FAUNA
of
AUSTRALIA

30. FAMILY VARANIDAE

Dennis King & Brian Green

Pl. 5.10. *Varanus gouldii* (Varanidae): Gould's goanna lives in the arid interior; an active forager, it is one of the largest Australian goannas, growing to 1.6 m overall; common throughout the mainland except in the wettest parts; also on Lizard Island. [J. Wombey]

Pl. 5.11. *Varanus rosenbergi* (Varanidae): inhabits far South-western and southern Australia; attains about 1 m in length. [R. Kuiter]

Pl. 5.12. *Varanus tristis* (Varanidae): is arboreal or inhabits crevices in rocky hills along the coast and in the arid interior of northern and central Australia; it grows to 0.8 m in length. [G. Shea]

Pl. 5.13. *Varanus brevicauda* (Varanidae): the smallest member of the family in Australia, inhabits sandy deserts with spinifex grass in central and western areas of Australia. [J. Wombey]

GENERAL DESCRIPTION AND DEFINITION

Australian varanids have a long and slender neck, a long body with strong, muscular tails, and well-developed, pentadactyl limbs with a strong claw on each digit. Autotomy does not occur. The whole body is covered with thick, loose-fitting skin with small, juxtaposed scales. The scales on the head are small. The eyelids are movable, and the tongue is extremely long, slender and deeply forked at the tip.

Approximately 40 species are known, all included in the single genus *Varanus*. At least 25 of these occur in Australia, where they are known as goannas. They are medium to large in size and are active, diurnal hunters (Pl. 5).

HISTORY OF DISCOVERY

The Nile Monitor, *Varanus niloticus*, was the first varanid named by Linnaeus in 1758, as *Lacerta monitor*. White (1790) described the first Australian species, *Varanus varius* (as *Lacerta varia*), from a specimen probably collected near Botany Bay, New South Wales. The holotype is presumed to be lost. *Varanus varius* was next referred to by Daudin (1802), and a designated holotype, from Sydney, New South Wales, is held in the Museum National d'Histoire Naturelle in Paris. Merrem first used the generic name *Varanus* in 1820.

Other Australian species were named during the remainder of the 19th and throughout the 20th century, as more of the continent became accessible to scientists. Thus up to 1869, all of the described species had coastal distributions, but more species were named from specimens collected on several of the major explorations into the deserts of central Australia between 1885 and 1903. Most new species described since 1942 were from northern Australia, or were named during revisions of previously described species. Several species that are currently recognised within Australia are still undescribed.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

The snout is elongate, the nares range in position from near the tip of the snout to close to the eyes (Bellairs 1949). The long, forked tongue fits into a sheath on the floor of the mouth (Smith 1986). The tail is round or laterally flattened in cross section, and its length in relation to the snout-vent length (SVL) is variable, ranging from approximately 100 to 220% in Australian species (Cogger 1975a). *Varanus* shows the widest size range of any vertebrate genus; adults of the smallest species (*V. brevicauda*) weigh approximately 17 g and reach a total length of 200 mm (James pers. comm.; Pl. 5.13), while adults of the largest species (*V. komodoensis*) can exceed 70 kg and are reported to reach a total length of 3.5 m (Auffenberg 1981). *Varanus salvator* and *V. giganteus*, respectively are the next largest species in terms of body mass. It is reported that *V. salvadorii* can reach a total length of over 4 m because it has an exceptionally long tail, but no specimens of that length have been documented.

Body Wall

The skin is loose and is covered by small, juxtaposed scales, and the scales on top of the head are small and fragmented (Cogger 1975a). There is a distinct, clear parietal scale on the top of the head.

Skeletal System

Cranial kinesis occurs in varanids, whereby the upper jaw can move independently of the rest of the skull (Rieppel 1979). This facilitates the functioning of the dentition and the swallowing of prey. The teeth are recurved and laterally compressed, and have serrated edges in some species (Greer 1989). The hyoid apparatus has greater mobility than in most lizards (Smith 1986), which assists in the movement of prey into the oesophagus. The roof of the nasal capsule is covered only by skin and connective tissue, unlike other lizards (Bellairs 1949).

Varanids have one cervical vertebra additional to those found in other lizards and the vertebrae are elongated. There is little variation in the number of pre-sacral vertebrae (27 to 32), and the number of post-sacral vertebrae varies from 56 to 139 in Australian species (Greer 1989).

The hemipenes contain ossified hemibaculae, and differences in the morphology of these structures have been used in constructing phylogenies of varanids (Branch 1982; Böhme 1988).

Locomotion

Terrestrial locomotion is generally quadrupedal, with a slow, swinging gait. A large varanid ambling through the bush in an almost arrogant manner, with its tongue flickering through the air, is very impressive.

Occasionally varanids raise the body and forelimbs from the normal position and run bipedally. Many species are arboreal as adults, particularly the smaller species. Some of the larger species, such as *V. tristis* and *V. varius*, also climb trees, and arboreal habits are common in the young of some of the larger species, including *V. komodoensis* (Auffenberg 1981) and *V. varius* (Weavers 1983). *Varanus varius*, *V. tristis*, *V. scalaris*, *V. gilleni* and *V. caudolineatus* often use tree holes and loose bark as shelters, and *V. prasinus* is aided by its prehensile tail when climbing (Greene 1986). Species such as *V. glauerti* (Pl. 5.11), *V. glebopalma* and *V. kingorum* are primarily saxicolous.

Several species (*V. indicus*, *V. mertensi*, *V. niloticus*, *V. salvator*, *V. semiremex*) are amphibious and most species, including some from Australian deserts, can swim well. When swimming, the limbs are held loosely alongside the body and horizontal strokes of the tail and undulations of the whole body are the main means of propulsion (Cowles 1930). Amphibious forms have a dorso-ventrally flattened tail, apparently to assist in swimming and, in *V. mertensi* (Hermes 1981) and *V. salvator*, to assist in hunting aquatic prey.

Feeding and Digestive System

Varanids possess large Jacobson's organs which are located in the front of the nasal capsules in the roof of the mouth. They augment the nose, and appear to play a major role in detecting prey by smell (Bellairs 1949). They are connected by ducts to the nasal sacs and enable the lizard to detect scent particles which have been collected from the air by the tongue and delivered to the roof of the mouth near the openings to the Jacobson's organs. A flickering tongue is highly characteristic of a foraging varanid (Pianka 1986). The tips of the deeply incised tongue move separately, thereby increasing the volume of air they sample and the scent particles they collect (Smith 1986). When the tongues of varanids are extended, they can increase in length by 70 to 90% (Smith 1986).

The tongue plays no part in manipulating prey (Smith 1986). Varanids use inertial feeding, movements of the neck, and the hyoid apparatus to force the prey down the throat and into the simple stomach. Small prey are swallowed whole. Large prey or carrion are dismembered by holding them with the forefeet

and using the sharp teeth and jerking movements of the head to tear off pieces of the carcass (Auffenberg 1981). The tongue is protected in its sheath on the floor of the mouth during feeding (Smith 1986) and when the food has reached the throat, the hyoid apparatus moves it back into the oesophagus (Smith 1986). The neck is then twisted from side to side to help move the food further down the throat. Sometimes large food items are forced down the throat by ramming; the lizard places the food item against a firm structure and pushes against it.

Circulatory System

Although reptiles do not possess a diaphragm, varanids (and *Heloderma* and *Lanthanotus*) have a well-developed septum that separates the thoracic and abdominal cavities.

The varanid heart is not a typical lizard heart. It is located further posterior in the body cavity than in other lizards and is surrounded by a thick pericardium. Oxygen transport by the blood is enhanced due to the arrangement of the chambers and valves, which results in limited ventricular mixing of pulmonary and systemic blood streams (Webb, Heatwole & De Bavay 1971; Heisler, Neumann & Maloiy 1983). Systemic blood pressure also exceeds pulmonary blood pressure because of the contact between a muscular ridge (muskelleiste) in the ventricle and the exterior wall of the heart during systole (Heisler *et al.* 1983) and effectively creates a four-chambered heart at that stage and largely separates the systemic and pulmonary blood streams.

During changes in body temperature, the pH of the blood is closely regulated by buffers, which enables a high level of oxygen transport and aerobic activity to continue (Bennett 1973a).

Varanids also have higher levels of myoglobin in the muscles than other lizards (Bennett 1973a), which facilitates the rapid transport of oxygen from blood to muscles.

Respiration

The intra-pulmonary ducts in the lungs are reinforced with cartilage and connect with a number of small chambers (multi-cameral). The lungs are larger than those of most other reptiles (Perry 1983). They provide an enlarged surface for gas exchange and a starting point for the evolution of high performance lungs which have large surface areas and can be ventilated easily at a low energy cost (Perry 1983). The lungs are attached directly to the body wall under the rib cage, have a strong compliance with body movements, and are efficiently ventilated by costal breathing alone. The gas exchange strategy is convection-dominated and the lungs do not have to be actively deflated like those of most lizards (Perry 1983).

Varanids have a greater aerobic capacity than other reptiles (Bartholomew & Tucker 1964; Bennett 1972) and, except for amphibious forms under water, do not function anaerobically for the long periods shown by other reptiles. Generally they maintain low blood levels of lactic acid through efficient blood buffering and gaseous exchange in the lungs (Hicks, Ishimatsu & Heisler 1987). Varanids can thus repay their oxygen debt quickly after exertion.

The chemical control of ventilation of the lungs is rapid and efficient (Glass, Wood, Hoyt & Johansen 1979) which increases and maintains their high level of performance. The advanced structure and performance of the lungs and circulatory system allow varanids to respire efficiently for long periods without becoming exhausted. These adaptations enable them to adopt an active, wide-ranging foraging strategy.

Excretion

Six species of varanid are closely associated with water, including the Australian species *V. mertensi* and *V. semiremex*. However, most species inhabit environments that are arid or semi-arid for substantial parts of the year. Evaporative water loss in varanids is low compared to that of most other squamates (Green 1969).

Renal studies show that *V. rosenbergi* and *V. gouldii* can regulate glomerular filtration rate, tubular reabsorption and secretion, and ureteral urine flow over a broad range in response to different environmental and experimental conditions (Green 1972; Bradshaw & Rice 1981). The ureteral urine is passed into the coprodaeum of the cloaca, where further water is removed from the excreta by solute-linked sodium transport (Braysher & Green 1970). Renal and cloacal function is regulated mainly by the anti-diuretic hormone arginine vasotocin (AVT) (Braysher & Green 1970; Green 1972; Bradshaw & Rice 1981), circulating levels of which vary in response to the lizard's environmental state (Rice 1982). The water contents of urinary pellets are quite low when they are finally expelled (Seshadri 1959; Green 1969) and the amount of water lost relative to nitrogen excreted is much lower even than in the urine of desert mammals (King & Green 1993).

Excess cations can be excreted via the nasal salt glands that have been identified in several varanid species, such as *V. rosenbergi* and *V. semiremex* (reviewed by Minnich 1979). Sodium is the main cation secreted by the salt glands of varanids, reflecting the predominance of this ion in their prey and habitats. The nasal secretion of hyperosmotic sodium facilitates the sodium-linked reabsorption of water from the kidney tubules, cloaca and rectum.

Field studies have been made of the total water fluxes of a number of varanids (Table 30.1). Clear seasonal patterns of water use are evident in *V. rosenbergi* and *V. varius* (Green 1972; Weavers 1983), and the water fluxes of some tropical species appear to be substantially higher than in species from semi-arid/arid environments.

Table 30.1 Water turnover rates of free-living varanid lizards in spring (sp) and summer (su).

Species	Season	Weight (g)	Percent body water	Water turnover (ml/kg/day)
V. acanthurus	sp	60	70.3	15.9
V. griseus	su	350	77.9	28.3
V. gouldii	su	493	77.0	23.5
V. rosenbergi	su	1086	76.7	22.0
	sp	1089	76.5	15.8
V. varius	su	4300	72.7	24.6
	sp	–	—	15.0
V. giganteus	su	7700	68.4	22.3
V. komodoensis	su	45000	74.9	25.5
Tropical varanids				
V. bengalensis	–	2560	–	60.5
				76.9
V. salvator	–	7600	74.9	54.4

There are few reports of metabolic rates in free-living varanids. However, it seems clear that seasonal variations are marked (Green, Dryden & Dryden 1991) and tropical species show higher CO_2 production rates than non-tropical forms (Dryden, Green, King & Losos 1990).

Sense Organs and Nervous System

Varanids rely heavily on the tongue, which collects scent particles and transfers them to the Jacobson's organs, to provide sensory stimuli during hunting and reproductive behaviour (Auffenberg 1981, 1988; Smith 1986). Vision seems less important than smell in food detection (Auffenberg 1988).

Reproduction

Some Australian and African species of varanids have sex chromosomes with female heterogamety (King & King 1975; King, Mengden & King 1982).

All varanids are oviparous. Clutch size is positively correlated with body length (Fig. 30.1) in varanids, (King 1991). In some species, gravid females become so distended with eggs that they are unable to feed for several weeks prior to egg laying (Auffenberg 1988).
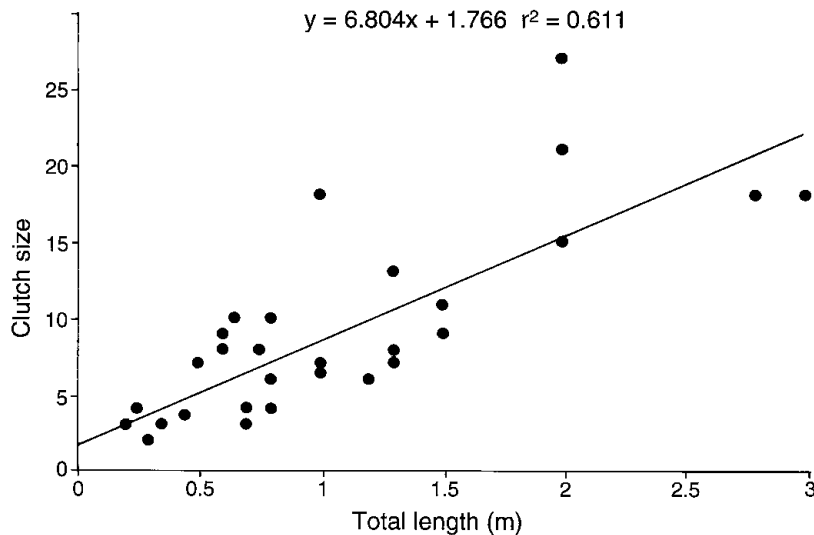

$$y = 6.804x + 1.766 \quad r^2 = 0.611$$

Figure 30.1 The relationship between clutch size and body size in varanid lizards. (After King & Green 1993)   [W. Mumford]

Although captive animals are able to produce two clutches a year (Horn & Visser 1989), wild varanids apparently breed only once a year.

Some species (*V. rosenbergi*, *V. varius*, *V. giganteus*, *V. gouldii*, *V. albigularis*, *V. niloticus*, *V. bengalensis*) lay their eggs in termite mounds (Cowles 1930; King & Green 1979; Carter 1990; Branch 1991) which maintain their temperature above 25°C, with high humidity, throughout winter (Green, MacKelvie & Rismiller unpub. data). This provides perfect conditions for the development of reptile eggs. Other species simply bury their clutch deep in the soil, while *V. olivaceus* reportedly lays its eggs in hollow trunks and limbs of trees (Auffenberg 1988). Some species appear to deposit their eggs in communal warrens (King & Green 1993).

The timing of breeding varies substantially between species and there can be marked differences between localities within a species (King, Masini & Robinson unpub. data), or between species at a particular locality, particularly in the tropics (Shine 1986d; James *et al*. 1992).

The age of sexual maturity for most species is not known, but it probably occurs at an older age in large species that in small species. It is estimated that *V. komodoensis* take about five years to mature (Auffenberg 1981) and four to six years in *V. albigularis* (Branch 1991). *Varanus olivaceus* reaches sexual maturity at about three years old (Auffenberg 1988). Captive *V. varius* bred at the age of seven to eight years (Horn & Visser 1991). It has been estimated that wild *V. acanthurus* may reach sexual maturity in one to two years (King & Rhodes 1982).

Embryology and Development

Incubation times in the field for the eggs of different species which do not lay in termitaria are variable, and range from an estimated 90 to 120 days in *V. acanthurus* (King & Rhodes 1982) to 250 or 265 days for eggs of *V. komodoensis* (Auffenberg 1981). Incubation times at similar temperatures in captivity vary from approximately 75 to 250 days (Horn & Visser 1989), and are related to maternal body size (Fig. 30.2; King 1991).

Growth rates of the young of all species are rapid during the first three months after hatching, and adult size is reached within one to two years in the smaller species (King & Rhodes 1982; Horn & Visser 1991), whereas the larger species may take up to five years to reach adult size (Auffenberg 1981; Horn & Visser 1991).
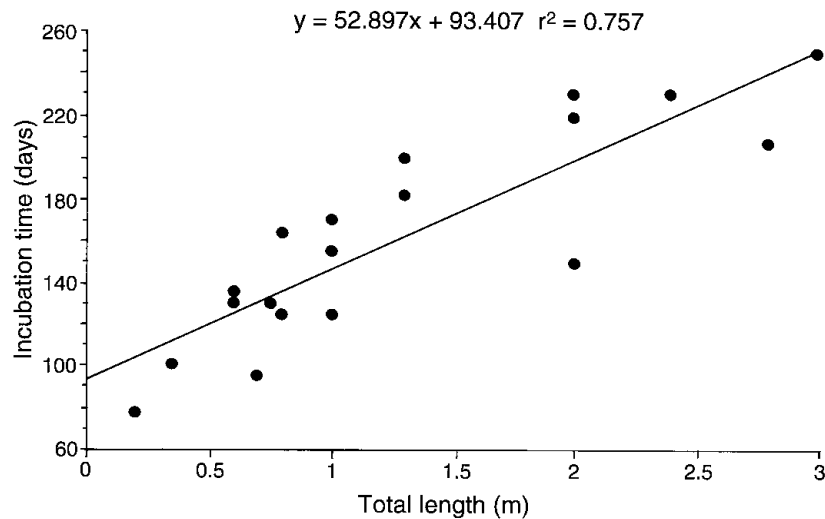
$$y = 52.897x + 93.407 \quad r^2 = 0.757$$

Figure 30.2 The relationship between incubation time and body size in varanid lizards. (After King & Green 1993)   [W. Mumford]

NATURAL HISTORY

Life History

There are few data on the longevity of varanids in the wild, on their age of maturity or age specific fecundity, or on other demographic parameters (Auffenberg 1988). Several species (*V. komodoensis*, *V. albigularis*, *V. niloticus*) have been held in captivity for periods of 15 to 20 years, suggesting long life

spans are also possible in the wild (Auffenberg 1981; Branch 1991). Auffenberg (1981) agreed with Darevsky's (1963) estimate of a probable lifespan of 50 years for *V. komodoensis* in the wild.

The sex ratios of varanids in museum collections are often strongly biased in favour of males (King & Green 1979) but this is probably a result of differences in activity patterns between the sexes (King & Rhodes 1982).

Ecology

Varanids utilise a wide variety of habitats, ranging from aquatic to terrestrial and arboreal, and from arid deserts to temperate shrublands with tropical forests (Cogger & Heatwole 1981).

Most varanids forage over large areas (Green, King & Butler 1986; Pianka 1986; Vernet, Lemire & Grenot 1988a). Population densities of varanids are generally low (Stanner & Mendelssohn 1987) although there are some exceptions (Auffenberg 1981). There are no indications that any of the six species of varanids whose movements have been well studied using radiotelemetry (*V. rosenbergi*, *V. komodoensis*, *V. olivaceus*, *V. varius*, *V. griseus*, *V. giganteus*) are territorial (Green & King 1978; Auffenberg 1981, 1988; Weavers 1983; Stanner & Mendelssohn 1987; King *et al*. 1989; Vernet, Lemire Grenot & Francaz 1988b). All six species have well-defined home ranges or activity areas. These overlap extensively, within and between sexes (Green & King 1978; Auffenberg 1981, 1988; Weavers 1983; Stanner & Mendelssohn 1987; Vernet et al. 1988b; King *et al*. 1989) and are highly variable in size. The activity areas of *V. olivaceus* are much smaller (Auffenberg 1988) than predicted by the formula of Turner, Jennrich & Weintraub (1969) on the basis of body mass, perhaps because of the importance of fruit in their diet (Auffenberg 1988). Those of the other species are larger than predicted, and all of those are strictly carnivorous (Stanner & Mendelssohn 1986). There is a positive correlation between the size of individual *V. komodoensis* and the size of their foraging areas (Auffenberg 1981). The home ranges of males are larger than those of females (Stanner & Mendelssohn 1987; Auffenberg 1988), and male varanids are more active than females (Auffenberg 1981; Stanner & Mendelssohn 1987).

The sizes of home ranges/activity areas are strongly influenced by seasonal conditions in *V. rosenbergi*, being larger in summer and smaller in spring and autumn. The animals generally do not move far away from the immediate vicinity of their burrows in winter (King & Green 1993).

Varanids are generally solitary and they are almost exclusively diurnal (Cogger, Cameron & Cogger 1983a), although some rock-dwelling species may occasionally be crepuscular (Wilson & Knowles 1988). They are also strictly carnivorous (Pianka 1986), with one exception (Auffenberg 1988). As far as is known all species are wide-ranging foragers (Pianka 1986). Most varanids eat a variety of invertebrates, including insects, molluscs and crustaceans, and an occasional large vertebrate (Losos & Greene 1988). Even some relatively large varanids (*V. gouldii*, *V. griseus*, *V. indicus*, *V. rosenbergi*) include considerable numbers of invertebrates in their diets (Dryden 1965; Cissé 1972; King & Green 1979; Stanner & Mendelssohn 1986), and they appear to be opportunistic predators. They forage over large areas and investigate fallen logs, burrows, nesting areas of birds or reptiles, leaf litter, crevices and recently disturbed areas, and will apparently eat almost anything they can capture (Losos & Greene 1988). Varanids can chase prey over long distances (Bennett 1973a).

As the size of the species of varanid increases, the range in size of the prey species broadens (Losos & Greene 1988; King unpub. data), and adults of some of the larger species (*V. giganteus*, *V. glebopalma*, *V. komodoensis*) specialise in feeding on vertebrates (Auffenberg 1981; King, Green & Butler 1989; James, Losos & King 1992). Large *V. komodoensis* use sit-and-wait tactics and ambush

pigs, deer and other large mammals beside game trails (Auffenberg 1981). Adults of the large species, such as *V. komodoensis*, *V. rosenbergi*, *V. salvator* and *V. varius* are able to dismember carcasses (Losos & Greene 1988; King & Green 1993) and frequently consume carrion. Smaller varanids consume their prey whole (Losos & Greene 1988).

Cannibalism has been recorded in several species of varanids, including *V. rosenbergi*, *V. komodoensis* and *V. giganteus*, (King & Green 1979; Auffenberg 1981; King *et al*. 1989).

Intraspecific differences in diet occur and generally reflect prey availability, habitat use or seasonal abundance of prey (Shine 1986d; Losos & Greene 1988; King *et al*. 1989; James *et al*. 1992; Thompson & King in press). Some species, such as *V. dumerili*, *V. mertensi*, *V. mitchelli* and *V. semiremex*, do specialise and primarily eat aquatic forms (Krebs 1979; Shine 1986d; Losos & Greene 1988; James *et al*. 1992), while species in Australian deserts such as *V. eremius* and *V. gouldii* (Pl. 5.10) prey heavily on the abundant and diverse lizard fauna (Pianka 1982). Eggs of birds or reptiles are frequently eaten by a number of species, such as *V. rosenbergi*, *V. tristis* and *V. giganteus* (King & Green 1979; Pianka 1982; King *et al*. 1989).

The diet of the arboreal *V. olivaceus*, from the southern Philippines, contains many invertebrates, however it also includes a large amount of fruit at some times of the year, particularly between May and September (Auffenberg 1988). A few other species of varanids have been reported to eat fruit in captivity but no others include vegetation in their diet in the wild (Auffenberg 1988).

Parasites

Varanids tolerate large numbers of internal and external parasites, seemingly with little or no discomfort or harmful effects. All species of varanids harbour a range of nematodes in their gastrointestinal tract. In Australia, these worms are generally species of *Abbreviata*. Each species usually occurs in several *Varanus* species, but some are specific to one host species (Jones 1985a). Each host species usually has one or two dominant species of nematodes, but may have four or more species parasitising them (Jones 1988). Almost all adult *V. rosenbergi* support numerous *Abbreviata antarctica* in their digestive tracts (Jones 1983). These nematodes can mature in either *V. rosenbergi* or in several species of elapid snakes. Their intermediate hosts are arthropods.

Cestodes occur commonly in the intestines of varanids and their larvae often are found in large numbers under the skin or in the connective tissue of the lizards (Auffenberg 1981).

Pentastomes of the genus *Elenia* parasitise varanids from the Australian region (Bosch 1991). The intermediate host is a vertebrate (amphibian, reptile or mammal) although auto-infections can also occur. Sexually mature parasites occur in the mouth–throat region of varanids.

Protozoans, particularly *Entamoeba* species and *Isospora* species., are also abundant in the gastrointestinal tracts of some species of varanids (Keymer 1981).

Varanids also host blood parasites, such as the protozoans *Trypanosoma* species and *Hepatozoon* species (Keymer 1981) and malarial plasmodia (Auffenberg 1988), but their effect on the lizards is unknown.

Ticks and mites are very common on monitors. Most ticks found on goannas in Australia belong to the genera *Amblyomma* or *Aponomma* (Roberts 1970; Sharrad & King 1981), and *Aponomma fimbriatum* is a common external parasite of *V. rosenbergi* and *V. gouldii* (Sharrad & King 1981). These ticks

generally attach themselves to the chest, at the base of the tail behind the cloaca, between the eyes and the nares, in the nares, or in the axillary regions. Up to 30, or occasionally more, of these ticks can be found attached to an individual.

Although various species of mites occur on varanids, they are not usually present in high numbers.

Behaviour

During courtship and mating, licking, stroking and scratching are used by the male to maintain the close attention of the female (Auffenberg 1988; Carter 1990; King & Green 1993).

During the breeding season, males engage in ritual combat behaviour, which involves bipedal clinches and wrestling by the larger species (*V. bengalensis*, *V. gouldii*, *V. komodoensis*, *V. mertensi*, *V. salvator*, *V. spenceri*, *V. olivaceus*, *V. varius*). They clutch each other with the forelegs only (Fig. 30.3), and try to overpower their opponent, which may result in the animals rolling on the ground. Occasionally, in some species, the victor may bite (*V. gilleni*, *V. komodoensis*, *V. niloticus*, *V. olivaceus*, *V. varius*), but apparently not in others such as *V. bengalensis* and *V. salvator* (Horn 1985; Auffenberg 1988; Twigg 1988). Severe wounds are sometimes inflicted by teeth or claws. Combat in the smaller species (*V. gilleni*, *V. semiremex*, *V. caudolineatus*, *V. timorensis*) does not include a bipedal phase, but mainly involves clutching with the forelegs and hindlegs and body-arching (Horn 1985). There appears to be a phylogenetic basis to this behavioural difference (Horn 1985).
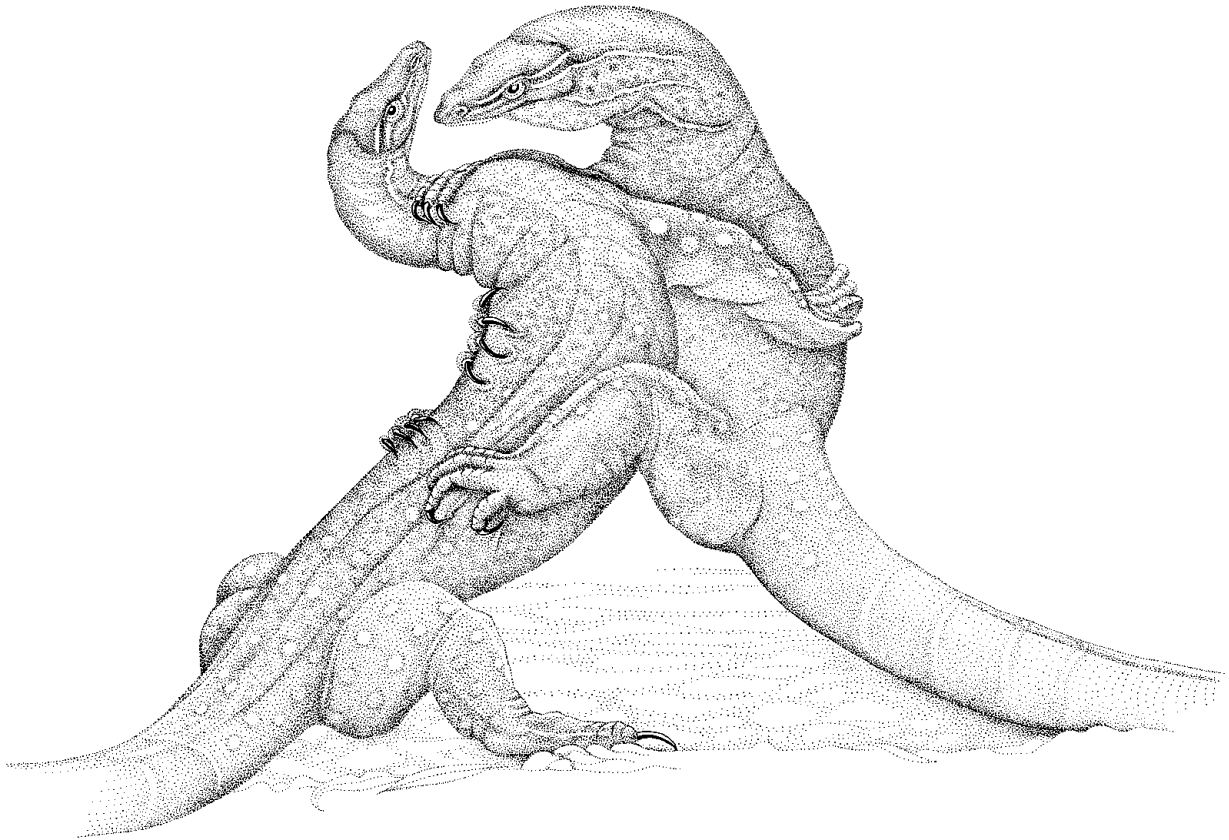

Figure 30.3 Male ritual combat in *Varanus gouldii*. (After photo by D. & T. O'Byrne/ANT)   [T. Wright]

Male *V. varius* with large wounds are often observed during the mating season, which suggests strong competition for mates (Carter 1990). Interspecific defensive behaviour involves a number of aggressive postures, such as assuming an upright threatening posture (Fig. 30.4), elevating the body on all four legs, inflating the gular pouch and tail-lashing, as well as the display of weaponry, including teeth (Auffenberg 1981; Auffenberg 1988). Hissing is used as a vocal threat (Auffenberg 1981).

Female varanids may mate frequently with one or several males over a period of a few days, and groups of males have been observed trying to mate with one female (Carter 1990). During mating, they communicate via olfactory, visual and tactile stimuli (Auffenberg 1981; Carter 1990). Both hemipenes are used, usually alternately, during copulation (Carter 1990; King & Green 1993).

A pair of *V. rosenbergi* will spend about 10 days engaged in intermittent copulation. Each bout of copulation lasts about 10 minutes. Between these bouts the female often retreats to the shared burrow. The male subsequently enters the burrow and coaxes the female outside by extensive licking, and by rubbing her body with his head. The male uses the base of his tail and his hind limbs to raise the females hindquarters sufficiently to enable penile penetration (King & Green 1993). In *V. bengalensis*, *V. komodoensis* (Auffenberg 1983), *V. varius* (Carter 1990) and *V. indicus* (McCoid & Hensley 1991) the male scratches the base of the female's tail with his claws, before intromission.

Figure 30.4 *Varanus panoptes* in bipedal threat display. (After King & Green 1993)   [T. Wright]

Males of some of the larger species (*V. bengalensis*, *V. komodoensis*) embrace the female during mating in such a way as to immobilise her by pinning her front legs to her side, preventing her from moving forward and escaping or damaging him (Auffenberg 1983).

The gravid female buries her eggs in a nest, and in some species (*V. rosenbergi*, *V. gouldii*, *V. niloticus*, *V. varius*, *V. giganteus*, *V. albigularis*, *V. bengalensis*) the nest is dug deeply into a termite mound. The female backfills the entrance shaft she has dug and, in *V. rosenbergi*, is sometimes assisted in this by the male (Green *et al*. unpub. data). The termites soon complete the task of sealing off the egg chamber.

The hatchlings of *V. niloticus* escape from termitaria without the assistance of adults (Cowles 1930), as do those of *V. rosenbergi* (Green, MacKelvie & Rismiller, unpub. data). However, parental assistance in hatchling release apparently occurs in *V. varius* and perhaps in other species (Carter 1992; Fig. 30.5). While the young of *V. niloticus* immediately desert the nest in the termitarium, hatchlings of *V. rosenbergi* may continue to use the termitaria as refuge sites for up to four months after hatching (Green *et al*. unpub. data). The young of *V. varius* spend most of their time in trees during the first weeks after emerging from the termitaria (Carter 1992).
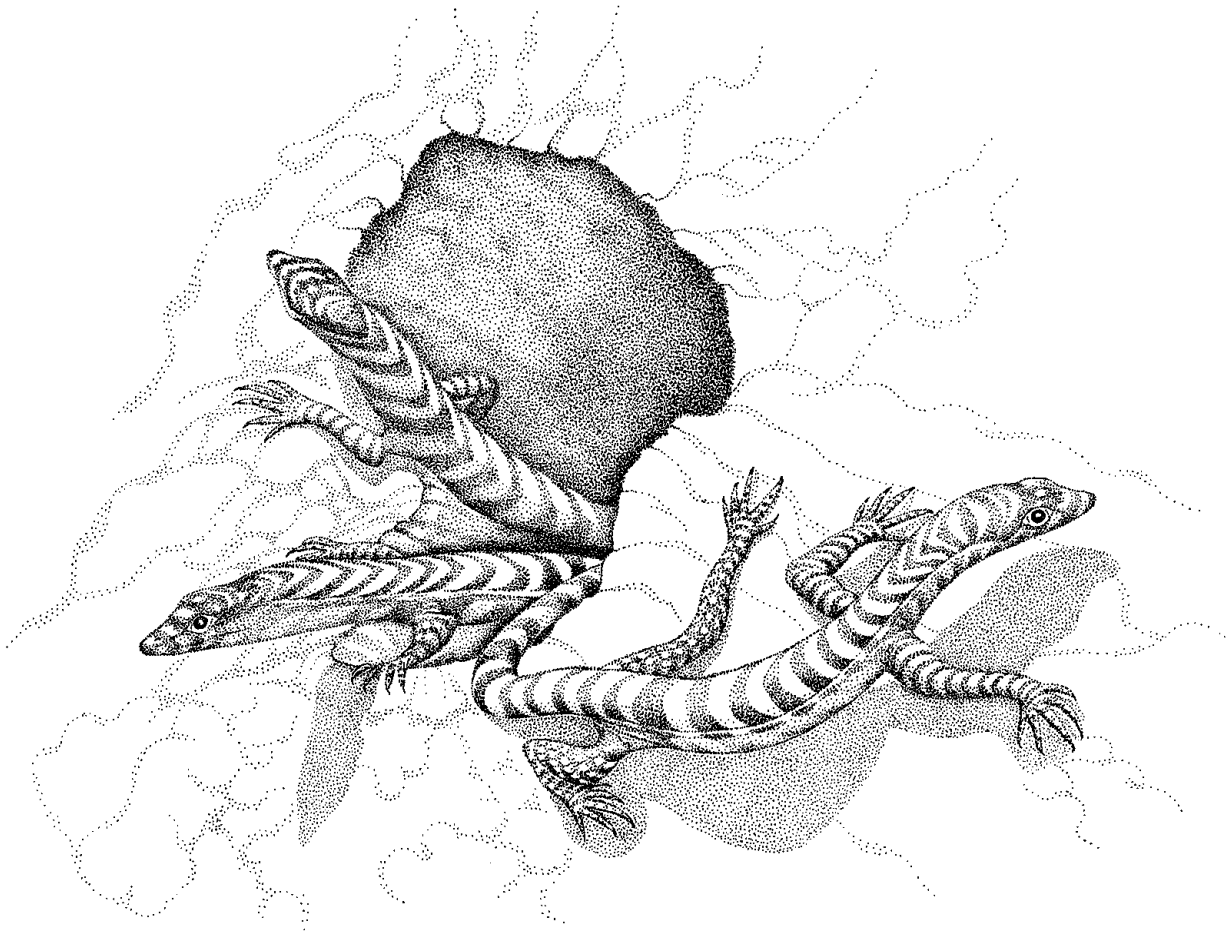

Figure 30.5 After incubation in the protection of a termite mound, newly hatched *Varanus varius* leave through a hole opened by one of the parents. (After BBC 1990)   [T. Wright]

Seasonal activity patterns of varanids vary greatly, as these lizards occur in a wide variety of climates and habitat types. Species in tropical regions (*V. komodoensis*, *V. olivaceus*, *V. giganteus*, *V. gouldii*, *V. panoptes* (Pl. 8.12)) are generally active throughout the year (Auffenberg 1981; 1988; Green *et al.* 1986; Shine 1986d). Some species from desert environments, such as *V. gouldii* and *V. griseus*, show seasonal inactivity during hot or cold periods (King 1980; Stanner & Mendelssohn 1987; Vernet *et al.* 1988b), whereas some of the smaller species, such as *V. eremius*, do not (Pianka 1986). Species in temperate regions of southern Australia are active year round, although activity is restricted in winter and they show different activity patterns during summer and winter (King 1980; Weavers 1983). Seasonal activity varies geographically in species which occupy several climatic regions, such as *V. gouldii* in tropical (Shine 1986d) or arid Australia (King 1980), and *V. niloticus* in South Africa (Cowles 1930) and Sudan (Cloudsley-Thompson 1966). *Varanus griseus* is active throughout the day in winter but shows a bimodal daily activity pattern in summer in Iraq (Corkill 1928); however it is inactive during the cold winters in north Africa (Vernet *et al.* 1988b), Israel (Stanner & Mendelssohn 1987) and Iran (Anderson 1963).

Table 30.2 Activity temperatures of 15 species of varanids. Single values of body temperature were taken by thermometer.

Species	Free-living (°C)	Captive (deg;C)	Total length (m)
Arboreal or terrestrial			
V. bengalensis	32–37	–	2.0
V. caudolineatus	37.8	–	0.25
V. eremius	37.5	35.9	0.45
V. exanthematicus	36.4	36.5	2.0
V. giganteus	36.1	–	2.4
V. gilleni	37.4	37.1	0.7
V. gouldii	37.0	35.3	1.0
V. griseus	38.5	36.4	1.3
V. komodoensis	36–40	36.3	2.8
V. rosenbergi	35.1	35.2	1.5
V. tristis	34.8	35.4	0.8
V. varius	34.7	33.5	2.0
Amphibious			
V. niloticus	32.7	34.8	2.0
V. mertensi	32.7	32.5	1.3
V. salvator	27–32	35.6	2.5

When active, all terrestrial varanids are able to maintain their body temperatures within two or three degrees of 36°C over a wide range of ambient temperatures (Table 30.2). They do not regulate their body temperatures as precisely as do some other reptiles. However, this allows them greater behavioural latitude during their periods of active foraging. Under extremely hot or cold conditions most species retreat to thermal shelters such as burrows and tree-holes. After several hours in thermal shelters the body temperatures of the lizards

approximate those of the shelter, and during winter those of *V. rosenbergi* or *V. varius* in southern Australia may fall below 10°C (King 1980; Weavers 1983). Amphibious species tend to exhibit lower active body temperatures than terrestrial species (Table 30.2), since they lose body heat quickly when foraging in water. Attempting to maintain body temperatures around 36°C would encroach on the time available to them for foraging.

Varanids can maintain temperature differences between the head and body by circulatory adjustments and evaporation from the buccal cavity/gular pouch (King 1977d; Weavers 1983). The brain temperature of *V. varius* can be as much as 6°C higher than the general body temperature before emergence in the morning and during the initial period of basking (Weavers 1983). However, once the animal becomes active, brain and body temperatures are similar (King 1977d; Weavers 1983).

If body temperatures exceed approximately 38°C, some varanids (*V. gouldii*, *V. griseus*, *V. komodoensis* and *V. rosenbergi*) hold their mouth open and start to flutter the gular pouch (King 1977d; King & Green 1993). This increases greatly the rate of evaporation from the buccal cavity (Green 1969) and maintains the temperature of the brain below that of the body (King 1977d). This behaviour is used to only a limited extent before the animal retreats to a thermal refuge such as a burrow or a shaded area.

The anterior nasal tubes of varanids have a large surface area (King 1977d). As inhaled air moves along the tubes it is warmed before reaching the lungs, and air being exhaled is cooled below deep body temperature. Water vapour is thus condensed onto the surface of the tubes, and water loss is also lessened.

Reflectivity of the skin is highly variable between species. Forms which inhabit areas of high insolation generally have a higher skin reflectivity, particularly in the near infra-red portion of the spectrum, than those from cooler or more vegetated areas (King 1977d; King & Green 1993).

Economic Significance

In Australia, all species of varanids are protected by state, federal and international legislation. Although they are hunted to some extent by Aboriginal people, it seems to pose no threat to their survival. There is no commercial harvesting of varanids in Australia.

Huge numbers of skins of several species (*V. salvator*, *V. bengalensis*, *V. indicus*, *V. flavescens*, *V. niloticus*, *V. exanthematicus*) have been exported from some countries in South-East Asia (425 000 to 1 300 000 per year) and Africa (275 000 to 800 000 per year) during the last decade, for use in the leathergoods industry (Luxmoore, Groombridge & Broad 1988). Little or nothing is known of the maximum sustainable levels of harvest for these species. The main exporters were Indonesia, Singapore, Sudan, Nigeria and Mali, and the main importing countries were Belgium, France, Italy, United States of America and Japan (Luxmoore *et al*. 1988). Although international legislation protects all varanid species, not all countries are signatories to the treaties and levels of legislative protection and enforcement are variable between countries in these regions (Luxmoore *et al*. 1988).

No data are available on threats to the survival of varanids through habitat alteration and industrial pollution in many third world countries.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Different karyotypic groups of the Varanidae occur in a broad array of habitats in South-East Asia, the Middle East, Africa and Australia (Fig. 30.6). They are found throughout the continent in Australia, except in Tasmania and parts of southern Victoria (Fig. 30.7). The Kimberley and Arnhem Land have the highest species densities (10 species each); both have extensive areas of sandstone plateau. Areas with the lowest species densities (two species; Fig. 30.7), are near the southern coast (Cogger & Heatwole 1981).

Affinities with other Groups

Varanids are anguimorph, platynotan lizards (Rieppel 1980b). The group Varanoidea, including Varanidae, Helodermatidae and Lanthanotidae was formed by McDowell & Bogert (1954) and it was regarded as a monophyletic assemblage within the Platynota by Rieppel (1980b). Each family contains only one extant genus (*Varanus*, *Heloderma* and *Lanthanotus*), and it appears that the lineages they represent are of considerable antiquity (Pregill, Gauthier & Greene 1986).

Affinities within the Taxon

Mertens (1942) was the first to attempt to classify the Varanidae. He based his work on the osteology and morphology of the group, and was hampered by restricted access to specimens. He did not attempt to construct a phylogeny for the Varanidae, and he named 10 subgenera, most of which are not supported by studies using more modern techniques.
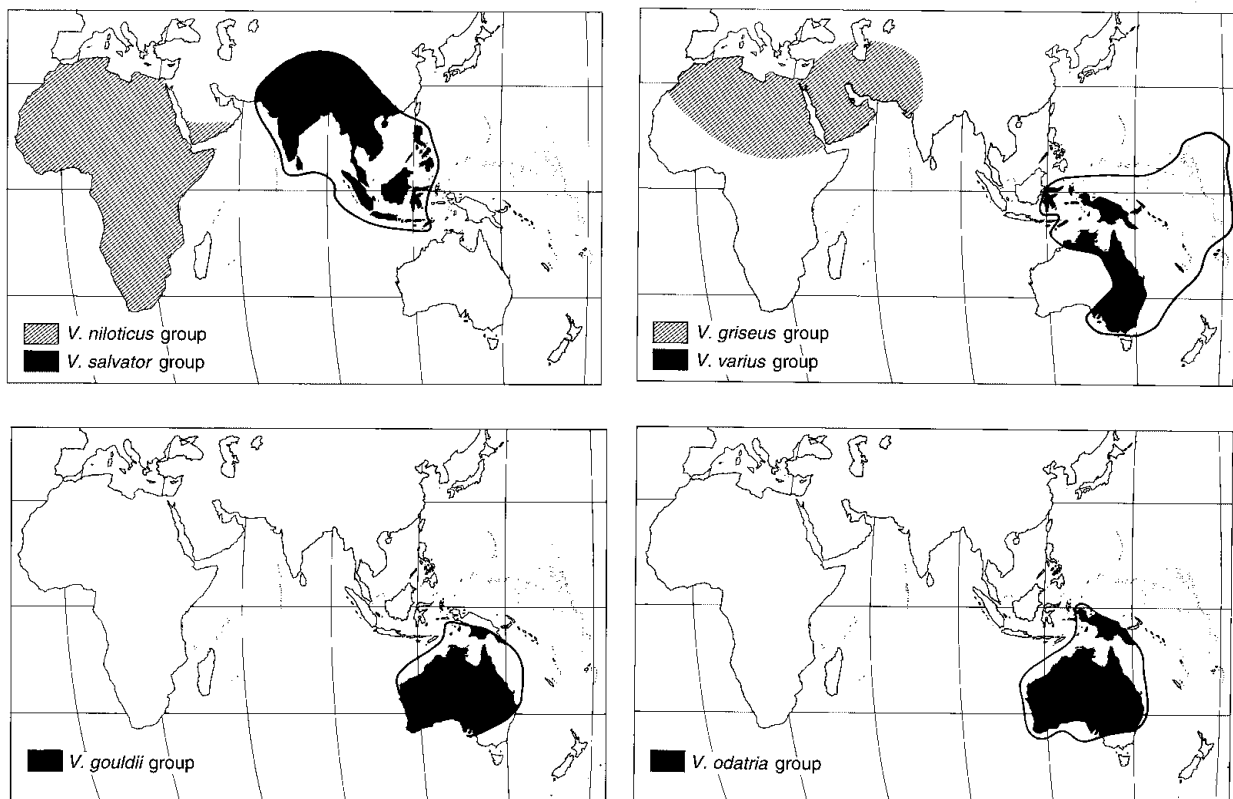

Figure 30.6 The world distribution of varanids. (After King & Green 1993)
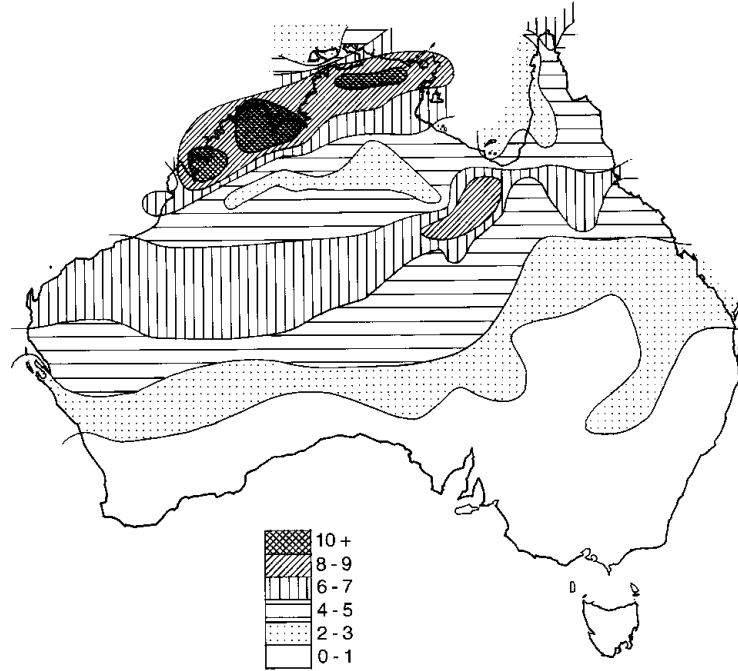
[W. Mumford]

Figure 30.7 The distribution and species density of varanids in Australia. (After Cogger & Heatwole 1984)   [W. Mumford]

A chromosomal analysis of 16 species in the family by King & King (1975) attempted to determine the most likely origin of the Varanidae and to construct a phylogeny for them. They recognised six karyotype groups (Fig. 30.8A) and suggested an Asian origin with two radiations into Australia and development of an endemic group there, and a westward radiation into the Middle East and North Africa, with a subsequent southern radiation into Africa. These and additional data have been reanalysed by King (1990) and the conclusions have been modified. The revised interpretation of these results agrees very closely (Fig. 30.8B) with the phylogeny proposed from a recent study (Fig. 26.8) based on microcomplement fixation (Baverstock, King, King, Birrell & Kreig in press).

Other phylogenies have been proposed recently, based on the results of studies on hemipenal morphology (Branch 1982; Böhme 1988) and lung morphology (Becker, Böhme & Perry 1989). Studies on hemipenes grouped most of the species in clusters similar to those of the chromosomal and immunological studies, whereas the lung morphology study grouped several species in assemblages not supported by other techniques. The phylogenies derived from the morphological studies of hemipenes and lungs do not agree closely with those based on chromosomal or immunological data (Fig. 30.8C, D; King 1990; King et al 1991; Baverstock *et al*. in press). The major differences between them relate to the position of the Asian species-cluster in relation to the African cluster and the two Australian clusters. Further studies using other techniques will be necessary to resolve these differences.

Fossil Record

The oldest fossil varanoids are in the extinct subfamily Saniwanae, from the upper Cretaceous of eastern Asia and North America (McDowell & Bogert 1954). Accurate conclusions on the history of the Varanidae cannot be drawn because of a lack of knowledge of Cretaceous fauna (Pregill *et al*. 1986). The subfamily Saniwanae is known from the Paleocene-Eocene of North America
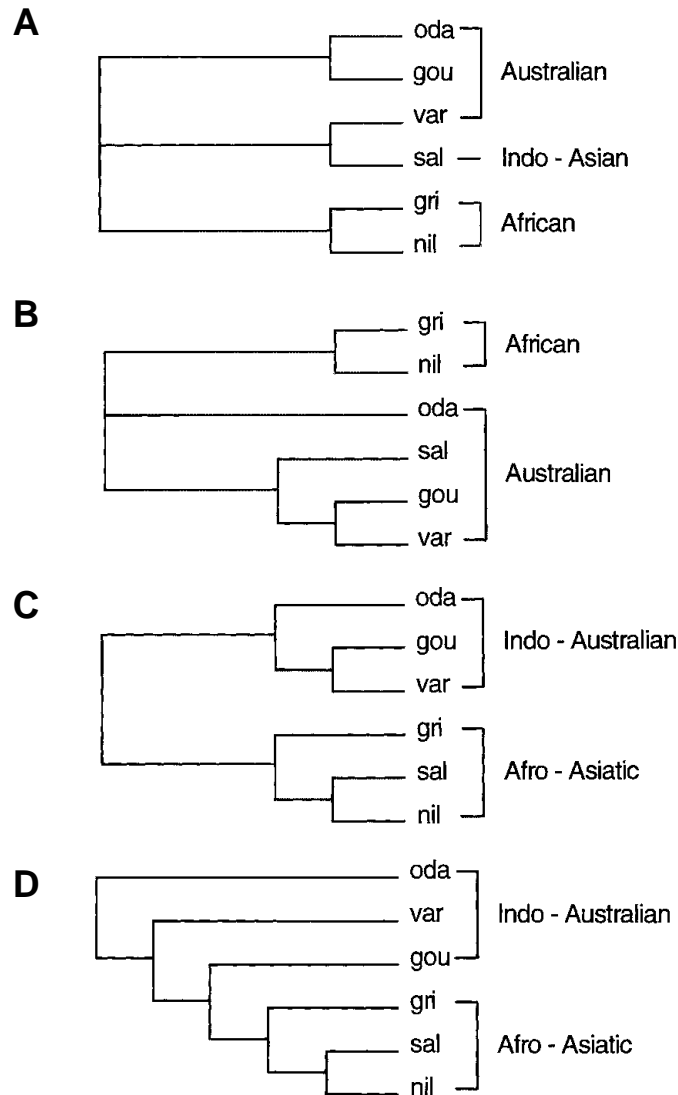
Figure 30.8 Comparison of phylogenies of the Varanidae. Based on **A**, chromosomal data; **B**, revised chromosomal and MC'F data; **C**, hemipenial morphology; **D**, lung morphology. **gou**, *gouldii* group; **gri**, *griseus* group; **nil**, *niloticus* group; **oda**, *Odatria* group; **sal**, *salvator* group; **var**, *varius* group. (A, after King & King 1975; B, after King 1990; C, after Böhme 1988), D, after Becker *et al.* 1989)   [D. Wahl]

and the Eocene of Europe (McDowell & Bogert 1954) and another varanoid family, the Necrosauridae, occurred in Europe from the Upper Paleocene to the Oligocene (Hoffstetter 1968). The earliest member of the Varanidae is *Telmatosaurus* from the Upper Cretaceous of Mongolia (Hoffstetter 1968). The oldest representative of the genus *Varanus*, subfamily Varaninae, is *V. hofmanni* from Miocene deposits in eastern Europe (Hoffstetter 1968). There is thus a large gap between members of the Saniwanae and the Varaninae in Europe. Hoffstetter (1968) proposed a possible origin of the Varanidae, suggesting that the genus *Varanus* differentiated from the Saniwanae in Asia and migrated from there into Europe, displacing the European descendants of the Saniwanae during the Miocene. The oldest varanid fossils in Australia (Estes 1984) and Africa (Estes 1983a) are also from the Miocene, suggesting a recent radiation (King & King 1975). Other varanid species, including the extinct giant *Megalania prisca* (estimated to have reached a total length of up 7 m and a mass of approximately 600 kg) and smaller *Varanus* species, occur in Australia in Pleistocene and Pliocene deposits in central Australia (Hecht 1975).