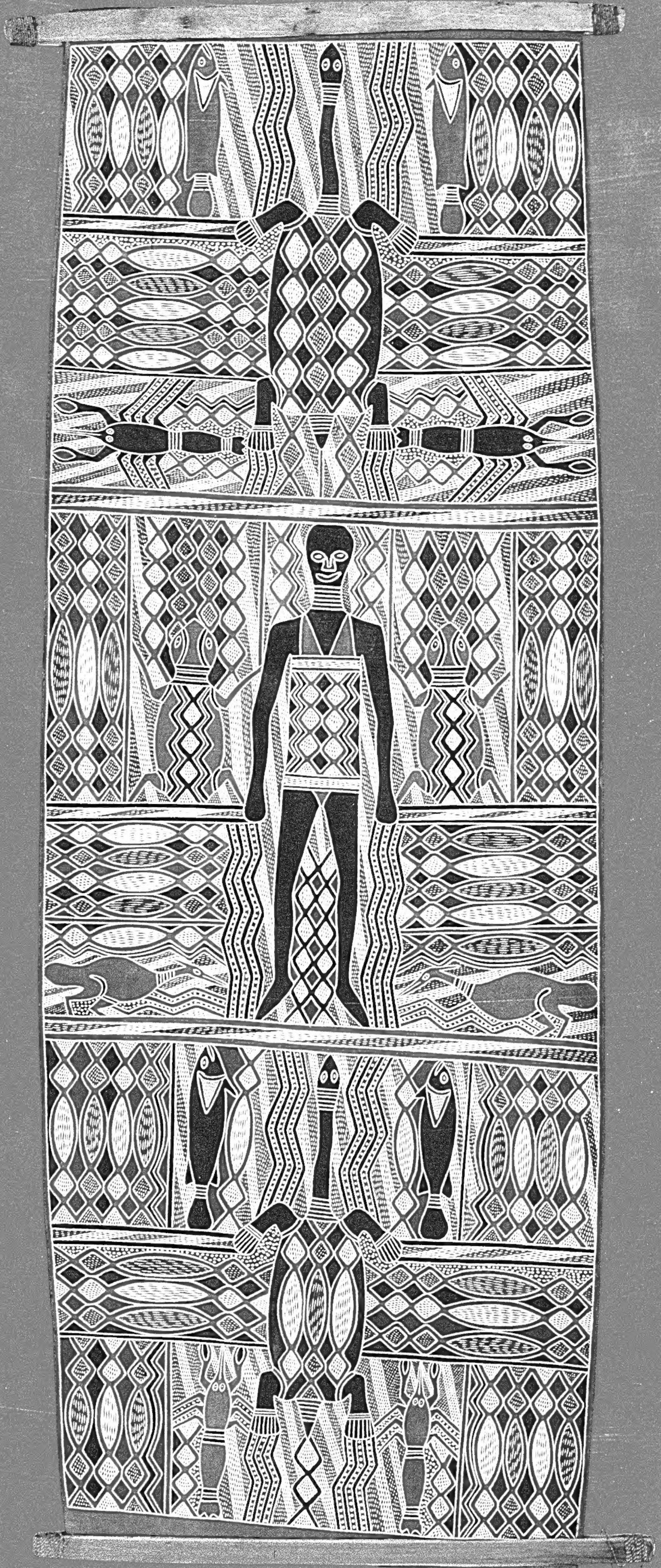


Yangarriny Dalwangu (1932 –)
Northeast Arnhem Land, Northern Territory
Ancestors of the Yirritja moiety circa 1979
ochres on *Eucalyptus* bark 155.0 × 56.0 cm
Collection: Australian National Gallery, Canberra



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