



FAUNA
of
AUSTRALIA



34. FAMILY COLUBRIDAE

Harald Ehmann



Pl. 8.1. *Boiga irregularis* (Colubridae): mainly arboreal in diverse habitats, from coastal heaths to rainforests in northern and eastern Australia. [J. Wombey]



Pl. 8.2. *Myron richardsonii* (Colubridae): inhabits mangrove flats and tidal creeks along the central north coast of Australia. [G. Shea]



Pl. 8.3. *Fordonia leucobalia* (Colubridae): feeds on crabs and fishes on mudflats and among mangroves along the north coast to eastern Cape York. [H. Cogger]

DEFINITION AND GENERAL DESCRIPTION

The family Colubridae is distinguished from other snakes primarily by the dentition, which usually comprises solid teeth on the maxilla, palatine, pterygoid and dentary, but never on the premaxilla. A few species have enlarged and/or grooved posterior maxillary teeth, which channel venom from the supralabial (Duvernoy's) gland. Envenomation is effected by chewing rather than by injection, and serves to subdue struggling prey and to initiate digestion (Goin, Goin & Zug 1978; McDowell 1987). Within Australia, the members of this family are characterised by a combination of attributes—enlarged ventral scales in a single row, a more or less cylindrical tail in which all subcaudals are divided, fewer than 30 mid-body scale rows, and the presence of a loreal scale (see Fig. 34.1) in all species except *Fordonia leucobalia* (Pl. 8.3).

Approximately 300 colubrid genera in nine subfamilies were recognised by McDowell (1987), including three subfamilies in Australia (Colubrinae, Homalopsinae and Natricinae). However, the subfamily classification of Cogger (1992), which includes the two subfamilies Homalopsinae and Colubrinae, is followed here (see also Affinities within the Taxon). Eight genera, *Boiga*, *Cerberus*, *Dendrelaphis*, *Enhydris*, *Fordonia*, *Myron*, *Stegonotus*, and *Tropidonophis* are found in Australia. These genera also occur in New Guinea and beyond. Although the family Colubridae comprises over 1600 species, or approximately two thirds of the world's living snakes, only 11 species are found in Australia, where they are considered to be relatively recent invaders from islands to the north.

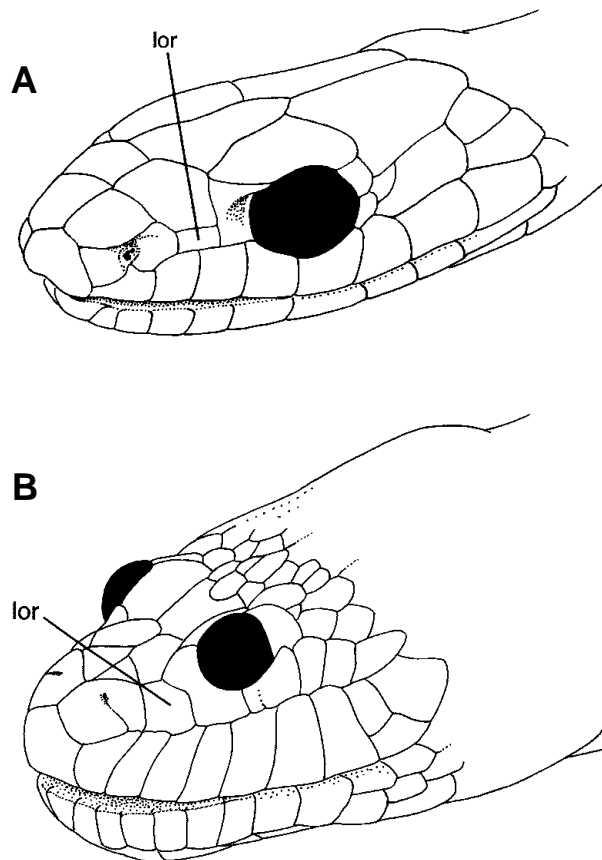


Figure 34.1 Oblique dorso-lateral views of the heads of **A**, a colubrine, *Dendrelaphis punctulata* and **B**, a homalopsid, *Cerberus rynchops*, comparing the form of the nostrils, eye and loreal scale. [R. Plant]

HISTORY OF DISCOVERY

The Australian colubrids were described over a century ago in Europe and their type specimens, several of which have been lost or destroyed, were lodged in European museums (see Cogger, Cameron & Cogger 1983a). *Cerberus rynchops*, described by Schneider in 1799 (as *Hydrus rynchops*), is the earliest described species occurring in Australia. Although the whereabouts of the type material and the type locality are unknown (Cogger *et al.* 1983a), the distribution of *Cerberus rynchops*, from northern Australia to India, suggests that the type material may have originated from outside Australia. The first colubrid to be described from indisputably Australian material was *Dendrelaphis punctulata* (as *Leptophis punctulatus*) by J.E. Gray (1826), based on a specimen from Careening Bay in Western Australia. Between 1826 and 1854, four species and two genera of currently recognised taxa were described by Gray, and two further species were described by Schlegel and by Duméril, Bibron and Duméril. Günther, Fischer and Meyer each described species between 1867 and 1886 that occur in Australia, of which only *Dendrophis calligastra* was based on Australian type material.

All but four of the 23 species that have been described from type material collected in Australia have been synonymised. The most prolific describer of Australian and New Guinean colubrids was William Macleay, who described 17 species and two genera more than a century ago, all of which are currently in synonymy. Several authors described between two and four separate species from type material which currently is considered to be conspecific (Cogger *et al.* 1983a). This in part reflects the significant morphological variability in the more common species that are widely distributed in northern Australia, south-eastern Asia and the intervening archipelagos.

There have been relatively few taxonomic studies of the Australian colubrids although their ecology and zoogeography have attracted considerable interest (Shine 1991c).

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Australian colubrid species are medium-sized snakes ranging from 500 to 2000 mm in adult total length. The two species in each of the genera *Boiga* (Pl. 8.1) and *Dendrelaphis* show slight to moderate lateral compression, and all other Australian species have relatively rounded bodies.

The head is moderately to obviously distinct from the narrower neck. The eyes are moderately large and set high on the head in the Homalopsinae, larger and set laterally in the Colubrinae. The external nares are valvular and on top of the snout in the Homalopsinae, but permanently open and on the side of the snout in the Colubrinae (see Fig. 34.1).

The tail is apparently prehensile in the four species of tree snakes (*Boiga* and *Dendrelaphis*), although the tail of *Dendrelaphis* does not have the extensive musculature near the tip of the tail present in arboreal pythons (McDowell pers. comm.)

Colouration within a species can vary remarkably. *Dendrelaphis punctulata* may be green, blue, black, golden yellow, or an intermediate colour. Dorsal patterning in *Enhydryis polylepis* may consist of small blotches of pigment, large blotches, or the entire back may be dark. In *Fordonia leucobalia* (Pl. 8.3), the combination of variable body colouration and dorsal patterning is complex, ranging from fawn to grey to orange with scattered small blotches, large blotches, to a near absence of any paler colour.

Body Wall

The body and head scales of colubrids are similar to those of other terrestrial and arboreal Australian snakes. Colubrids of moist habitats have very glossy, water repellent scales, which presumably reduce the risk of microbial attack. The dorsal and lateral scales of the aquatic species *Cerberus rynchops* and *Tropidonophis mairii* are strongly keeled. These keels may aid in maintaining directional stability and reduce friction during rapid movement, especially on slippery, muddy substrates. In *Dendrelaphis* species, the lateral ends of each ventral scale are angled abruptly to form a pair of latero-ventral keels. These provide purchase even on fine irregularities of a twig or branch, and allow a secure grip that facilitates rapid body movement in a precise direction.

Skeletal System

The skull (Fig. 34.2) is highly kinetic between the anterior elements and the braincase. Solid teeth are present on the upper and lower jaws and on the palate, but not on the premaxilla. Both *Dendrelaphis* species (Fig. 34.2A), both *Stegonotus* species and the sole *Tropidonophis* have numerous, ungrooved, fine, pointed teeth. The two *Boiga* species and all four homalopsines have two enlarged, grooved teeth on the posterior maxilla that are associated with prey envenomation (Fig. 34.2B). The homalopsine *Fordonia leucobalia* is unusual in having relatively short and blunt teeth (Gyi 1970) which facilitate the capture, holding and swallowing of crabs (Savitzky 1983).

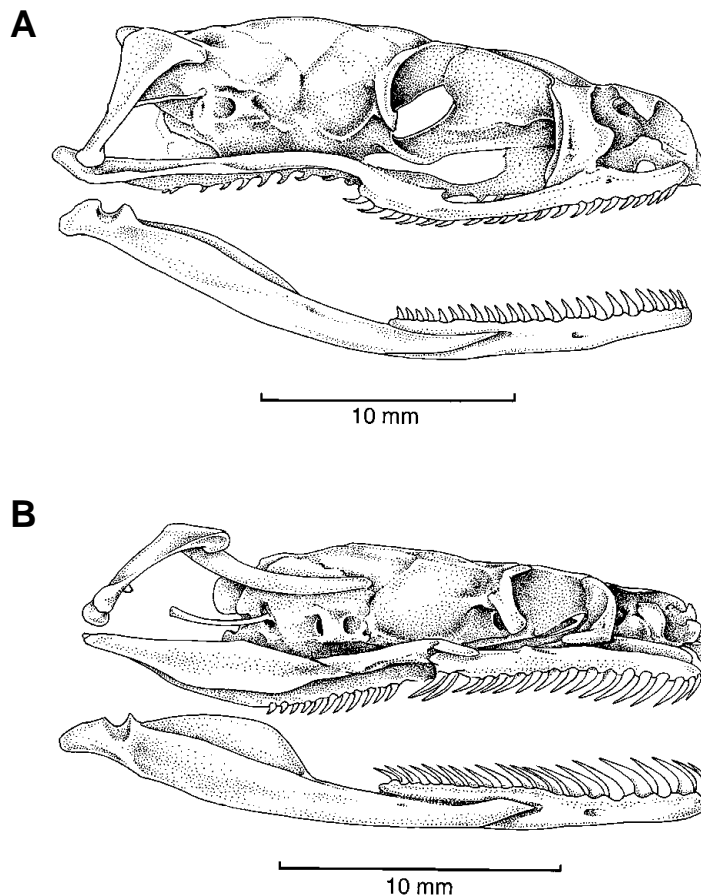


Figure 34.2 Lateral view of the skull of colubrid snakes. **A**, the solid-toothed species, *Dendrelaphis punctulata*; **B**, a rear-fanged colubrine species, *Cerberus rynchops*. [R. Plant]

The skeletal anatomy of Australian species was described by Gyi (1970) (*Cerberus rynchops rynchops* and *Fordonia leucobalia*) and Malnate & Underwood (1988) (*Tropidonophis mairii*). Bellairs & Kamal (1981) reviewed the development of the skull in snakes extensively and provided access to earlier literature.

The axial skeleton consists of pre- and post-cloacal vertebrae and ribs; there are no vestigial girdles or limb bones. The vertebrae are procoelous with well-developed condyles, and accessory articulating facets, namely the zygosphenes (anterior) and the zygantrum (posterior), are present in addition to the zygapophyses found in other amniotes.

One rarely reported feature of *Tropidonophis mairii* is the ease with which it can break its tail distally when it is firmly grasped. Tail autotomy is not known in other Australian snakes (Lyon 1973; Ehmann pers. obs.). Tail fragility may be a characteristic of the genus, as incomplete tails are common in many overseas *Tropidonophis* (Malnate & Underwood 1988). There is no tail regeneration.

Locomotion

Lateral undulation is the most common type of locomotion used by Australian colubrids. It is used in swimming, movement on land, and in climbing. Concertina locomotion is often used by arboreal snakes when moving between or along widely spaced elevated branches and vines or inside naturally occurring vertical hollows and channels. Sidewinding occurs in *Fordonia*, *Cerberus* and *Myron* (Cogger & Lindner 1974; Jayne 1987, Wall 1919) but rarely in *Tropidonophis* (Ehmann pers. obs.). Rectilinear locomotion has been observed in all Australian colubrids (Ehmann pers. obs.).

Feeding and Digestive System

Constriction, or a modification of it, is used in some species to subdue and/or hold prey. Species of *Boiga*, *Fordonia*, *Myron* and *Stegonotus cucullatus* are all known to constrict prey (Irvine 1954; Shine & Schwaner 1985). Australian *Boiga* species constrict prey with anterior body loops (Ehmann 1992) whereas several overseas colubrids, including *Boiga*, use the tail and posterior body (Murphy 1977). The most bizarre feeding in any Australian colubrid is that of *Fordonia leucobalia* which has very effective crab venom (Kopstein 1931). It constricts its crab prey or clamps it into the muddy substrate with an overbearing body loop, and then proceeds to break off and partly crush and crack individual appendages, before swallowing them. When the crab's overall size and defences are suitably reduced, the snake partly crushes and swallows the body (Savitzky 1983; Shine & Schwaner 1985). Savitzky (1983) indicated that *Fordonia* has hypertrophied gastric musculature that presumably aids in coping with the hard and often jagged crab exoskeletons. At least six of Australia's eleven colubrids can envenomate their prey, in some cases apparently as an aid to digestion rather than to subdue the prey (Irvine 1954). Other Australian species have venom which is highly effective in subduing/immobilising prey (Kopstein 1931; Parker & Grandison 1977; Shine 1991c).

Cundall (1987) reviewed the functional morphology of feeding and envenomation in snakes and Mushinsky (1987) reviewed several specific aspects of foraging ecology in snakes, including non-Australian colubrids.

Respiration

The Australian homalopsine snakes possess some specialised, aquatic adaptations. These include valvular nostrils on the top of the snout (see Fig. 34.1). The oxygen carrying capacity of blood in *Cerberus rynchops*, a frequent inhabitant of mangroves, is close to the lower end of the range for land

snakes (Feder 1980; Heatwole 1987). Its ability to take in oxygen through the skin is lower than other snakes (Heatwole 1987). The concurrent low transport rate of carbon dioxide would be advantageous in mud of mangroves, which has high carbon dioxide levels (Heatwole 1977a).

Heatwole (1987) provided an excellent overview of the respiratory/circulatory function in aquatic/marine snakes, and Johnson (1975a) has reported on head-body temperature differences in *Boiga irregularis* as a function of circulation.

The respiratory physiology of Australian colubrine snakes has yet to be investigated. One interesting observation is that *Tropidonophis mairii* can remain submerged for 20 to 30 minutes (Lyon 1973).

Excretion

The Australian terrestrial colubrine snakes, and at least the homalopsines *Cerberus* and *Fordonia*, all excrete nitrogenous waste as uric acid paste, usually with faecal material (Ehmann pers. obs.). It is possible that the freshwater-inhabiting *Enhydryis polylepis* can excrete primarily urea, as it is not subject to the same desiccation risks as the terrestrial colubrines or to the salty environments of other homalopsines.

A premaxillary salt gland in the anterior roof of the mouth of coastal and estuarine homalopsines excretes excess salt. In *Fordonia*, the salt gland is extremely large, probably as an adaptation to the relatively high salt content of crabs (Savitzky 1983). These snakes also have significantly reduced rates of cutaneous water loss (Heatwole 1987).

Sense Organs

The slightly elevated placement of the eyes in the homalopsines is the only obvious difference from the position and function of sense organs of terrestrial snakes. Otherwise the five senses are believed to be similar to those found in other relatively unspecialised terrestrial forms. The pupils are vertically elliptical in nocturnal species of *Boiga* and *Stegonotus* and round in diurnal species of *Dendrelaphis* and *Tropidonophis*. Scale pits present in many head shields, dorsal scales and sometimes in the subcaudals of *Tropidonophis mairii* (Malnate & Underwood 1988) may have a sensory function.

Exocrine and Endocrine Glands

As well as the premaxillary salt gland in the homalopsines (see Excretion) the colubrines *Dendrelaphis* and *Stegonotus* are known to produce distinctively odoriferous secretions from the cloacal glands. These are particularly obvious when a snake is first handled. Normally docile captive snakes become quite agitated when exposed to their species' smell, for example, on a contaminated hand. These odours are surprisingly strong (relatively nutty-sweet in *Dendrelaphis punctulata* but offensively pungent in *Stegonotus cucullatus*) in newly hatched and juvenile snakes. They probably occur in response to stress and serve as a pheromonal danger signal to nearby conspecifics (Ehmann pers. obs.). *Stegonotus* produces scent from anal glands (Cogger 1992).

The most significant exocrine gland in some colubrids is associated with prey envenomation (see Feeding and Digestive System). Duvernoy's gland (in the supralabial gland) secretes a venom that drains to the vicinity of the teeth (sometimes grooved and/or enlarged) of the posterior maxilla (see Cundall's 1987 review). The studies by Kopstein (1931) demonstrated the high specificity and effectiveness of two colubrid venoms, and the importance of relating functional venom studies to the natural prey species.

For a comprehensive review of reproductive endocrinology in snakes, including non-Australian colubrids, see Seigel & Ford 1987.

Reproduction

A major review of snake reproduction by Seigel & Ford (1987) covered many non-Australian colubrid studies, and included *Cerberus rynchops* studied outside Australia. Reproduction in Australian colubrids is discussed by Shine (1991c) and Ehmann (1992).

All Australian colubrines are oviparous whereas the homalopsines are viviparous. The mean litter or clutch size ranges from 5.5 to 13.0 per female, and is significantly correlated with maternal body size in four species. Some Australian colubrids exhibit reproductive seasonality. Oviposition in *Boiga* species throughout Australia occurs in summer; east coast *Dendrelaphis punctulata* have a similar pattern, but in the Northern Territory the species shows no obvious seasonality. Gravid *Fordonia* have been collected from July to October, gravid *Cerberus* in February and August, and gravid *Enhydris* in June and November. *Tropidonophis* can reproduce almost year-round, even in southern populations, although no gravid females have been recorded from August to October, probably because these months are relatively dry within the species' range.

Embryology and Development

Shine (1991c) published data on artificially incubated eggs of four Australian colubrids. The most notable feature of these data is that in *Tropidonophis* the egg size, mass and incubation time are all remarkably lower than in *Boiga*, *Dendrelaphis* and *Stegonotus*. In the wild, the eggs of *Boiga*, *Dendrelaphis* and *Tropidonophis* are laid in moist or very humid sites that are not exposed to temperature extremes (Lyon 1973; Ehmann 1992). During development, eggs of *Boiga* and *Dendrelaphis* absorb moisture and increase in size, sometimes becoming strongly cohesive and constrained within rigid-sided oviposition sites (Ehmann pers. obs.).

NATURAL HISTORY

Life History

The only Australian colubrid for which information on growth and longevity is available is *Cerberus rynchops*. Two small specimens from Burma, 19.4 and 20 cm long, doubled their lengths in the first year and by the end of the second year were approximately three times their original length (Wall 1921).

A detailed, recent review of snake life histories, based substantially on North American colubrids, is provided by Parker & Plummer (1987).

Ecology

The habitats of the Australian colubrids are summarised in Ehmann (1992). All Australian colubrids occur in mesic, moist, or wet habitats associated with permanent watercourses, swamps, estuaries or bays. *Boiga* species can inhabit drier habitats probably because their surface activity is nocturnal and the risk of desiccation is less. Shine (1991c) suggested that the colubrids in Australia are not in significant competition with the endemic elapids and pythons because they have invaded Australia with ecological specialisations that are rare amongst the endemics.

The diets of Australian colubrids are diverse. Homalopsines feed largely on fishes and crustaceans, *Tropidonophis* consumes mostly frogs, *Dendrelaphis* eats mostly frogs and lizards, *Boiga* takes birds, lizards and mammals (Green 1989), and *Stegonotus* feeds mainly on reptile eggs, frogs and lizards (Shine 1991c).

Frog-eating Australian colubrids frequently have subcutaneous swellings that contain the sporogony stage of tapeworms (Ehmann pers. obs.).

Australian *Boiga irregularis*, *Dendrelaphis punctulata*, *Tropidonophis*, *Cerberus*, *Enhydris* and *Fordonia* are sometimes locally abundant and aggregated (Worrell 1963b; Covacevich & Limpus 1973; Lyon 1973; Cogger & Lindner 1974; Gow 1976; Ehmann pers. obs.).

Behaviour

Aggregations of Australian colubrids are relatively small compared to those in the large dens seen in some higher latitude species in the northern hemisphere (Gregory 1984). In a long-term opportunistic study of *Boiga irregularis* at Calga, north of Sydney, Ehmann (1992, unpub. data) found two females associated with egg clutches laid in deep recesses in rock crevices. Both females remained in the vicinity of their eggs for 18 and 27 days. Habitation of spring-summer refuges by adult males or females averaged two days (range one to four days, n=4).

The defensive behaviour of Australian colubrids towards humans varies from the pugnacious (if mildly aroused) members of *Boiga* and *Stegonotus*, to the less easily provoked *Dendrelaphis*, *Tropidonophis*, *Cerberus*, *Fordonia* and *Enhydris*. *Myron* is not inclined to bite even when provoked (Ehmann 1992).

The arboreal, diurnal *Dendrelaphis* species bask in sunlight, usually using elevated, leaf-camouflaged platform sites, such as forks, dense twigs and/or vines (Thompson 1935; Ehmann pers. obs.), whereas the terrestrial and semi-aquatic diurnal *Tropidonophis* basks on low vegetation, open ground and even lying on the surface of shallow still water (Lyon 1973; Ehmann 1992). The aquatic crepuscular and nocturnal homalopsines also may engage in thermoregulatory behaviour by emerging in the late afternoon either to bask or to lie in shallow warm water. The nocturnal *Boiga irregularis* north of Sydney, basks one or more body loops in full morning or afternoon sunlight usually remaining within a recess or crevice (Ehmann pers. obs.). Colubrids, and especially colubrines, restrict their surface activity during dry or drought conditions, but the same species become quite active and mobile during very humid warm weather or soon after warm rains. This behaviour minimises the risk of desiccation.

Gillingham (1987) reviewed courtship and mating behaviour, social aggregation, and aggression in snakes including many North American colubrids. Mushinsky (1987) summarised the behaviours associated with foraging, and Lillywhite (1987b) reviewed the behavioural components of the thermal ecology of snakes.

Economic Significance

The Australian colubrids are not dangerously venomous to humans. Some homalopsines in South East Asia and India are important predators of invertebrate pests, frogs and fishes in the natural food chains of rice cultivation areas.

None of the Australian colubrids is considered to be endangered (Ehmann 1992). The conservation status of *Stegonotus parvus* on Murray Island (its only Australian occurrence, based on four collected specimens) is unknown, but the species appears to be common in Papua New Guinea (McDowell 1972b). All Australian colubrids are potentially put at risk by habitat change and aquatic or marine pollution.

The limitations of *Tropidonophis* as a potential biological control organism for *Bufo marinus* were outlined by Shine (1991c). Shine indicates that they eat *Bufo marinus*, and therefore may have the capacity to overcome the toad's toxicity.

In Australia, *Boiga* species are known to prey on aviary birds on rare occasions, but appropriate caging easily excludes them. However, the accidental introduction of *Boiga irregularis* to Guam, probably from the Admiralty Islands in salvaged materials from World War II, has resulted in a population explosion of the species and the extinction or endangering of most of Guam's native vertebrates, especially birds. There is no doubt that *Boiga irregularis* potentially poses a severe conservation threat to the native faunas of other Pacific islands (Rodda, Fritts & Conry 1992; Fritts 1988).

BIOGEOGRAPHY AND PHYLOGENY

Distribution

The Australian colubrid populations are outliers of much wider distributions in the islands of New Guinea, south-eastern Asia and further north. *Myron* and some *Enhydris* are endemic to Australia and New Guinea while *Cerberus* and *Fordonia* are distributed widely throughout the Indo-Australian region. Of the colubrines, some *Tropidonophis* and *Dendrelaphis* are also endemic to Australia–New Guinea, while *Stegonotus* (Philippines, Borneo, Moluccas, New Guinea and Australia) is a possible recent arrival in the Australasian region. Most *Boiga* are widespread in the Indo-Australian region (Cadle 1987); *Boiga fusca*, currently considered a synonym of *B. irregularis* by some authors, may be an Australian endemic.

Australian colubrids are restricted to mesic habitats in the northern tropical and eastern tropical, subtropical and temperate regions (Fig. 34.3) (Ehmann 1992). *Boiga irregularis* and *Dendrelaphis punctulata* have the southernmost and furthest inland populations, and *Enhydris polylepis* is the homalopsine most highly adapted to freshwater (Wilson & Knowles 1988; Cogger 1992; Ehmann 1992).

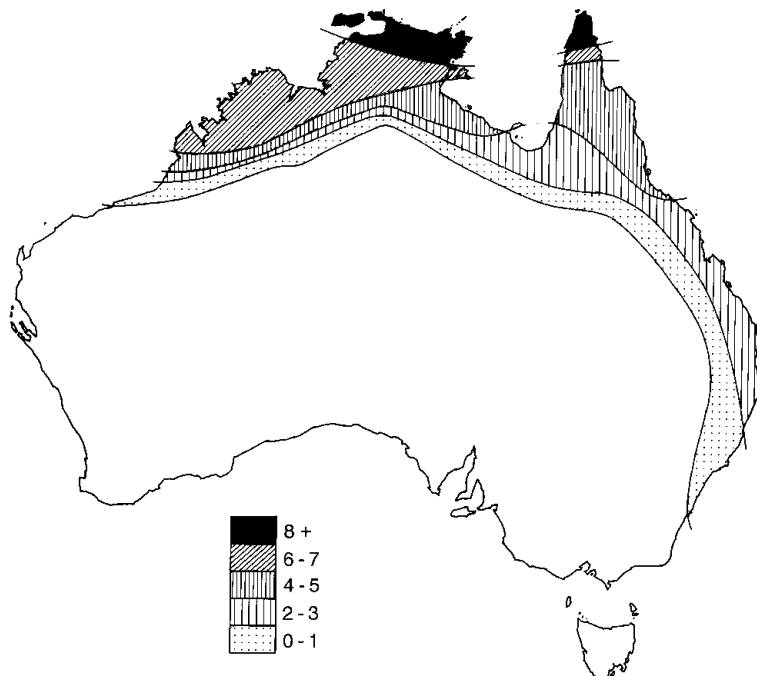


Figure 34.3 Species density map of colubrids. (After Shine 1991c)

[W. Mumford]

The colubrines are almost cosmopolitan in distribution whereas the homalopsines occur in southern Asia, the Indo-Australian Archipelago and Australia (Cadle 1987).

Affinities with Other Groups

The Colubridae are placed in the superfamily Colubroidea which is considered to comprise two series. The more primitive Proteroglypha contain the Elapidae, *Calliophis*, *Atractaspis* and some other African genera, and the Opisthoglypha contain the Colubridae and Viperidae. The systematics and phylogeny of the Colubroidea are uncertain. The available morphological, anatomical, cytogenetic and molecular data are conflicting, but the greatest promise for resolution probably lies with immunological investigations (Cadle 1987; McDowell 1987).

Affinities Within the Taxon

The number and definition of subfamilies in the Colubridae is uncertain (Cadle 1987). In this account the Australian colubrids have been treated conservatively as belonging to two subfamilies, but other authors have suggested four: Homalopsinae, Natricinae (for *Tropidonophis*), Boiginae (for *Boiga*), and Colubrinae (Cadle 1987; McDowell 1987; Cogger 1992). Furthermore, Cadle (1987) places *Enhydris polylepis* in the Colubrinae.

The colubrids radiated extensively in all zoogeographic regions other than the Australian region, with some minor radiation in New Guinea (Cadle 1987). Cogger & Heatwole (1981) postulated that the colubrids arrived recently in Australia by land-bridge migration or by swimming, and Storr (1964a) suggested that of the homalopsines, *Enhydris* entered from the north-east and the other three genera entered from the north-west. Some ecological preadaptations that may have facilitated and ensured the successful invasion of Australia by colubrids were discussed by Shine (1991c).

Fossil Record

As yet no colubrid fossils have been reported from Australia, but the vast Riversleigh fossil deposits in northern Queensland may yield fossils, as they include many snake remains yet to be identified (Archer, Hand & Godthelp 1991).

The earliest known colubroid fossils date from the Late to Early Eocene of Italy, the Early Eocene of France and Portugal; there are possible primitive colubroids from the upper Eocene beds of England (see Rage 1987). However, the first undisputed colubrid fossils date from the middle Oligocene of Europe and North America, and are at least 30 million years old. By the Miocene—times that have been referred to as the ‘Age of Colubroidea’ (Rage 1987)—an astonishing array of colubrids existed in North America and Europe; other areas are poorly studied, but a few are known from Morocco, Asia and South America.