



FAUNA
of
AUSTRALIA



33. FAMILY BOIDAE

Harald Ehmann



Pl. 7.2. *Aspidites ramsayi* (Boidae): a nocturnal, terrestrial snake, often found sheltering in hollow logs or thick vegetation; occurs in dry areas and deserts across central Australia. [J. Wombey]



Pl. 7.3. *Chondropython viridis* (Boidae): juveniles are often yellow, and coil in the manner shown; (see also Pl 7.4). [H. Cogger]



Pl. 7.4. *Chondropython viridis* (Boidae): adults of this species are bright green (see also Pl. 7.3); a nocturnal, arboreal python of the rainforests, north-eastern Cape York. [H. Cogger]



Pl. 7.5. *Antaresia stimsoni* (Boidae): found frequently near rock outcrops, in stone fields, around large trees or other isolated features in sandy deserts; throughout arid central and western parts of Australia. [H. Cogger]

DEFINITION AND GENERAL DESCRIPTION

Worldwide the boids include terrestrial, arboreal, burrowing, semi-aquatic and saxicoline species. They are non-venomous, medium-sized or very large snakes. Many of the Australian species are nocturnal and many feed on mammals or birds as adults. Most boids immobilise their prey in tight coilings of the body, and use sustained constriction to kill prey by suffocation (Fig. 33.1).

The Boidae are distinguished from other snakes by the presence of vestiges of the pelvis and, usually, hindlimbs which appear as cloacal spurs in live snakes. The supratemporal and quadrate bones are long, resulting in a relatively large mouth. Uniform, large, recurved sharp teeth are present on the dentary, maxilla, palatine, pterygoid. Teeth are present also on the premaxilla of most pythonines. The rigid lower jaw has a coronoid element, and the anterior skull elements are moderately flexible and mobile on the brain case. The pupils of all boids are vertically elliptical (Underwood 1976; Kluge 1993). Most boids have a functional left lung that is up to 75% the size of the right one (Parker & Grandison 1977). Most pythonines and some boinines possess heat sensitive pits in the labial region of the head.

The family comprises about 85 species, in two subfamilies, distributed through most of the tropical and temperate regions. In Australia, the subfamily Pythoninae includes 15 species in five genera (Kluge 1993). The subfamily Boinae does not occur in Australia. Kluge (1993) proposed that the Pythoninae originated in the Australasian region.

HISTORY OF DISCOVERY

The earliest discoveries of Australasian pythonines are associated with early voyages of discovery and early European settlement in eastern Australia and the islands to the north. The first described species that is undeniably Australasian in distribution is *Morelia amethystina* (as *Boa amethystina* Schneider, 1801); the type is presumed lost and the type locality is not known (Cogger, Cameron &

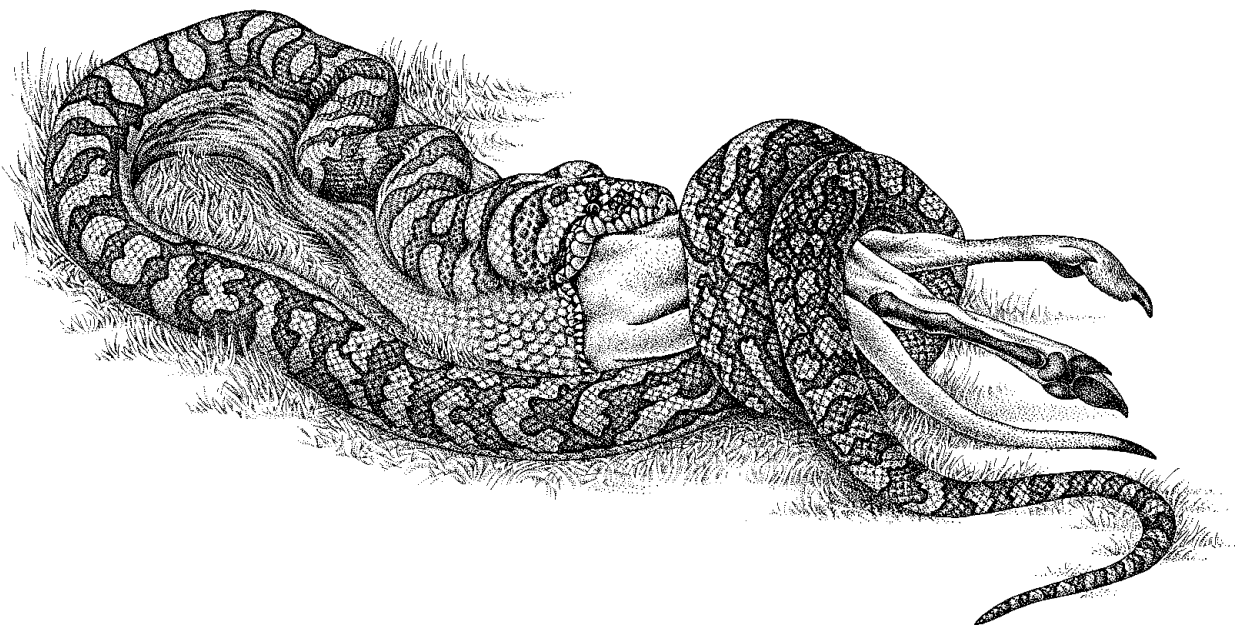


Figure 33.1 A large *Morelia spilota variegata* constricting and eating a young Whip-tailed Wallaby, *Macropus parryi*. (After photo by W. Farrugia/ANT)
[K. Hollis]

Cogger 1983), though it may have come from the Moluccas or Timor (Kluge 1993). *Morelia spilota* was the first species described from Australian type material (Cogger *et al.* 1983).

European-based workers described eight Australian species last century, and deposited the type specimens in European institutions. Two species of *Aspidites* were described by Australian-based zoologists last century. Krefft deposited the type specimen of one of these (*A. melanocephalus*) in the British Museum, while the type specimen of *A. ramsayi* (Macleay, 1882) is believed lost. Three of the five species described this century were recognised as a result of careful re-assessment of known species (see Cogger *et al.* 1983; Kluge 1993); two of these, *Morelia oenpelliensis* and *M. carinata*, are recently-discovered, spectacular and remotely distributed species.

During the past two decades Shine and his co-workers have investigated many aspects of the biology of most Australian pythons (summarised in Shine 1991a). The natural history of the Australian pythons was summarised by Ehmann (1992).

MORPHOLOGY AND PHYSIOLOGY

External characteristics

The Pythonines are robust, muscular snakes (Pl. 7). The tail is prehensile in many species, and moderate in length compared to the long tails of some arboreal colubrids and the short tails of burrowing elapids. The head is distinct from the neck in most species (except *Aspidites*) and the eyes are moderate (*Aspidites*) to large (*Morelia*) in size. The smallest adult pythonines are 0.45 m in length; the largest are reported to exceed 10 m (Kluge 1993). The streamlined, rounded head, with non-protrusive eyes of *Aspidites* may be an adaptation for entering hollows, burrows and earth cracks for shelter and finding prey. The neck of adult *Antaresia* (= *Liasis childreni* group of Smith 1981) is distinctly slender while the body is often quite thickset. This combination allows rapid and long strikes at flying prey, such as bats entering caves, where anchor points are scarce and precarious (Shine 1991a; Ehmann 1992). The longest Australian python on record, *Morelia amethistina*, exceeded 8 m; Aboriginal people from Arnhem Land report that *Morelia oenpelliensis* may be longer, though more slender (Ehmann 1992).

The greatest range of colour variants is found in the widespread species *Morelia spilota* (Ehmann 1992). In *Morelia viridis* (formerly *Chondropython*; see Kluge 1993), juveniles may be rich yellow (Pl. 7.3), reddish orange or orange, and change between one to 12 weeks to the typical adult green colouration (Pl. 7.4) when they are one to three years old (Ross & Marzec 1990; Ehmann 1992).

Photographs of all Australian pythons appear in Wilson & Knowles (1988) and Ehmann (1992). Hoser (1989) published many photographs of variants, and Ross & Marzec (1990) provide photographs of many boids in Australia and elsewhere.

Body Wall

The dorsal overlapping body scales are rhomboidal in shape, and the single row of enlarged ventral scales is narrower relatively than those of colubrids and elapids. The body scales are small and mid-body scale row counts are high (mean 51, range 31 to 80; after Cogger 1992) for Australian species. These high counts reflect the need for greater stretching of the skin between semi-rigid scales to accommodate bulky mammalian prey, especially in the larger species (Fig. 33.1). The smallest species (*Antaresia* spp.) have the lowest scale row counts.

Morelia carinata is the only pythonine with keeled scales (albeit weakly keeled), whereas rugose or finely keeled scales occur in many Boinines. Such scale carinations or keeling may provide grip and/or directional stability when moving through vegetation or over muddy substrata (cf. *Candoia*, *Tropidonophis*) or when restraining struggling prey, and may provide air channels that reduce suction attachment when crawling on soft muds.

The frequency of skin-shedding in some captive boids was reported by Hoser (1982). Banks (1985a) reported a sloughing cycle of 10 to 250 days, and an exceptional period of 645 days in an adult male of *Antaresia childreni*, the longest sloughing cycle ever reported. Generally boids shed less frequently than the more active elapids and colubrids.

SKELETAL SYSTEM

The skull (Fig. 33.2) is long compared to colubrids and elapids, especially in the snout and temporal regions. The extensive gape of boids reflects the posterior elongation of the supratemporal, quadrate and the lower jaw, which is enhanced by the mobility of the anterior bones of the upper snout (especially the maxilla and its associated bones). The supraorbital bone, which forms the upper margin of the orbit in pythonines, is absent in boinines (McDowell 1987). The osteology of boids and a detailed morphological study of the skull bones and dentition of pythonines are described by McDowell (1975) and Kluge (1993), respectively.

Solid, long, pointed and razor-sharp teeth are present on the maxillary and dentary, on the palate (palatine and pterygoid) and on the premaxilla (except in *Aspidites*). The numerous teeth gradually decrease in size posteriorly, except on the very short median premaxilla. There is no diastema, nor are there large teeth or fangs as in some other snakes.

The vertebrae are procoelous with well-developed condyles. Accessory articulating facets, namely the zygosphene and the zygantrum are present, as are zygopophyses and small, inconspicuous accessory prezygopophysial processes (McDowell 1987; Underwood 1976). The ribs have tuber costae and simple terminal cartilages.

The vestigial hindlimbs and pelvic structures, seen in live pythons as a spur-like projection on either side of the vent, are important appendages during mating (see Reproduction; Shine 1991a).

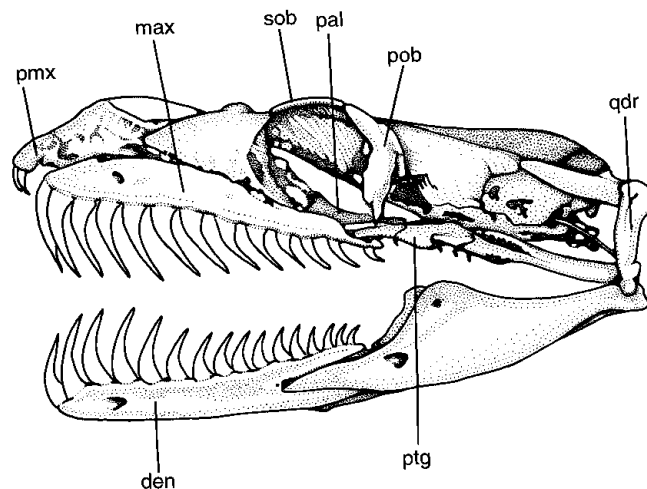


Figure 33.2 Lateral view of the skull of *Morelia amethystina*, illustrating the supraorbital and the arrangement of the teeth. **den**, dentary; **max**, maxilla; **pal**, palatine; **pmx**, premaxilla; **pob**, postorbital; **ptg**, pterygoid; **qdr**, quadrate; **sob**, supraorbital. (After McDowell 1979) [T. Wright]

LOCOMOTION

The following summary of locomotion in boids is based partly on Gans (1974) and Cundall (1987). Boids, like other terrestrial snakes, use lateral undulation in swimming, in rapid movement on land and sometimes in hasty climbing during escape. In this mode of locomotion all parts of the snake are in motion.

Rectilinear locomotion ('belly walking') is most commonly used by boids for slow forward progress when stalking prey or foraging. In concertina locomotion, one third to two thirds of the body is held static in relatively tight 'S' bends while the remainder, which appears much straighter, moves forward. Then the previously static part of the body is moved forward in similar fashion, so there is an alternation of movement of the front and the hind portions of the body. This mode is mostly used during arboreal activity when moving between or along widely spaced elevated branches and vines or inside naturally occurring vertical hollows and channels.

Morelia viridis is the only truly arboreal Australian boid. Most are at least partly terrestrial. All pythonines swim, although species of *Aspidites* and *Antaresia* do so only when necessary, for example when the ground is flooded. Species of *Morelia* occasionally enter the water, and *Liasis mackloti* (previously *L. fuscus*; Kluge 1993) and *Liasis olivaceus* habitually enter the water (Ehmann 1992).

FEEDING AND DIGESTIVE SYSTEM

Detection and capture of endothermic prey in many boids (including most pythonines) is facilitated by the heat sensitive labial pits. Active ectothermic prey, especially reptiles, may have a body temperature that is significantly higher than the ambient temperature or that of the substratum, and therefore is presumably detectable by pythons. The absence of labial pits in *Aspidites* (Kluge 1993) and the boinines *Eryx* and *Charina* (Parker & Grandison 1977; Ross & Marzec 1990) is perhaps not surprising in view of the semi-fossorial lifestyle and/or hunting behaviour of these genera. *Morelia viridis* and *Aspidites ramsayi* (Pl. 7.2) may attract potential prey by caudal luring (Murphy, Carpenter & Gillingham 1978; Wilson & Knowles 1988).

Prey constriction in snakes is best developed in the Boidae. Most boids use three to eight body coils to constrict prey. As in other snakes, prey ingestion involves major relocations of the lower jaw bones, particularly in adult snakes taking in a large meal (Fig. 33.1). Cundall (1987) reviewed the functional morphology of snake feeding and provided many references to boids.

During digestion some pythons, for example *Morelia spilota*, may position the stomach in a warm spot thereby elevating its temperature (Webb in Heatwole & Taylor 1987; Slip & Shine 1988c).

CIRCULATORY SYSTEM

Underwood (1976) and Kluge (1993) reviewed some aspects of the circulatory system of boids, and the intercostal arteries in particular. Thermoregulatory aspects of circulation in Australian and New Guinean boids have been reported by Webb & Heatwole (1971) and Johnson (1975a, 1977). Thermoregulation is described under Behaviour below.

RESPIRATION

Oxygen consumption and energy metabolism during intense movement has been studied in one boid, the Desert Rosy Boa *Lichanura trivergata roseofusca*. Its energy output/consumption was the lowest of six snake species studied (Ruben

1976; Lillywhite 1987b). Bennett & Dawson (1976) reviewed snake metabolism (including oxygen consumption) and Lillywhite (1987b) has summarised research on snake cardiorespiratory function.

Several Australian pythons are known to be able to remain fully submerged in water for between 20 and 45 minutes (*Liasis mackloti*, *L. olivaceus*, *Morelia amethystina*, *M. spilota*; Ehmann pers. obs.). *Liasis mackloti* (as *L. fuscus*; Shine 1991a) and *L. olivaceus barroni* (Ehmann 1992) spend considerable periods of time partly or almost fully submerged. The submergence capacity of pythons is perhaps not unexpected since they are generally large-bodied, with large lungs and a relatively low metabolic rate (Andrews & Pough 1985).

EXCRETION

Australian pythons (except *Morelia carinata*) excrete nitrogenous waste as uric acid paste, usually with faecal material (Ehmann pers. obs.). Excretory and evaporative water losses are minimised by behavioural factors. Australian pythons usually are freely active on the surface only at night when relative humidity is usually high, or during overcast or rainy conditions by day (Ehmann pers. obs.). The arid-adapted pythons of the genera *Antaresia* and *Aspidites* may have more efficient excretory systems and water conservation mechanisms compared to their relatives from more mesic habitats (*Liasis* sp. and *Morelia* sp.).

SENSE ORGANS AND NERVOUS SYSTEM

The most noteworthy sense organs in many boids are the infra-red or heat sensitive labial pits that allow these snakes to detect, stalk and strike prey accurately in the dark. These pits (Fig. 33.3) are found within the labial scales (absent in *Aspidites*) in pythonines, and in boinines they are between the labial scales (present only in a few species). Kluge (1993) made a detailed morphological study of the labial pits in pythonines, and de Cock Buning, Terashima & Goris (1981) analysed the warmth reception of pit organs.

Many boids and especially pythonines have scale pits, or apical pits, that are believed to be sensory (McDowell 1975; Kluge 1993).



Figure 33.3 The labial pits of *Morelia spilota*, within the labial scales, sense the heat emitted by ectothermic prey. Note the opaque spectacle over the eye, indicative of incipient skin shedding. [Photo by H. Ehmann]

EXOCRINE AND ENDOCRINE GLANDS

Anal glands are reported in some pythons (McDowell 1975) and Ross & Marzec (1990) describe and illustrate probing the 'musk glands' for gender determination. Anal glands probably produce pheromones that act as mate attractants in adults (especially females). They may function as predator repellents in young snakes.

Seigel & Ford (1987) provided a comprehensive review of reproductive endocrinology in snakes. Testosterone levels in males of the cuban boa *Epicrates striatus* peak during mating (Seigel & Ford 1987).

REPRODUCTION

Observations on captive boids have contributed substantially to the literature on boid reproduction. A major review of snake reproduction by Seigel & Ford (1987) included some boid examples, especially concerning parental care. Heatwole & Taylor (1987) also reviewed many important aspects of reptilian reproduction.

Available information indicates that most Australian pythons are oviparous (Ross & Marzec 1990; Shine 1991a; Ehmann 1992); no information is available for *Morelia carinata*. McDowell suggested that all pythonines are oviparous (McDowell 1975), whereas the boinines as far as is known are viviparous (Parker & Grandison 1977; Ross & Marzec 1990).

In south-western Australia, spermatogenesis in *Morelia spilota imbricata* starts in late summer or autumn and culminates in November when mating is believed to occur (Kuchling 1991). In many species, the male must experience an episode of cooling to breed successfully (Ross & Marzec 1990). Mengden *et al* (1980) published photomicrographs of normal and heat-affected (abnormal) python spermatozoa.

The morphology of the paired hemipenes of boids has been extensively studied as an adjunct to systematics. Boids hemipenes lack spines, in contrast to those of colubrids and elapids. The club shape, flounces and terminal loops of the engorged everted hemipenes of *Liopython albertisi* are illustrated by Ross & Marzec (1990).

The seasonal timing of boid reproduction varies considerably (Shine & Slip 1990; Ross & Marzec 1990). In Australia, ovigenesis usually occurs from October to January, especially in the southern and eastern sections of the continent, at least in species for which there are sufficient data. In the monsoonal north, oviposition occurs earlier in *Liasis mackloti* (August-October) and possibly serves to avoid nest inundation by rains in the wet season from December onwards. A high proportion of non-reproductive females in large collections suggests that many female pythons probably do not reproduce each year.

Courtship and copulation of boids, mostly in captivity, is well documented (Goin, Goin & Zug 1978; Murphy, Carpenter & Gillingham 1978; Murphy, Lamoreaux & Barker 1981; Charles, Field & Shine 1985; Charles 1988; Ross & Marzec 1990; Shine 1991a; Vandermark 1992). During courtship the male crawls over the female, flicking his tongue, and frequently touches his chin on the female's back. The male rakes his larger spurs (Shine & Slip 1990) back and forth (termed spurring) over the female's posterior body. In some boids, the male stimulates the female with his spurs to move her cloaca into an accessible position juxtaposed to his own cloaca. One of the male's two hemipenes is partly everted and inserted into the relaxed cloacal opening (vent) of the female, and is then fully everted and engorged with blood so that it swells in the female's cloaca and cannot be easily withdrawn (Ehmann pers. obs. of *Morelia spilota*

variegata). Copulation may occur one to many times over several days and sometimes with several males, each copulation lasting between 10 and 150 minutes.

After copulation, many female boids refuse food or eat very little as eggs develop. In pythonines, the distended female often lies with her mid and posterior belly uppermost (Christian 1978; Murphy *et al.* 1978, 1981; Charles *et al.* 1985; Charles 1988; Ross & Marzec 1990).

Oviposition in pythonines occurs at a site presumably selected by the female. Seven nests of *Morelia spilota variegata* were associated with bales of hay, a pile of grass or densely matted vegetation (Charles *et al.* 1985; Slip & Shine 1988c, 1988e). Shine (1991a) reported oviposition by *Liasis mackloti* in goanna burrows on high ground near a swamp.

The clutch size of eleven Australian python species varied from five to 21. Mean clutch size was not significantly correlated with mean adult size, although three of the smallest pythons had consistently small clutches of five, six and seven eggs (Shine & Slip 1990; Shine 1991a). In a re-evaluation using data from Shine (1991a), a significant positive correlation was found between an estimator for reproductive effort (mean hatching size x mean clutch size) and mean female body size. The eggs (and hatchlings) of *Aspidites melanocephalus* are surprisingly large (Charles *et al.* 1985), but quite small in *Morelia spilota* (Ehmann pers. obs.).

After laying, the female python brings the eggs together firmly with a body loop and then coils herself around them. The eggs are soon stuck together into a coherent mass (Fig. 33.4). At this stage the females of some species become aggressively protective of their clutch (Charles *et al.* 1985; Ross & Marzec 1990), and lunge and bite at any threatening intruder.

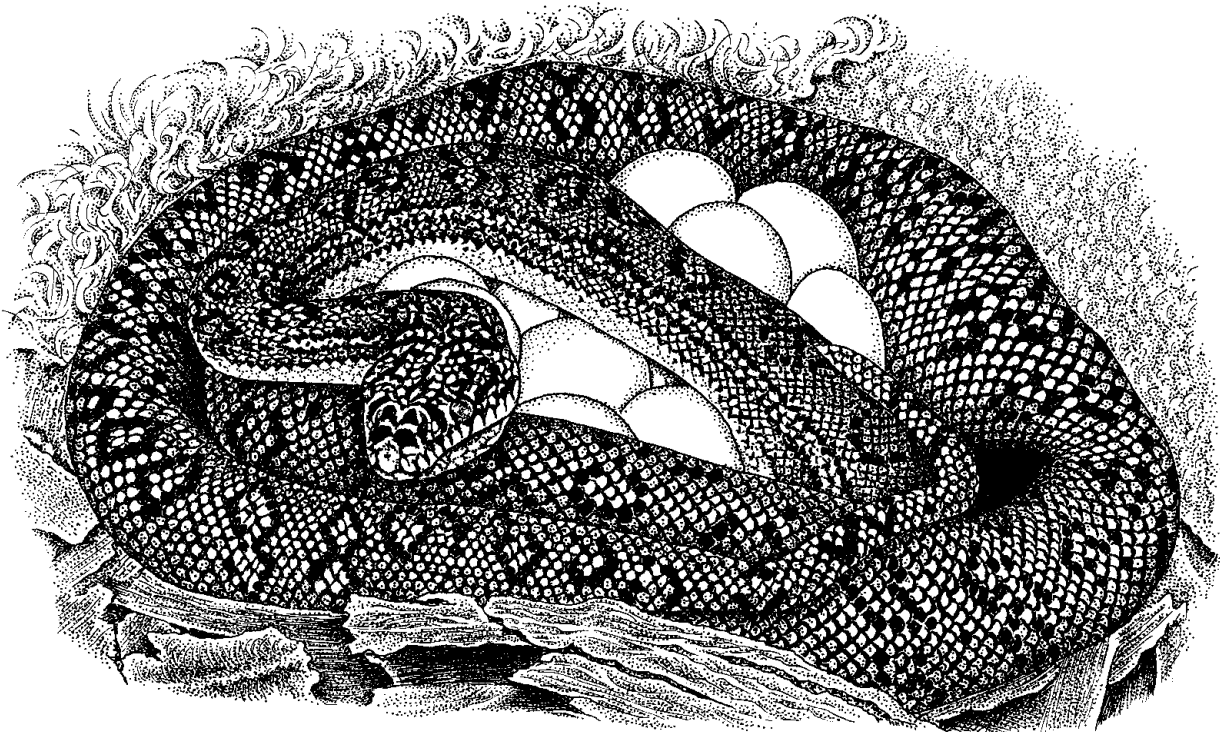


Figure 33.4 A brooding female *Morelia spilota* coils around her clutch of eggs to warm and protect them. (After Shine 1991) [K. Hollis]

In some species, female pythons are known to maintain relatively high and stable egg temperatures during incubation by leaving the eggs in the morning, basking nearby, and when warm, returning to their eggs to warm them. If temperatures fall to a certain point, a brooding female may ‘shiver’, producing heat by anaerobic respiration (Harlow & Grigg 1984; Charles *et al.* 1985; Slip & Shine 1988c). Females may also leave the brood to drink, and Shine (1991a) reported captive *Liasis mackloti* wetting her eggs on returning with water held in her cloaca, presumably to rehydrate them. Seigel & Ford (1987) and Shine (1988c) have reviewed parental care in reptiles, including the pythonines.

Hatching of pythonine eggs has been reported many times (Murphy *et al.* 1981; Sheargold 1979; Charles *et al.* 1985; Charles 1988; Ross & Marzec 1990). The hatchling first slits the leathery egg shell using its egg tooth. Kluge (1993) has summarised the egg tooth’s occurrence and its attachment. The neonate may remain inside the slit egg for up to 48 hours, presumably absorbing remaining egg yolk and fluids. Sheargold (1979) reported that neonates of *Liasis maculosus* (as *L. childreni*) left their eggs in rapid succession, as if on cue, some time after the last egg had pipped. Such synchrony may improve each hatchling’s chance of surviving predators. Shine (1991a) provided data on the average lengths of neonates in eleven species of Australian pythons, and Ross & Marzec (1990) provided additional data for many boids bred in captivity.

Hybrids between genera, species and subspecies are known for captive snakes from Australia (Banks & Schwaner 1985; Hoser 1989; Kortlang 1989). In eastern Australia, *Morelia s. spilota* ö *M. s. variegata* hybrids are sometimes found in the wild. Captive interspecific and intergeneric crosses, *Morelia spilota* ö *M. amethystina*, *Morelia spilota* ö *Liasis mackloti* and *L. stimsoni* ö *L. childreni* are between species that are sympatric over much of their common ranges, yet hybrids have never been found in the wild. This suggests that there are strong pre-mating isolating mechanisms that operate between wild pythons, and that genetically even the genera are closely related, supporting McDowell’s (1975) view of close relationships based on the morphology of the species.

EMBRYOLOGY AND DEVELOPMENT

Embryonic development in boinines occurs *in utero* and the young are born as small snakes, whereas in pythonines most embryonic development occurs *in ovum* following oviposition. A novel and potentially valuable technique for observing the later embryonic development of reptile eggs was developed by Barnett (1979, 1987) in response to *Liasis maculosus* eggs that split open during incubation through absorption of excess water. The wide open egg was suspended in an improvised humicrib and developed to full term.

The neonates of *Morelia viridis* and the very similar *Corallus caninus*, undergo similar dramatic colour changes as they grow (Ross & Marzec 1990). Changes in body shape are associated with the ontogenetic changes in diet, from lizards and/or frogs to endotherms, of some Australian pythons (Shine & Slip 1988), especially in some *Antaresia* (Ehmann pers. obs.)

NATURAL HISTORY

Life History

The size or age at which boids become sexually mature is known for a few species. Shine & Slip (1988) determined that sexual maturity is attained at approximately 70 to 75% of mean adult length in most of 13 species of Australasian pythons. Males are consistently smaller than females at maturity. *Liasis mackloti* reaches sexual maturity about one year after hatching (Shine

1991a). Pythonines generally reach maturity in 18 months to four years, whereas boinines mature in 18 months to seven years; in both subfamilies males often mature earlier than females (Ross & Marzec 1990).

Longevity in captivity was summarised for some boids by Ross & Marzec (1990), but these data may not apply to wild animals. Growth curves have been published for *Liasis mackloti*, in which size-biased mortality occurs in larger animals (Shine 1991a).

Ecology

The diet of the small and more xeric-adapted *Antaresia* comprises frogs and lizards. Reptiles predominate in the diets of medium to large sized, xeric-adapted *Aspidites*, and form 92% of all dietary items in *A. melanocephalus* (Shine 1991a). Mammals and birds are major dietary items of the larger Australian boids. Murid rodents predominate and possums, bandicoots, rabbits and bats also eaten (Shine & Slip 1990). Macropods, especially wallabies, are also eaten by large pythons. The eggs of magpie geese, *Anseranus semipalmata*, are eaten by large, mostly female, *Liasis mackloti* (Shine 1991a). At Humpty Doo in the Northern Territory, *Liasis mackloti* shows habitat and dietary lability, and assumes a semi-aquatic, terrestrial or arboreal life style, depending on the availability of water and associated prey (Shine 1991a). In this area, the population density of *Liasis mackloti* was estimated at hundreds of snakes per hectare (Shine 1991a). The diet of many species changes ontogenetically (Shine & Slip 1990; Ross & Marzec 1990; Shine 1991a; Ehmann 1992).

Shine & Slip (1990) proposed that sparse vegetation cover and a scarcity of large endothermic prey has, through lack of habitat and prey selection, resulted in the evolution of smaller species (especially *Antaresia*) and reptile eating (*Aspidites*) specialists.

Worrell (1963) described winter concentrations or aggregations of *Morelia amethystina* on open ground in deep rainforest gorges of the Atherton Tableland. These aggregations disperse with the onset of warm weather. Webber (1978a) reported a large mass of adults and at least one juvenile *Morelia s. spilota* in the Grose Valley, New South Wales, and aggregations of one large female and one to three courting males of this species are common (Shine 1991a). Two spring breeding aggregations of four and five *M. spilota* were observed on the Murray River near Blanchetown (Ehmann pers. obs.).

Many diseases and parasites are known from captive boids (see Ross & Marzec 1990), but their impact on wild populations is unknown. Shine (1991a) outlined some examples for snakes generally, including pythons.

Dispersal and migration of boids is poorly documented. It is likely that neonates and young boids disperse into and through areas unsuited to adults, where smaller, suitable shelter sites and lizard or frog prey are available.

Behaviour

Male-male combat under captive conditions is well documented in some boids. Such behaviour may be rare in free-ranging snakes. In such combat, two male *Aspidites melanocephalus* tightly entwine their tails, align and overlay their bodies loosely, and elevate the head and forebody. Each rakes his spurs on his opponent's body 0.5 to 2 times per second; no biting was seen (Barker, Murphy & Smith 1979; Murphy *et al.* 1981; Ross & Marzec 1990). In contrast, Charles *et al.* (1985) observed tight coiling and biting by a larger male when a smaller male was substituted for a female mate. Male-male aggression is reported in *Liasis olivaceus*, *Morelia spilota variegata* and *Morelia viridis* (Moran 1988; Charles *et al.* 1985; Walsh 1985; Ross & Marzec 1990), but is believed to be absent in *Morelia spilota spilota* (see Shine 1991a).

Thermoregulatory behaviour has been extensively studied in Australian and New Guinean boids. Cogger & Holmes (1960) first reported basking and coiling to elevate and maintain body temperature in *Morelia spilota variegata*. Coiling into a tight ball-like mass significantly reduces loss of stored heat and extends the time that digestion and ambush hunting can occur. This behaviour has been reported in several species (Johnson, Webb & Johnson 1975; Johnson 1975a; Slip & Shine 1988b).

The patterns of heat distribution within the bodies (and associated thermoregulatory behaviour) of several Australian and New Guinean boids has been studied (Webb & Heatwole 1971; Johnson 1975a, 1977). Most species showed elevated head temperatures while warming, with more precise temperature control in the head region. When overheated, boids maintain head temperatures lower than that in the body. These physiological controls are linked to behavioural/position adjustments.

Slip & Shine (1988a, 1988b, 1988c, 1988d, 1988e) reported the first detailed study of thermoregulation and associated behaviour in boids (see also Feeding and Digestive System, and Reproduction). They reported that *M. s. spilota* are mostly solitary (Slip & Shine 1988d). In warm weather, these snakes bask once in the morning to elevate body temperature before seeking shelter for the rest of the day, where heat loss is minimised, assisted usually by body coiling. At night, snakes relocated sometimes to a new foraging area or ambush site.

Defensive behaviours in boids are described by Bustard (1969f), Johnson (1975b) and Delean & Harvey (1982). Boids, like many other snakes, give warning by body inflation, hissing, and making bluff strikes with a closed or partly open mouth. *Liasis stimsoni* rolls into a ball with the head concealed, if aggressive posturing and striking fails to deter a human offender (Delean & Harvey 1982).

Aspidites is the only pythonine to exhibit burrowing behaviour. Murphy *et al.* (1981) reported that four captive *A. melanocephalus* excavated gravel by bending the head and neck into the shape of a 'J', moved the head and neck sideways into the loose substratum and then pulled the entrapped material towards the posterior body. Fyfe & Harvey (1981) observed six captive *A. ramsayi* using the chin and anterior ventral area to scoop out large quantities of sand, and suggested that wild snakes probably 'enlarge existing animal burrows for shelter or while hunting'. Captive specimens also completely buried their anterior 0.5 m under loose sand for 15 to 20 minutes, leaving the rest of the body exposed, emerging for about one minute before repeating the behaviour (Fyfe & Harvey 1981).

Economic Significance

In Australia and elsewhere there are extensive husbandry and breeding programs for boids by private keepers, researchers and institutions such as zoos and animal parks. Boids, especially those species that are easily tamed, are used most widely in public education (Ross & Marzec 1990). Captive husbandry and breeding of boids is an important adjunct to research and conservation efforts.

No Australasian boid species is considered to be threatened, but some races of *Morelia spilota* are vulnerable due to habitat loss and alteration, especially from extensively cleared areas of southern Australia. The race from the Murray-Darling drainage (see Ehmann 1992) is threatened and has been the subject of a Conservation Action Statement in Victoria (Allen 1993). Populations of *Morelia spilota imbricata* and *Aspidites ramsayi* in south-western Australia are similarly threatened (Smith 1981) and have been given additional protective status in Western Australia. A detailed study of the cryptic and secretive *Morelia s. spilota* around Sydney (Slip & Shine 1988a, 1988b, 1988c, 1988d, 1988e)

showed that the species is not as threatened as was previously believed, and it has since been removed from Schedule 12 of the New South Wales National Parks and Wildlife Act.

Some Australian python populations could be threatened by over-collecting. The insular populations of St Francis Island in South Australia (Schwaner, Francis & Harvey 1988), and the small populations of *Antaresia stimsoni* (Pl. 7.5, as *Liasis stimsoni*) in isolated rocky outcrops and small ranges in southern Australia may be at risk, and require monitoring and possibly management.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

The distributions of Australian pythons are mapped in Cogger (1992) and Ehmann (1992), and Shine (1991a) provided a species density map for Australian pythons. Species density is highest (eight species) on eastern Cape York and Torres Strait, and six species occur in the warm tropical areas of the western Kimberley and in Arnhem Land, where rainforest, relictual rainforest patches or deep mesic gorges occur. Pythons are absent from the cold winter areas of the south-eastern Australian mainland and Tasmania.

The distribution of 11 species of boids in New Guinea, Indonesia, and the Western Pacific is provided by McDowell (1975, 1979). Of particular interest are the four species shared with Australia: *Liasis mackloti* and *Morelia amethystina* are widespread in New Guinea and Indonesia; *Morelia viridis* is widespread in New Guinea and is restricted to small pockets of rainforest on eastern Cape York; *Morelia spilota* is widespread in Australia, and in southern New Guinea restricted to drier habitats. The first two species probably reached Australia by southward invasions, *L. mackloti* being first, followed by some evolutionary divergence. The last two species are most likely a reciprocal exchange northwards across the Torres Strait landbridge in Pleistocene times (see also McDowell 1975).

Beyond Australasia, pythonines occur in greater Asia and Africa, whereas the boinines occur in Europe, Africa, Central and South America and the West Indies (Cadle 1987). Cadle (1987) also discussed the various hypotheses and evidence explaining boid distribution in the Australasian Region.

Affinities with other Groups

McDowell (1987) concluded that the superfamily Booidea is a well-defined group without clear relationships to any other, and without clear palaeontological evidence of being particularly ancient. However, pelvic vestiges, premaxillary teeth and other osteological peculiarities suggest this is an old group. McDowell places the group into the infraorder Alethinophidia containing six superfamilies (and 16 families) of snakes, which were previously classified into the infraorders Henophidia and Caenophidia, with a total of eight families (Parker & Grandison 1977).

Affinities within the Boidae

The Boidae comprise two subfamilies: the distinctive Pythoninae, and all other snakes historically referred to as boinines, namely the Boinae and Erycinae of McDowell (1987). McDowell (1987) recognised a superfamily Booidea comprising the Pythonidae and the Boidae (Boinae plus Erycinae); three of the boinine subfamilies of Parker & Grandison (1977) were removed to other superfamilies. This scheme has not been fully accepted and is still the subject of study and debate.

On the basis of a detailed systematic study using both behavioural, and external and internal morphological characters, Kluge (1993) reassigned six of the 15 Australian species to three other genera and synonymised *Liasis fuscus* with *L. mackloti*. These are significant changes to recent Australian usage (*cf.* Wilson & Knowles 1988; Ehmann 1992; Cogger 1992). Kluge (1993) developed a phylogeny of the Pythoninae and found that *Aspidites* is the sister lineage of all other pythonines, and the remaining Australia-New Guinea taxa constitute a paraphyletic assemblage. The southeast Asia-Africa *Python* forms a highly derived clade.

Fossil Record

Before McDowell's (1987) transfer of the Madtsoiidae (Madtsoiinae of Boidae) to the infraorder Chlorophidia, *Wonambi* from Naracoorte Caves Pleistocene, was the first and most impressive 'boid' fossil from Australia (Smith 1976b). The oldest Australian snake fossils are the Miocene boids *Montypythonoides riversleighensis*, approximately 14 million years old, and *Morelia antiqua*, some 12 million years old, from Queensland and the Northern Territory, respectively (Smith & Plane 1985). Archer, Hand & Godthelp (1991) reported the occurrence of many boid remains in the Riversleigh deposits.

Kluge (1993) reassessed these Miocene boids and concluded that the first was *Morelia spilota* and the second *Liasis olivaceus*. He cast doubt also on the assignment of three snake fossils from elsewhere to the Pythoninae by Rage (1984). Rage (1987) reviewed ophidian fossil history and disagreed strongly with the removal of madtsoiines from the Boidae. He presented an overview of snake evolution based on fossil remains including many species he assigned to the Boidae.