



# FAUNA *of* AUSTRALIA



## 35. FAMILY ELAPIDAE

Glenn Shea, Richard Shine &  
Jeanette C. Covacevich



Pl. 8.4. *Vermicella annulata* (Elapidae): a burrower, feeds on blind snakes (Typhlopidae) in diverse habitats, from wet coastal forests to spinifex deserts; central and eastern Australia to central west coast. [J. Wombey]



Pl. 8.5. *Simoselaps warro* (Elapidae): a nocturnal burrower, inhabiting forests and woodland along the north-eastern coast and ranges of Queensland. [G. Shea]





Pl. 8.6. *Demansia psammophis* (Elapidae): found from coastal habitats to the arid interior, this species is widespread in mainland Australia except in the central north. [J. Wombey]



Pl. 8.7. *Notechis scutatus* (Elapidae): occupies a wide range of habitats from rainforests to open woodlands and floodplains; its main food is frogs; found in south-eastern mainland Australia. [J. Wombey]



Pl. 8.8. *Pseudonaja guttata* in aggressive posture; inhabits tussock grassland of interior north-eastern Australia. [H. Cogger]



Pl. 8.9. *Acanthophis pyrrhus* (Elapidae): occurs in desert regions and adjacent arid lands in central and western Australia. [H. Cogger]





Pl. 8.10. *Oxyuranus microlepidotus* (Elapidae): Australia's most venomous snake; it feeds mainly on rats and occurs on floodplains in the central east of the continent.  
[J. Wombey]



Pl. 8.11. *Furina diadema* (Elapidae): raises its characteristically coloured head high when alarmed; often associated with ants and termites in eastern Australia.  
[H. Cogger]



Pl. 8.12. *Suta suta* (Elapidae): in coil-spring offensive posture; found in sandy-stony deserts to savannah woodlands in central and eastern Australia.  
[H. Cogger]

## 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).

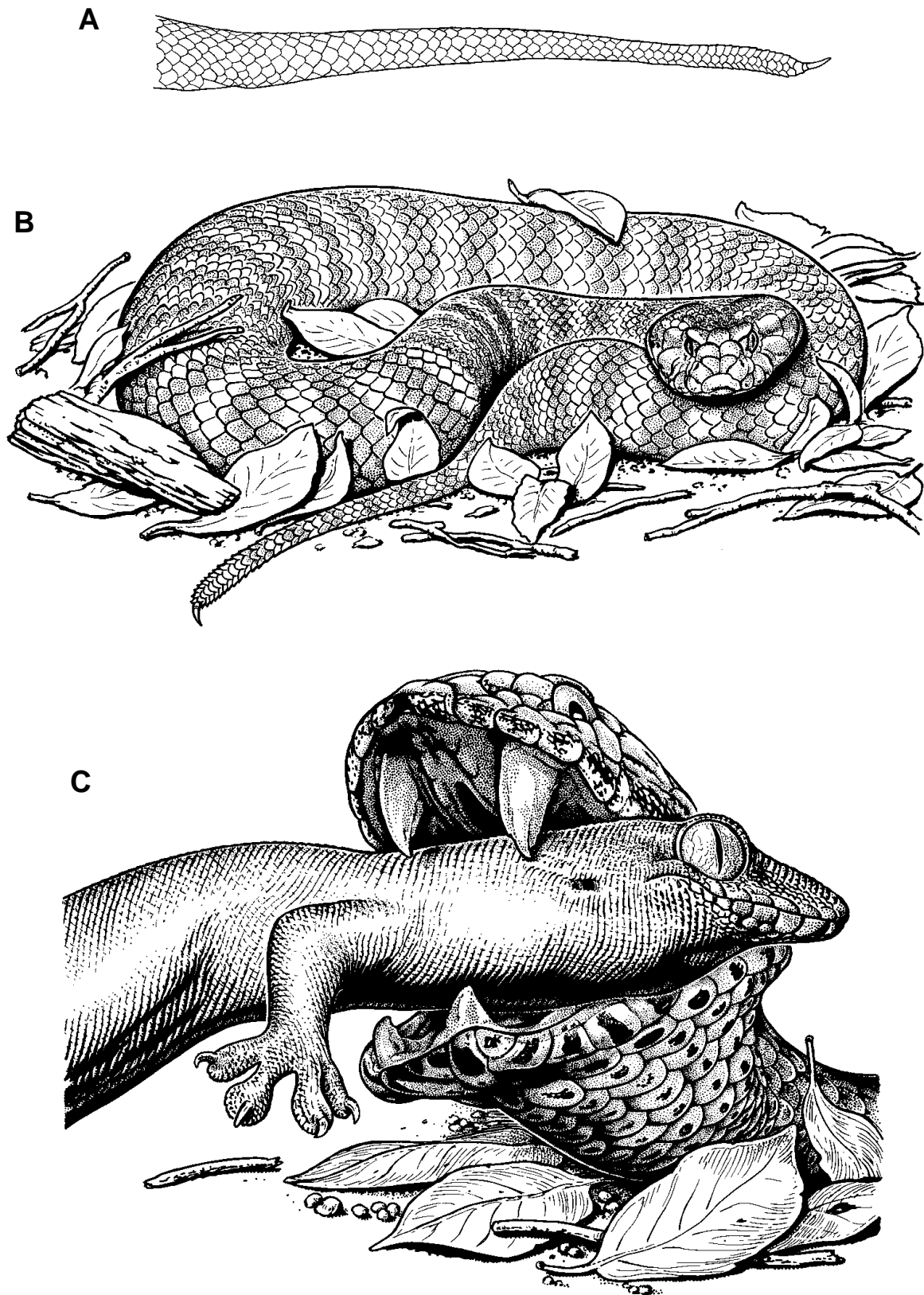
Venoms of Australian elapids have a predominance of pre- or post-synaptic neurotoxins. Some are extremely potent to humans. Venoms also have significant myotoxic, coagulant, and anti-coagulant effects, and less significant impacts on platelet function and haemolytic activity (White 1987a).

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.





**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]



## 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).

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 allozyme 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).

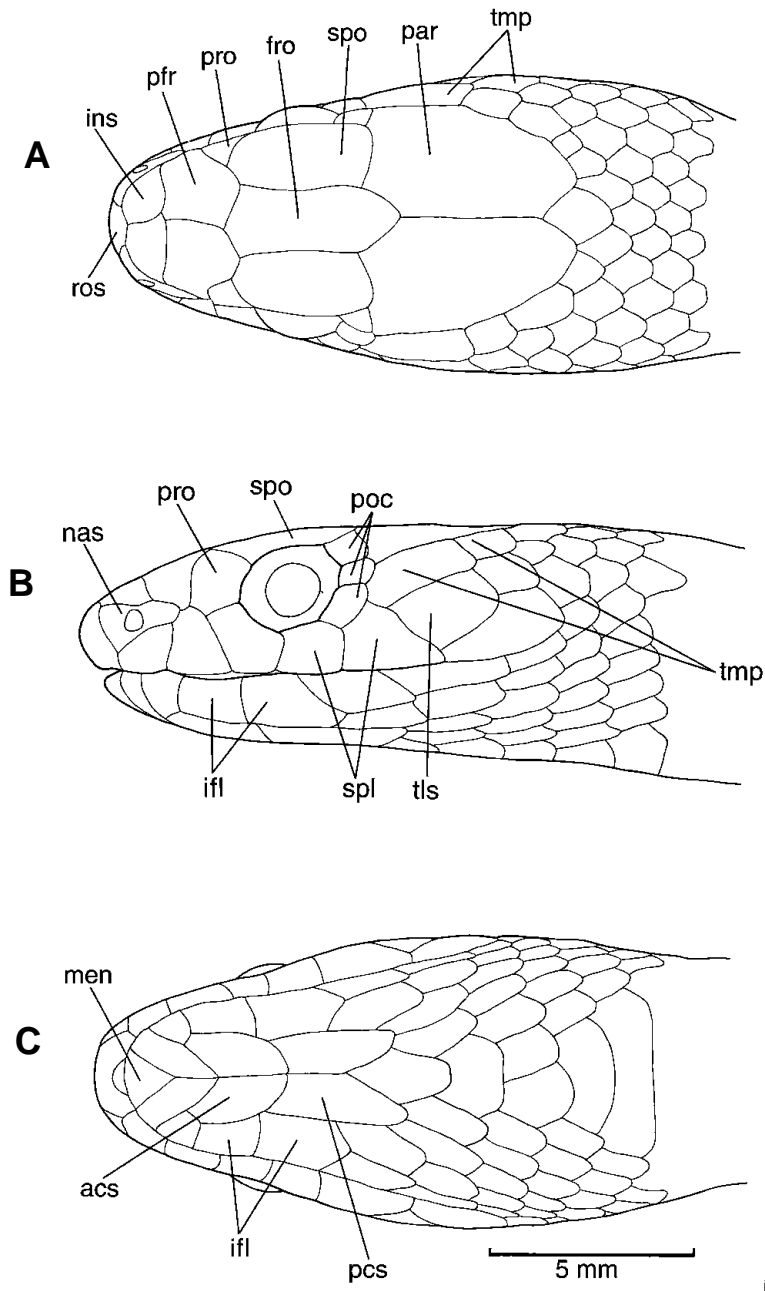
Mass of adult elapids is rarely reported. However, large adult *Notechis ater* from Chappell Island weigh nearly 1.7 kg (Schwaner & Sarre 1988). Neonates of small elapid species may weigh as little as 0.8 g (*Rhinoplocephalus*; Shine 1984a) and 1.2 g (*Hemiaspis*; Shine 1987a).

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 (Fig. 35.1A). This structure forms a lure for attracting prey (Fig. 35.1B, C).

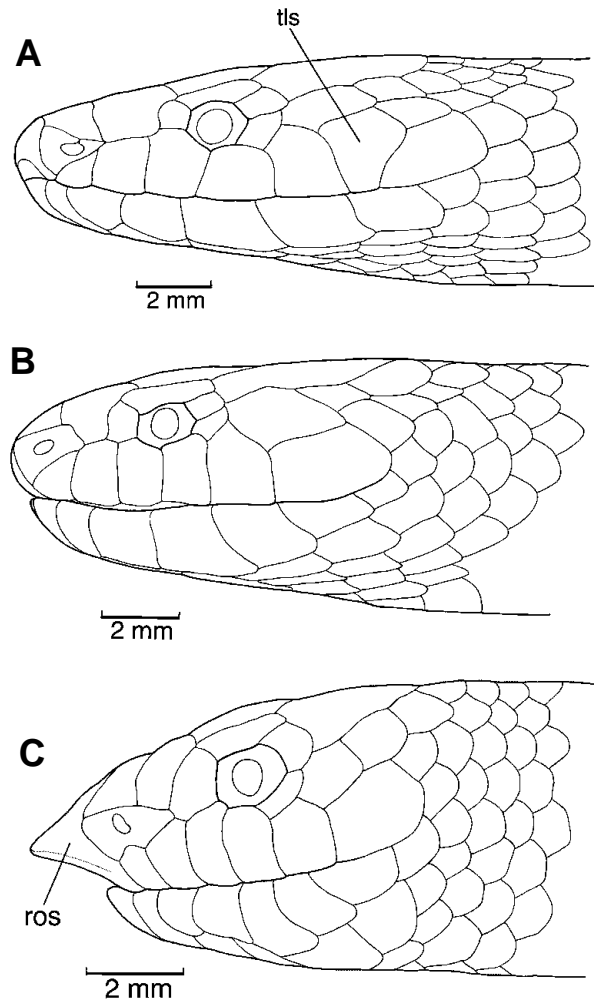
All elapids have a regular pattern of large head shields (Fig. 35.2). Along the head dorsum, these are the rostral, paired internasals, paired frontonasals, frontal, and paired parietals. Laterally, each nostril lies within a nasal scale, which may be deeply grooved. In *Rhinoplocephalus bicolor* and *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.



**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]

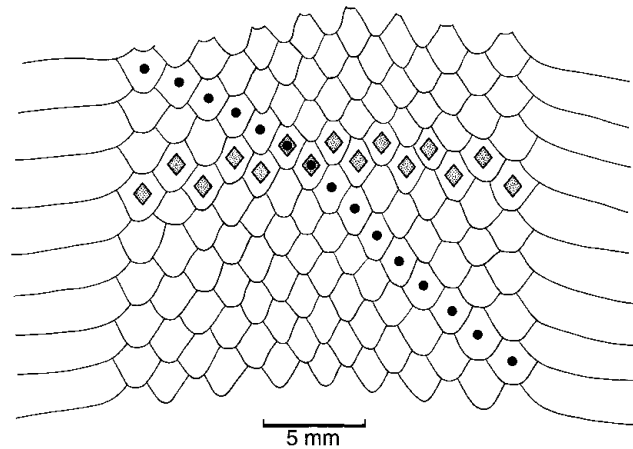


**Figure 35.3** Head shields in lateral view. **A**, *Furina ornata*, in which the temporolabial reaches the lip; **B**, *Cacophis krefftii*, which lacks the temporolabial; **C**, *Simoselaps roperi*, a burrowing species in which the rostral shield is modified to form a cutting edge. **ros**, rostral shield; **tls**, temporolabial. [B. Jantulik]

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 ventrolaterally (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).





**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 characteristic of this species. Alternative methods of counting scale rows are indicated by round and rhombic symbols. [B. Jantulik]

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).

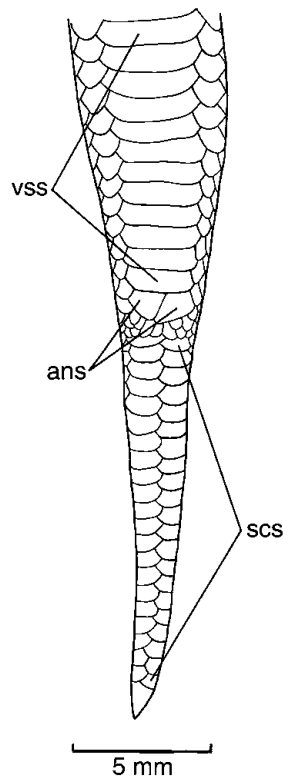
*Vermicella* (Pl. 8.4) and many *Simoselaps* species have a strong body pattern of alternating brightly coloured light and dark transverse bands. Transverse bands, often less distinct, narrower or less regular, also occur in *Acanthophis*, *Denisonia devisi*, *Hoplocephalus bungaroides*, *H. stephensii*, *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).

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).



**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]

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.

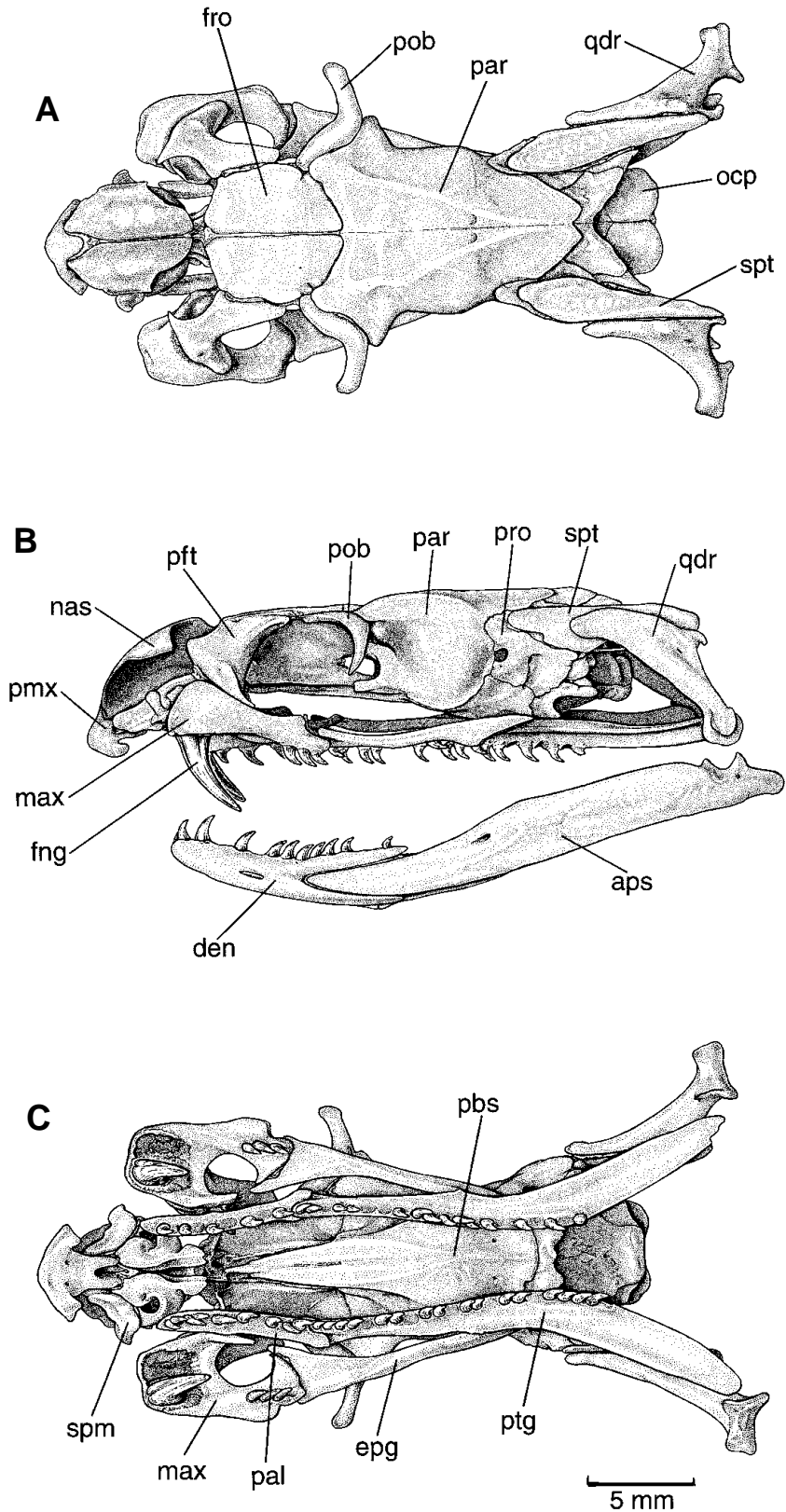
Sexual dimorphism in head size relative to body length occurs in several species. Males have significantly larger heads than females of the same body length in *Austrelaps*, *Rhinoplocephalus*, *Suta*, *Furina*, *Pseudechis* and *Simoselaps*, but head sizes tend to be larger in females in some other 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 1985a). 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).



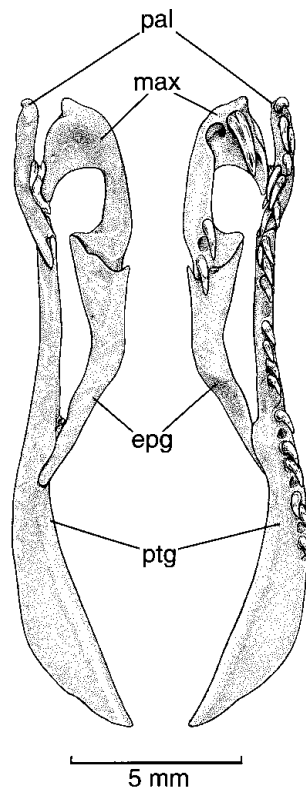


**Figure 35.6** The skull of *Pseudechis guttatus*. **A**, dorsal view; **B**, lateral view; **C**, ventral view. **aps**, fused articular, prearticular and surangular; **den**, dentary; **epg**, ectopterygoid; **fng**, fang; **fro**, frontal; **max**, maxilla; **nas**, nasal; **ocp**, otoccipital; **pal**, palatine; **par**, parietal; **pbs**, parabasisphenoid; **pft**, prefrontal; **pmx**, premaxilla; **pob**, postorbital; **pro**, prootic; **ptg**, pterygoid; **qdr**, quadrate; **spm**, septomaxilla; **spt**, supratemporal. [B. Jantulik]

### Skeletal System

Australian elapid skulls have been illustrated by a number of authors, including Fairley (1929), Thomson (1933), Worrell (1956a, 1956b, 1961a, 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).

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.



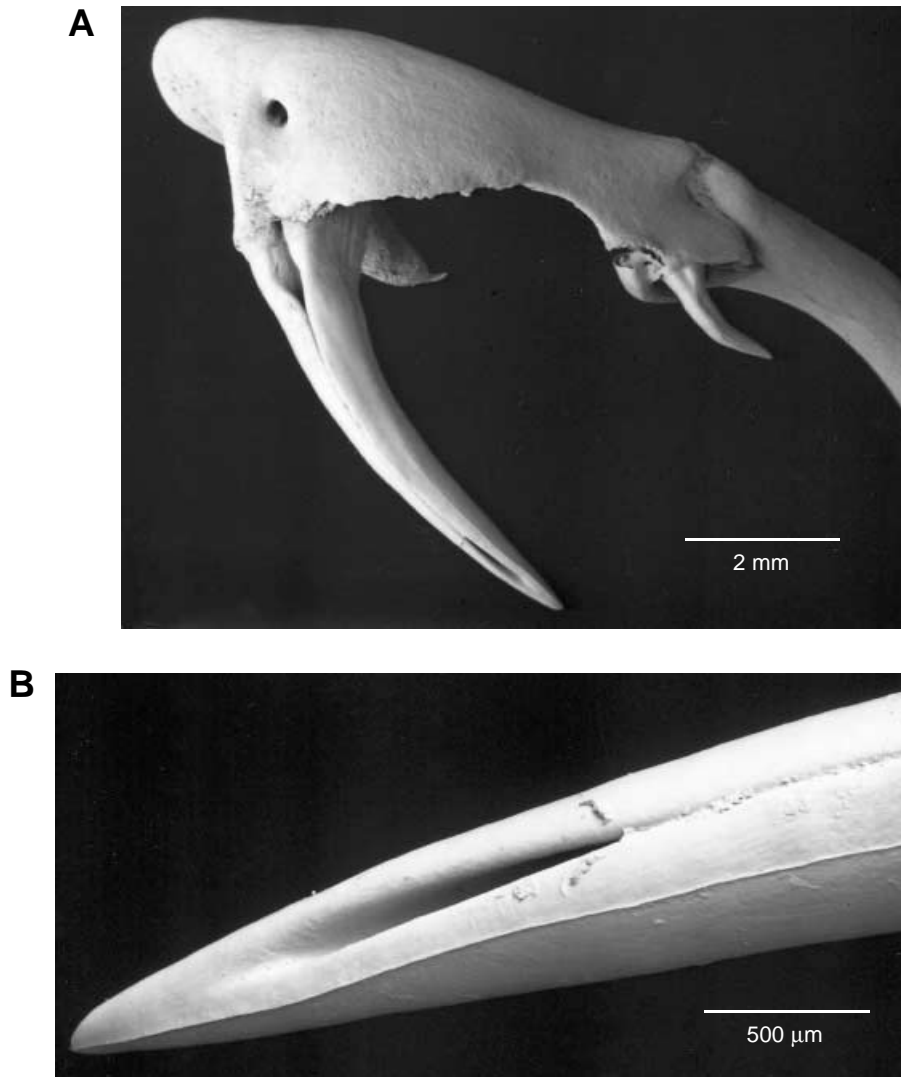
**Figure 35.7** Left palatal complex of *Echiopsis curta*. **A**, dorsal view; **B**, ventral view. **epg**, ectopterygoids; **max**, maxillae; **pal**, palatines; **ptg**, pterygoids. [B. Jantulik]

The 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





**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]

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 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.

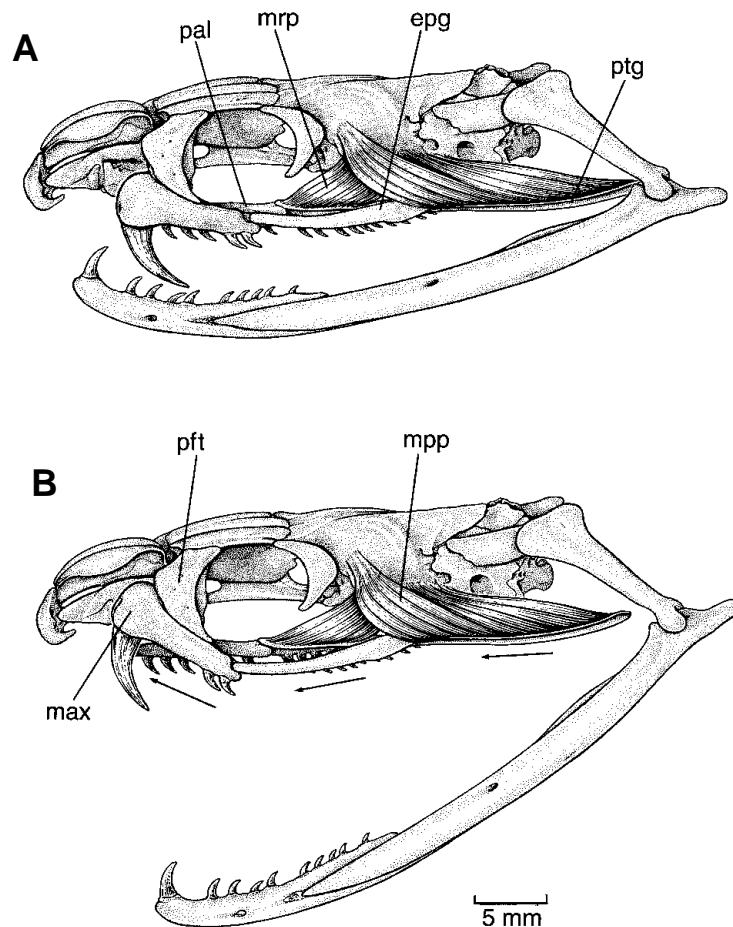
The number of maxillary teeth behind the fang varies (for examples, see Boulenger 1896; Kinghorn 1921, 1923a, 1939; Fairley 1929; Coventry & Rawlinson 1980; Covacevich *et al.* 1981). In most genera of Australian elapids, there are several teeth (Underwood 1967). Very large numbers (up to 13 teeth) are 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*.



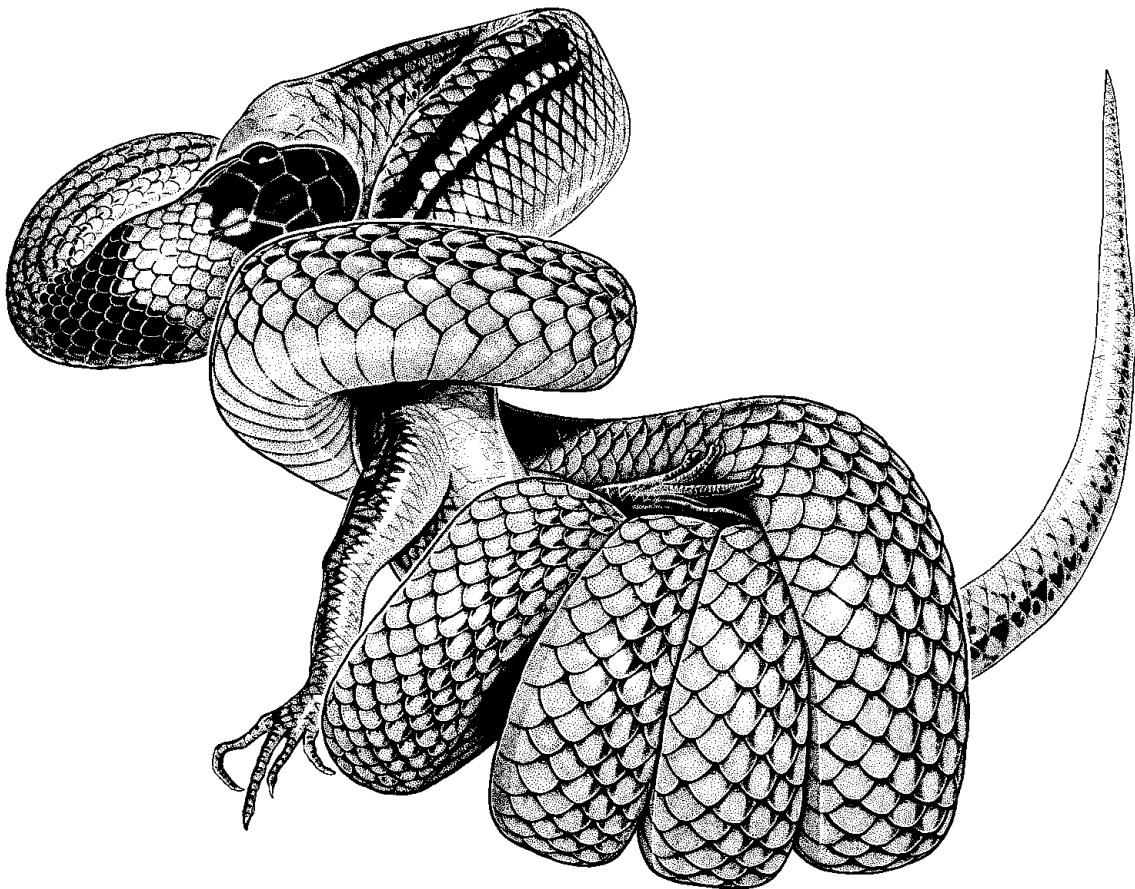
**Figure 35.9** Fang erection mechanism in the taipan, *Oxyuranus scutellatus*. **A**, The palatal complex is drawn caudally by the *m. retractor pterygoidei*, when the mouth is closed; **B**, when preparing to bite, the mouth is opened and the palatal complex is drawn rostrally by the *m. protractor 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]



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.



**Figure 35.10** Constriction of prey following envenomation by a juvenile *Furina ornata*. [B. Jantulik]

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 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 parabolooids 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).

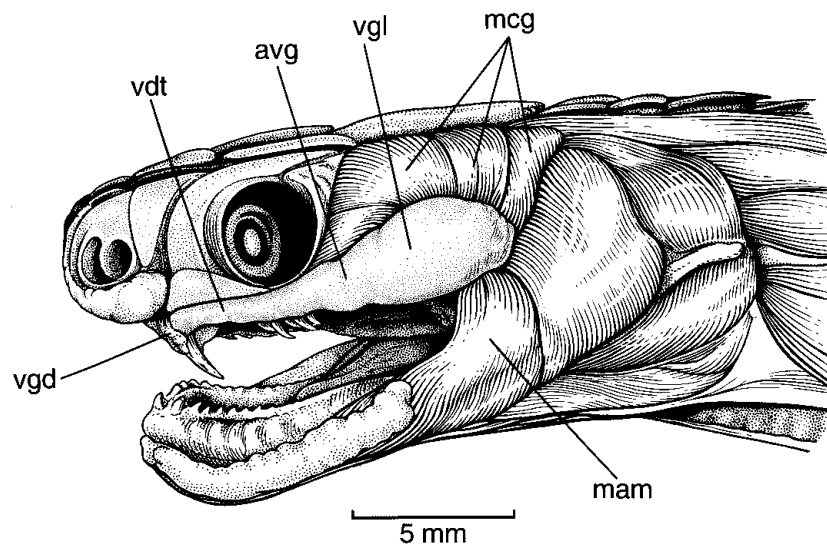
The compact, triangular pancreas is similar to that of other snakes (Underwood 1967; Shea pers. obs.); however, its histological structure and physiology have not been unstudied. It lies dorso-dextrally along the duodenum, immediately caudal to the pylorus, and is perforated by the bile duct.

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. 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



**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*; **mvg**, *m. compressor glandulae*; **vdt**, venom duct; **vgd**, *vagina dentis*; **vgl**, venom gland. [B. Jantulik]

(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, 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-Riemslog, 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<sub>50</sub> 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).

**Table 35.1** Relative toxicity of Australian elapid snake venoms to mice (from Broad et al. 1979). LD<sup>50</sup> 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<sup>50</sup> 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 <sup>50</sup> (a)	LD50 (b)
<i>Oxyuranus microlepidotus</i>	0.025	0.010
<i>Pseudonaja textilis</i>	0.053	0.041
<i>Oxyuranus scutellatus</i>	0.09	0.064
<i>Notechis scutatus scutatus</i>	0.118	0.118
<i>Notechis scutatus niger</i>	0.131	0.099
<i>Notechis scutatus occidentalis</i>	0.194	0.124
<i>Notechis scutatus serventyi</i>	0.338	0.271
<i>Acanthophis antarcticus</i>	0.400	0.338
<i>Pseudonaja nuchalis</i>	0.473	0.338
<i>Austrelaps superbus</i>	0.560	0.500
<i>Pseudonaja affinis</i>	0.660	0.560
<i>Pseudechis papuanus</i>	1.09	1.36
<i>Hoplocephalus stephensii</i>	1.36	1.44
<i>Tropidechis carinatus</i>	1.36	1.09
<i>Pseudechis guttatus</i>	2.13	1.53
<i>Pseudechis colletti</i>	2.38	–
<i>Pseudechis australis</i>	2.38	1.91
<i>Pseudechis porphyriacus</i>	2.52	2.53
<i>Cryptophis nigrescens</i>	2.67	–
<i>Demansia olivacea</i>	>14.2	–

## 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 brown snakes 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 typhlopoid 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 nighttime 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 particular 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* (Johnston & 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*, *Diocetowittus*, *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).

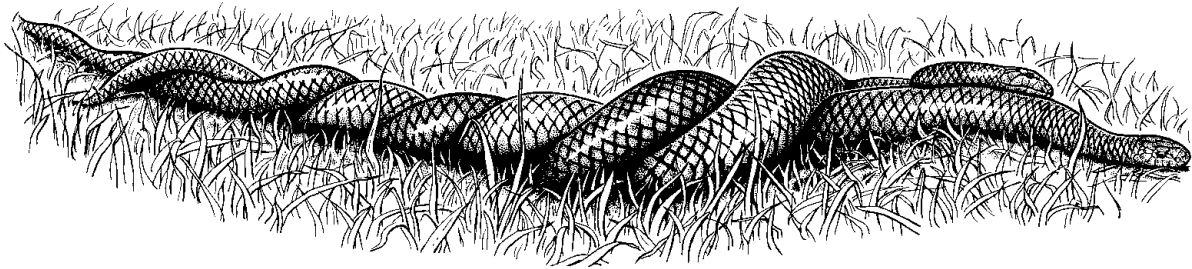
### Behaviour

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, 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.



**Figure 35.12** Male–male combat in *Austrelaps superbis*. (After photo by C. & S. Pollitt/ANT) [B. Jantulik]

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 Oxyurinae 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.

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 electrophoretic, 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.

**Intragenetic affinities.** Phylogenetic relationships within genera are not nearly so well understood as those between genera. The first examination of intragenetic 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.

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.

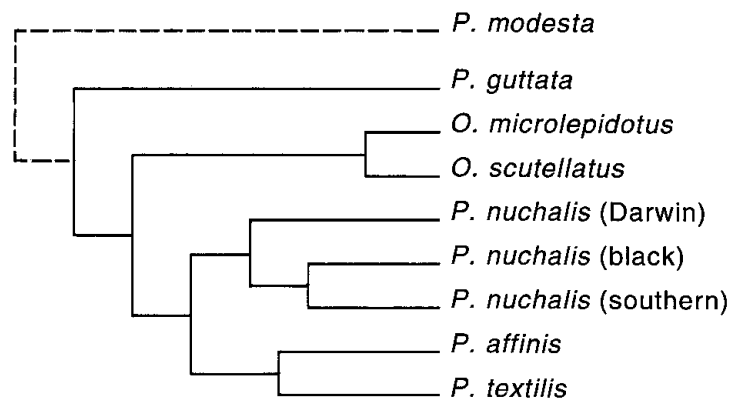
Mengden’s phylogenetic hypothesis for the genus, based only on electrophoretic data (Fig. 35.13) is in accord with the general picture of the group as determined from reviews of morphology and venoms. Exceptions, however, are the placement of *Oxyuranus* within the genus *Pseudonaja*, and the *P. nuchalis* 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*.

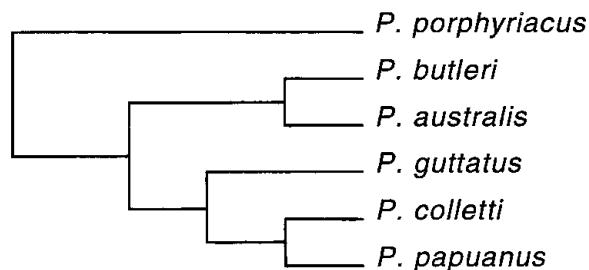


Most species are endemic to Australia. *Pseudechis australis*, and the endemic *P. papuanus* are found in southern New Guinea (Whitaker, Whitaker & Mills 1982). Chromosomes, scale counts, general morphology, and blood protein electrophoretic patterns reveal that the viviparous *P. porphyriacus* is most 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.



**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]



**Figure 35.14** Relationships within *Pseudechis*, based on Mengden *et al.* (1986). [D. Wahl]

### 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).