



FAUNA
of
AUSTRALIA



29. FAMILY AGAMIDAE

Geoffrey J. Witten



Pl. 5.1. *Tympanocryptis cephalus* (Agamidae): its cryptic colour matches its surroundings in a range of arid central and western Australian habitats.
[H. Cogger]



Pl. 5.2. *Lophognathus longirostris* lives in shrub and on the ground along streams in arid central and western Australia.
[J. Wombey]



Pl. 5.3. *Physignathus lesueurii* (Agamidae): an omnivorous, arboreal water dragon common along creeks and rivers of the east coast. [H. Cogger]



Pl. 5.4. *Ctenophorus pictus* (Agamidae): a swift inhabitant of sandy soils in drier parts of southern Australia. [H. Cogger]



Pl. 5.5. *Diporiphora* sp., a member of the most slender Australian agamid genus, from the Edward River, north Queensland.

[J. Wombey]



Pl. 5.6. *Moloch horridus* (Agamidae):: a distinctive, well-camouflaged, slow moving species; occurs in central and western Australian deserts, where it feeds on ants.

[H. Cogger]



Pl. 5.7. *Hypsilurus boydii* (Agamidae): a forest dragon with distinctive head ornamentation, endemic to the wet tropics, northern Queensland. [H. Cogger]



Pl. 5.8. *Pogona barbata* (Agamidae): a semi-arboreal species, showing its defensive display; commonly found in south-eastern and eastern Australia. [J. Wombey]



Pl. 5.9. *Chlamydosaurus kingii* (Agamidae): the frill-necked lizard, in upright defensive posture with raised frill and open mouth; occurs in dry forests in the north and north-east. [H. Cogger]

DEFINITION AND GENERAL DESCRIPTION

The family Agamidae is one of three families belonging to the infraorder Iguania. Known as dragons in Australia, agamids are small to moderate-sized lizards at maturity, and vary from a snout-vent length less than 50 mm to nearly one metre. Most Australian agamids are terrestrial, a few are arboreal or semi-arboreal and one species is riparian. Some species are swift, while others depend on cryptic colours and shape to avoid predation. Some 62 species are known, placed in 13 genera.

Frost & Etheridge 1989) suggested that the Agamidae cannot be diagnosed as a monophyletic group, although the group containing the agamids and the chameleons can be diagnosed. These authors proposed to include the Agamidae within the Chamaeleonidae. However, as discussed in Affinities with Other Groups, until further supporting evidence is forthcoming, the traditional classification will be used here.

Agamids have acrodont teeth and, like most other lizard families, anterior pleurodont teeth (Fig. 29.1B). Acrodont teeth are fused to the superior part of the mandible and maxilla, and are not replaced once they are formed. As the animal grows, further teeth are added to the tooth row posteriorly (Cooper, Poole & Lawson 1970). The Chamaeleonidae is the only other lizard group in which acrodont teeth are known; this family also lacks pleurodont teeth (Fig. 29.1C). Pleurodont teeth are adherent to the inner aspect of the tooth-bearing bones and are replaced continuously through life. In most agamids the anterior pleurodont teeth are caniniform. The scales are rough and irregularly shaped in many species. Enlarged head scales are absent. The tongue is broad and flat, and all species have movable eyelids.

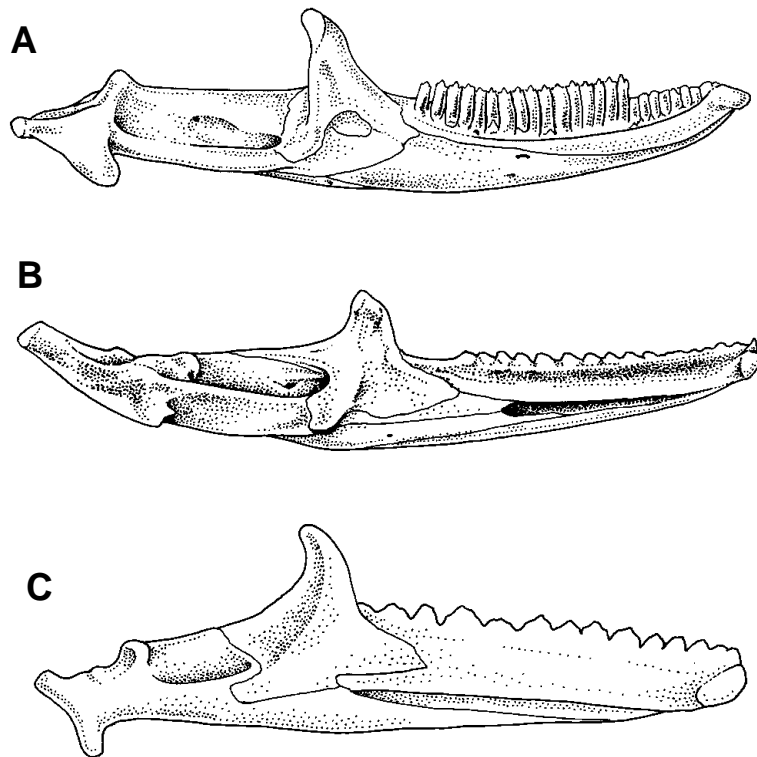


Figure 29.1 Mandible and teeth in the infraorder Iguania. **A**, the iguanid *Morunasaurus annularis*; **B**, the agamid *Pogona vitticeps*; **C**, the chamaeleonid *Brookesia stumpffi*. (After Estes 1983b) [R. Plant]

HISTORY OF DISCOVERY

The first dragon from Australia was described as *Lacerta muricata* by White in 1790. John Edward Gray named the three most distinctive Australian agamid genera: *Chlamydosaurus* (as *Clamydosaurus*), based on the frilled lizard, *C. kingii* in 1825 (Pl. 5.9); *Moloch*, based on the thorny devil, *Moloch horridus* in 1841 (Pl. 5.6); and finally in 1845, *Chelosania*, based on *C. brunnea*. By the time he wrote on the last of these, representatives of most Australian genera had been described.

Not long after Gray, Girard (1857) described *Oreodeira gracilipes*, based on a single female specimen supposedly collected in New South Wales by Charles Wilkes of the United States Exploring Expedition. The holotype was re-discovered by Moody (1988), and proved to be an *Agama* from Liberia in west Africa! The USNM received many specimens from west Africa during the 1840s as well as the results of the United States Exploring Expedition. Apparently the African *Agama* was tossed in with the Australian specimens, leading to Girard's later error (Moody 1988).

Boulenger (1885) consolidated much of the lizard taxonomy since Gray's (1845) catalogue, and rightly became the most authoritative worker of the day. Unfortunately, his coverage of the Australian agamids was not as complete as it should have been. Generic distinctions recognised by European taxonomists (for example, Fitzinger 1843) were ignored, and some of his own generic placements were puzzling.

Lophognathus was first described in 1842 by Gray for *L. gilberti*. Boulenger (1883) described a further species in the genus, *L. longirostris* (Pl. 5.2), but in his catalogue placed all *Lophognathus* species in the very dissimilar *Physignathus*. This error was corrected formally by Cogger & Lindner (1974).

Houston (1978) synonymised *Lophognathus* with *Amphibolurus*, and was supported in this by Storr (1982), though Storr attempted to resurrect the long forgotten name of *Gemmatophora* for the combined genus. Witten (1985b) reinstated *Lophognathus*, based on body proportions, but this has not been followed in the latest major work on Australian lizards (Greer 1989). In contrast, *Diporiphora*, which also closely resembles the type species of *Amphibolurus*, retained its generic status. Boulenger (1885) placed all other Australian agamids without spectacular or obvious modification into the genus *Amphibolurus*. This large conglomerate presented a large task for any reviewer, and it remained untouched for almost a century.

Glenn Storr of the Western Australian Museum contributed greatly to agamid taxonomy. Most of his work was at the species level, but he described *Caimanops* (Storr 1974) and began to correct the generic disarray left by Boulenger (Storr 1982). He described the genus *Pogona* for the bearded dragons and resurrected *Ctenophorus* Fitzinger, 1843.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Typical agamid scales have a ridge or keel along the exposed surface, leading to a short posterior spine. In the more primitive genera, the scales are tubercular or granular and do not overlap; also they are relatively small and uniform in size, creating a surface like sandpaper. Many species have scattered enlarged scales over the dorsum. Head scales usually lack spines and are relatively smooth. Ventral scales commonly overlap (imbricate). Keels of ventral scales are often less prominent and are absent in some species.

Dorsal scales are modified greatly in some genera. The scales of *Moloch horridus* (Pl. 5.6) have a central spine instead of a keel. The mid-dorsal scales in species of *Pogona* are thickened towards their posterior margin, and are much larger than other dorsal scales. These form a rasp-like raised area along the back. In species of *Amphibolurus* the dorsal scales imbricate widely and are heterogeneous. The surface of agamid scales has a honeycomb micro-ornamentation (Maclean 1980). Modified skin helps *Moloch horridus* to take up water from rain or condensation. Interscalar channels carry water to the corners of the mouth where it can be swallowed (Bentley & Blumer 1962; Gans 1985a). Other agamids appear to lack this ability (Gans 1985a).

Agamid skin is rather loose and may form permanent folds. Most Australian agamids have a well-defined transverse, gular fold. This fold usually continues laterally into a 'scapular' fold, which passes above the insertion of the forelimb, and in some species, continues along the lateral border of the body to above the hind limb. The gular fold is very narrow mid-ventrally in *Chelosania brunnea*. It is absent in some *Diporiphora*, though the scapular fold persists in some species without its ventral continuation. In *C. brunnea*, the skin behind the tympanum is covered by tubercular scales arranged in five or six postero-dorsal rows. Each row is separated from the next by a deep fissure. This mobile skin presumably allows the neck to be distended, but its functional significance is unknown.

Femoral glands open through pores on the ventral surface of the thigh. These pores have been used extensively in the taxonomy of agamids. They are present in most Australian agamids, but are absent in *C. brunnea*, *Hypsilurus* species and *Moloch horridus*. The position of each pore relative to scales has received some attention. Humphries (1972) noted that pores of some species open between scales, while others are within a single scale. However, many apparently interscalar pores are in fact contained within the posterior margin of a scale (Witten 1982a). When ventral scales have a keel, the opening of a posterior intrascalar pore is hidden on the posterior surface of the pore-bearing scale. If the ventral scales are smooth, the opening of the pore is clearly on the exposed surface of the scale. An ontogenetic shift may occur in this character. Hatchlings with ventral intrascalar pores may develop posterior intrascalar pores as the glands become active and the secretion hides the posterior part of the scale, or the enlarged pore may obliterate the scale entirely, giving the appearance of an interscalar pore (Fig. 29.2D).

Most Australian agamids have posterior intrascalar pores (Fig. 29.2C). This type of pore is apparently the primitive condition as it occurs in the three most primitive agamid genera, *Uromastyx*, *Leiolepis* and *Physignathus*.

Two types of intrascalar pore, apparently derived, occur in Australian agamids. In most members of the *Amphibolurus* group the pore occurs on the ventral surface of the keeled ventral scales, thus interrupting the keel, rather than lying posterior to it. However, many *Diporiphora* species have posterior intrascalar pores (Fig. 29.2A). Some individuals have both pore types.

Interscalar pores (Fig. 29.2B) are present universally in *Tympanocryptis* species, and occasionally in some species of *Ctenophorus* and *Pogona*, but otherwise are rare (Witten 1982a). The ventral scales of these species imbricate more than those of most agamids, such that a pore is hidden unless the associated gland has produced considerable secretion. Females often have less active glands, which has led several authors to report, in error, an absence of pores in female *Tympanocryptis* (for example, Storr 1964b).

The tympanic membrane is superficial and obvious in most Australian agamids. It is sunken in some *Pogona*, particularly in larger specimens. Juvenile species of *Hypsilurus* have a few scales on the posterior part of the tympanum, which do not persist in adults. The tympanum is covered with scales in two groups. The scale-covered tympanum of *Ctenophorus maculatus* is functional and appears

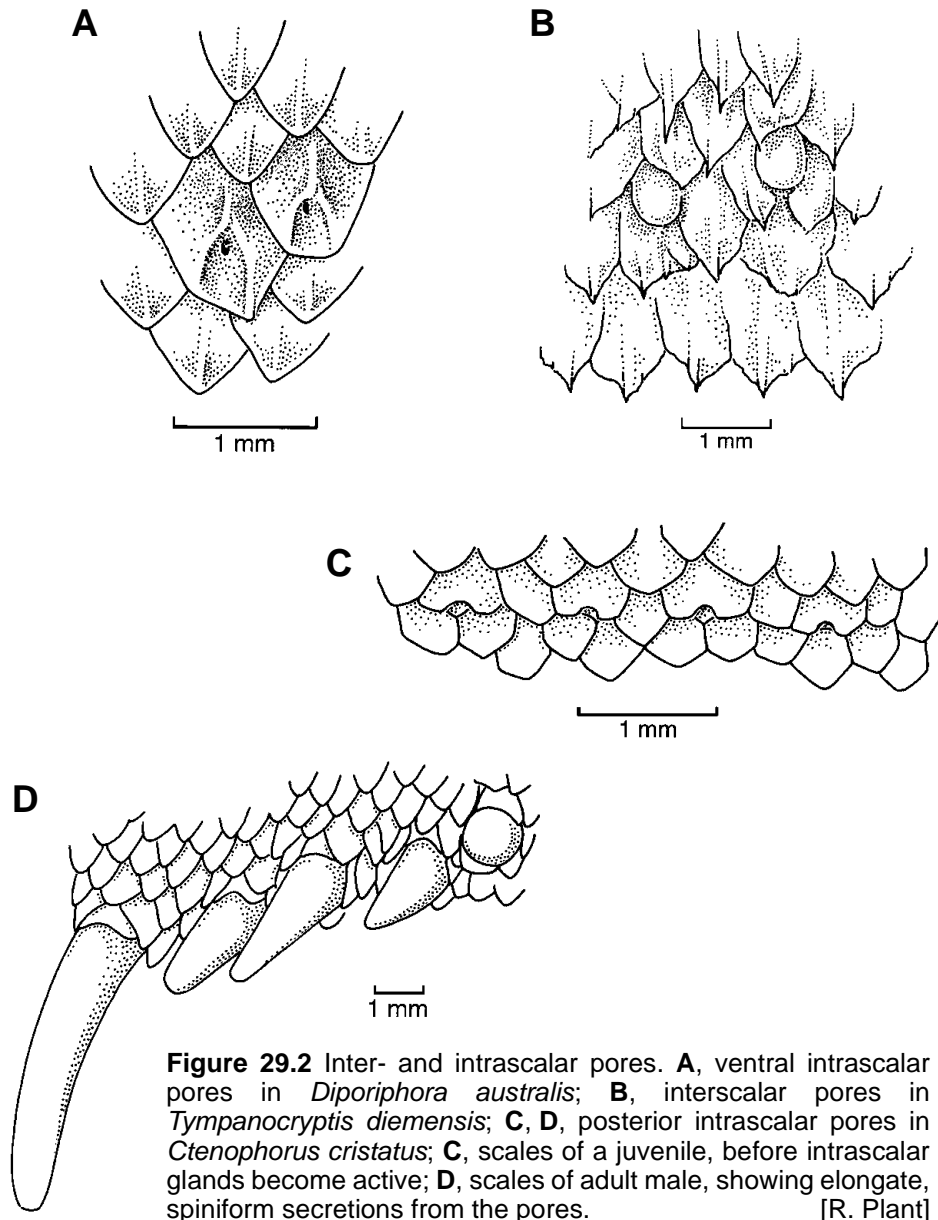


Figure 29.2 Inter- and intrascalar pores. **A**, ventral intrascalar pores in *Diporiphora australis*; **B**, interscalar pores in *Tympanocryptis diemensis*; **C**, **D**, posterior intrascalar pores in *Ctenophorus cristatus*; **C**, scales of a juvenile, before intrascalar glands become active; **D**, scales of adult male, showing elongate, spiniform secretions from the pores. [R. Plant]

on the side of the head as a depression. The succession of conditions within *Tympanocryptis* probably indicates the direction of evolutionary change (Witten 1982b). *Tympanocryptis diemensis* has a naked tympanum, *T. adelaidensis* normally has a naked tympanum, but occasional specimens have a few scales on the tympanum, and *T. parviceps* has a reduced tympanum which is completely covered by scales. The other species in the genus lack a tympanum.

Body Wall

The presence of a stiff outer coating on an animal creates the need for special sensory structures. The scales of agamids have epidermal sensory organs which resemble volcanic craters in shape. In *Pogona* species, these sensory organs occur on either side of the dorsal scales, just beneath the scale lip of the ventral scales, and are scattered over the larger head scales (Maclean 1980). The number on each head scale increases with age (pers. obs.). A dermal papilla, which extends into the base of these sensory organs, contains a nerve plexus with terminals in the cell layer immediately beneath the floor of the crater. The keratin is very thin in the floor of the crater, but the rim of the crater extends inwards to surround and support the dermal papilla (Maclean 1980).

Large melanophores are prominent in the dermis of agamids. These cells consist of a large central body, from which numerous processes radiate. Dark pigment within the central body of the cell disperses into the processes under the influence of melanophore stimulating hormone, and causes the skin to become darker. Melanophore stimulating hormone is apparently produced by the pituitary gland or hypophysis. Removal of the hypophysis causes the lizard to remain permanently pale (Rice & Bradshaw 1980). Darker skin allows a lizard to absorb heat more rapidly. Thus, the activity of melanophores in the skin is important in the control of heat uptake and therefore in thermoregulation in lizards (Rice & Bradshaw 1980). Males defending territories also change colour in a way that highlights different patterns. The melanophores in the white lip stripe of *Lophognathus* species contain a pigment which transmits red light and may give the distinctive white colour typical of the group (Witten 1982a).

Some agamids are able to raise skin folds along their dorsal midline. Such crests are obvious and apparently permanent structures in species of *Hypsilurus*, but are transitory in *Lophognathus* and *Ctenophorus*.

In all Australian genera, except *Moloch*, a sheet of connective tissue passes from the neural processes of the trunk vertebrae to the skin of the midline. Over the anterior part of the trunk, this fascia receives aponeuroses from muscles of the pectoral girdle and forms a thickening about halfway between the neural spines and the skin. This rhomboidal connective tissue block provides a thick sheath around vascular tissue in many species. The vascular tissue is mainly loose connective tissue with numerous veins and some arteries. The arteries are surrounded by thicker connective tissue (Fig. 29.3); the lumina of most of the veins in the non-erectile vascular tissue are flattened dorso-ventrally (Witten 1982a).

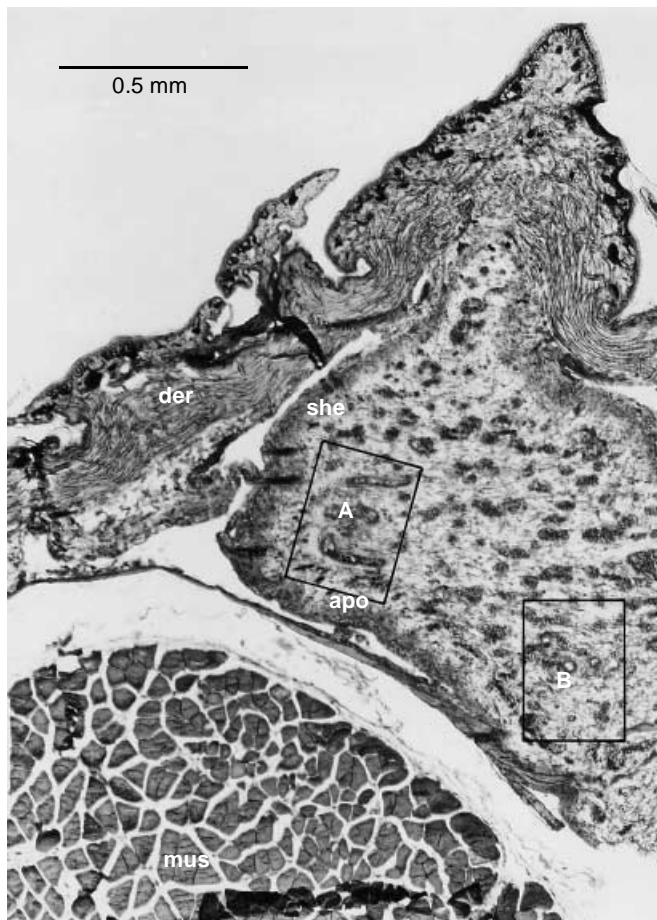


Figure 29.3 Transverse section of mid-dorsal region of *Amphibolurus muricatus*. Within the large erectile body note the flattened veins and the arterioles surrounded by denser connective tissue. Inset **A** outlines three flattened veins; inset **B** encloses two arteries; **apo**, aponeurosis of forelimb muscle; **der**, dermis; **mus**, muscle; **she**, dense connective tissue sheath. [Photo by B. Bowdern]

Vascular blocks are largest in males of *Lophognathus*, *Amphibolurus* and *Diporiphora*. They are either lacking or poorly developed in females of these genera. In *Ctenophorus* species the vascular block is relatively less dense, with fewer blood vessels (Witten 1982a). This variation may be related to differences in the way crests are erected in the two groups. In *Lophognathus* and its relatives, raising of the crest takes several minutes; it remains erect for long periods. In *Ctenophorus*, the crest is a much more transitory structure, and is raised and lowered during territorial displays (Pl. 5.4; Gibbons 1979).

The hyoid apparatus of the bearded dragon, *Pogona barbata*, is modified to support its 'beard' (Pl. 5.8). The second ceratobranchial, a posteriorly projecting, medial element has been lost, and the relatively broad body of the hyoid is placed anteriorly. The entoglossal process at the anterior point of the hyoid extends further forward through the tongue than in other lizards, and actually emerges from the tissue of the tongue to lie in a mucous membrane sheath on the floor of the mouth. The hyoid apparatus is suspended in a sling of muscles passing from the inner mandible to bones of the pectoral girdle, with an attachment to the elongate first ceratobranchial. In frill erection, the muscles anterior to the ceratobranchial contract and pull the whole hyoid apparatus forward (Fig. 29.4B, E). The entoglossal process quickly abuts the mandibular symphysis, preventing further forward movement of the body of the hyoid. With

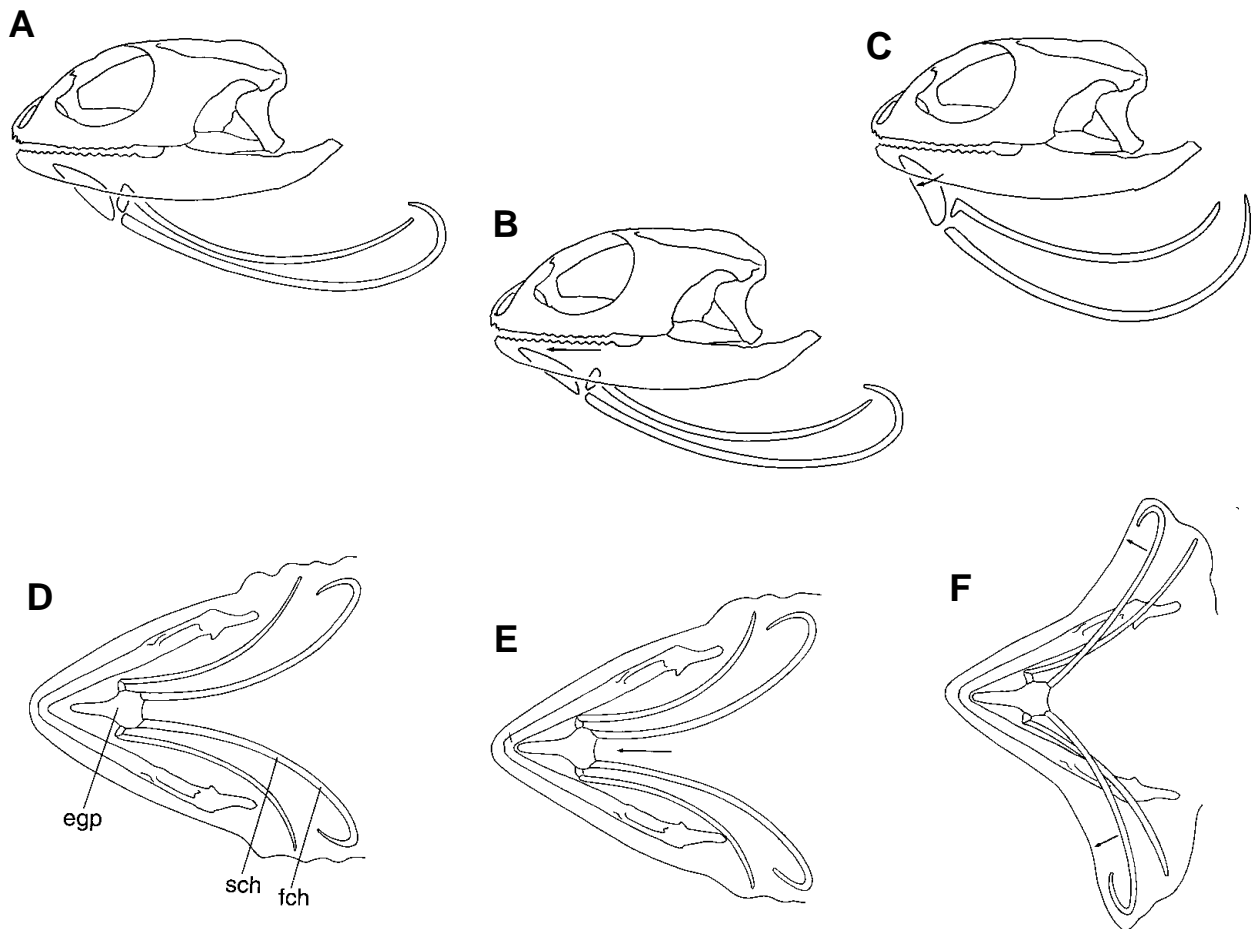


Figure 29.4 Erection mechanism of beard of *Pogona barbata*. **A–C**, in lateral view; **D–F**, in ventral view. **A, D**, beard in relaxed position; **B, E**, forward movement after initial contraction of anterior mandibular muscles, and contact of the entoglossal process with the mandibular symphysis; **C, F**, full contraction of mandibular muscles, outward and downward rotation of hyoid, resulting in full erection of beard. **egp**, entoglossal process; **fch**, first ceratohyal; **sch**, second ceratohyal. (After Throckmorton *et al.* 1985)

[R. Plant]

continued muscle activity the hyoid rotates ventrally, and the ceratobranchials swing laterally and ventrally to support the overlying skin as the beard (Fig. 29.4C, F). While all *Pogona* are known as bearded dragons, it seems the degree of specialisation in *P. barbata* has been a recent development, as most members of the genus retain the second ceratobranchials (Badham 1976). The entoglossal process also passes forward from the tissue of the tongue in the related *Amphibolurus muricatus*, but not in other lizards (Throckmorton, de Bavay, Chaffey, Merrotsy, Noske *et al.* 1985).

Camp (1923) distinguished three parts of the *m. rectus abdominis* muscle: *m. rectus abdominis pyramidalis*, *m. rectus abdominis medialis* and *m. rectus abdominis lateralis*. Camp reported the *m. rectus abdominis lateralis* in some primitive agamids, but Moody (1983) demonstrated that the observed muscle was a cutaneous slip of the pectoral muscle. Its nerve supply comes from the brachial plexus in a nerve also distributed to the pectoral muscle. Spinal segmental nerves supply the *m. rectus abdominis*. The *m. rectus abdominis medialis* has no attachment to the skin. It extends from the pubis to the xiphisternum (Moody 1983).

Physignathus is the only Australian genus having a cutaneous slip of the *m. pectoralis*. It is present also in *Uromastyx*, *Leiolepis* and in one of seven specimens of *Hydrosaurus* examined by Moody (1983). This cutaneous muscle is apparently a primitive feature which has been lost in other agamids. Though this muscle may have been present in the ancestor of all lizards, there is no evidence for its presence in either the chameleons or iguanids (Moody 1983), so it is probably best considered as peculiar to agamids.

SKELETAL SYSTEM

The agamid skeleton is very conservative. The skull is typical of primitive lizards and there is little variation between taxa. Differences in skull shape which might be used to infer relationships between genera are generally less than occur in the development of an individual.

Skull shape can vary ontogenetically as a result of the differential, or allometric, growth of some elements. The skull of most juvenile agamids is much shorter than that of the adult. The parietal bone contributes greatly to this elongation. In hatchling *Chlamydosaurus*, the parietal is roughly quadrangular. In adults, this bone bears large postero-lateral processes (Cogger 1961). Such allometric changes have made differences between species difficult to define.

Allometric changes are minimal in *Ctenophorus fordi*, a small species. This diminution of size reflects maturation at an earlier stage of development, a process referred to as neoteny, and adult *C. fordi* closely resemble juveniles of similar size from larger related species (Cogger 1961).

The lacrimal bone is one element of the skull which does vary between a number of Australian taxa. This element persists only in *Physignathus*, *Hypsilurus*, and *Chelosania*. Its loss in all other Australian genera coincides with the palatine extending further laterally in the floor of the orbit. In some specimens this lateral process intrudes into the lower margin of the orbit. The lacrimal of *Physignathus* and *Hypsilurus* (Fig. 29.5B, C) occupies the antero-inferior corner of the orbit, including the anterior part of the lower margin. In *Chelosania* the lacrimal is reduced to a small element in the anterior margin of the orbit (Cogger pers. comm.). *Moloch* lacks the supratemporal bone (Moody 1980).

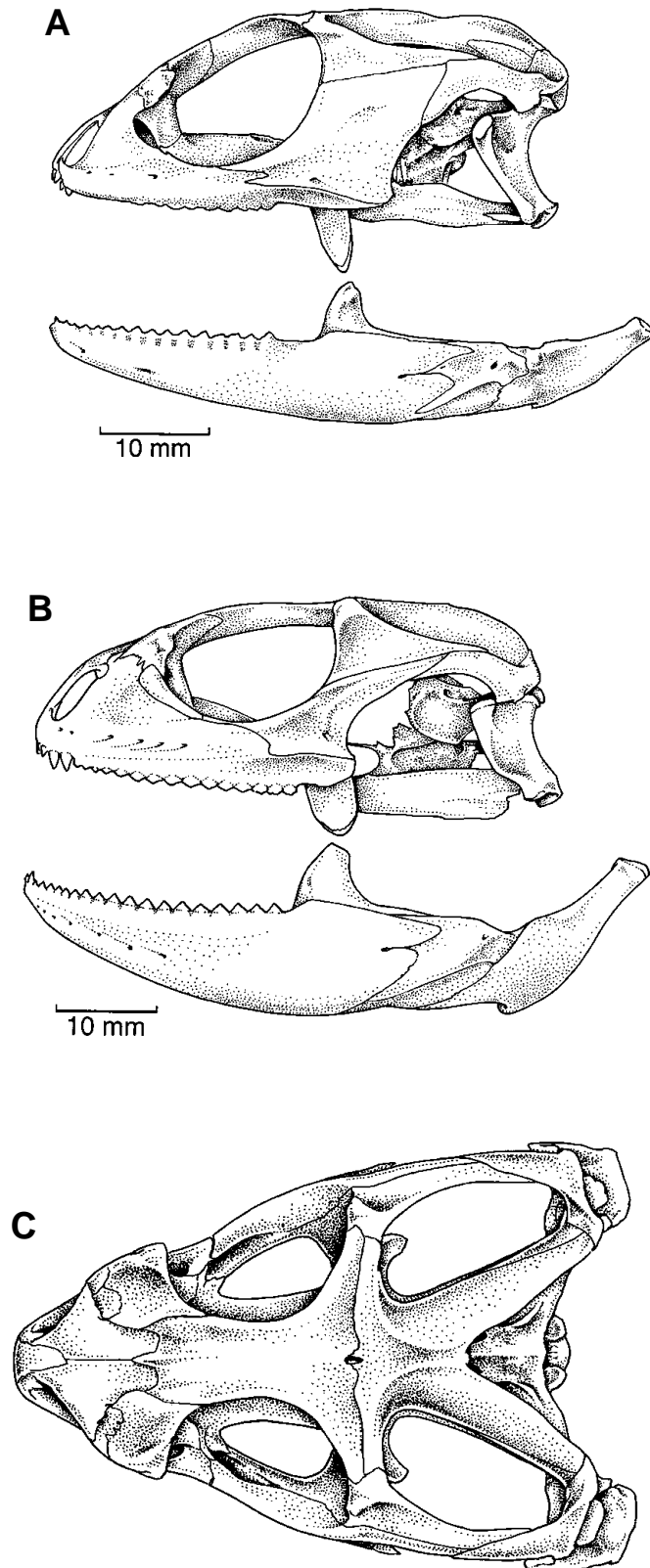


Figure 29.5 Skull of agamids. **A**, *Pogona barbata*, in lateral view, in which the lacrimal forms no part of the orbital margin; **B**, *Hypsilurus boydii* in lateral view, showing anterior pleurodont caniniform teeth and the large lacrimal in the lower anterior orbital margin; **C**, *Hypsilurus boydii*, in dorsal view.

[R. Plant]

The pleurodont teeth of Australian agamids are generally caniniform, and tend to be relatively larger in adults. They are particularly prominent in *Chlamydosaurus kingii*, but relative to size are most prominent in species of *Tympanocryptis*. They are generally not as well developed in the genus *Ctenophorus*.

The maxillary teeth of *Moloch horridus* project medially from the inner edge of the bone (Cogger 1961). The tricuspid mandibular teeth (Cogger 1961) have an elongate central cusp and two lateral ‘shoulders’. Each mandibular tooth slopes outwards, such that the central cusp fits between two maxillary teeth. This forms a shearing apparatus, which may be related to *Moloch*’s diet of hard-bodied ants. *Moloch horridus* has lost the anterior pleurodont teeth which, in other agamids, are presumably used in seizing prey; their loss in *M. horridus* may reflect the method of prey capture using only the tongue (Robinson 1976).

The number of presacral vertebrae is usually 22 or 23, except in *Pogona* species and *Chelosania brunnea* which have one more and *Moloch horridus* which has one less (Greer 1989). There is no adaptive alteration in the number of presacral vertebrae as is found in the skinks, for example. The number of postsacral vertebrae varies with the length of the tail, from 22 in *M. horridus* to 79 in *Lophognathus longirostris* (Greer 1989).

Most Australian agamids retain the ancestral phalangeal formula of 2.3.4.5.3/2.3.4.5.4. Each number represents the number of bones (phalanges) in each digit of the hand (manus) and foot (pes) respectively. The advanced *Tympanocryptis* species, which lack a functional tympanum, have lost one phalanx of the fifth toe (Cogger 1961; Mitchell 1965). A small percentage of *T. diemensis* have also lost this bone (7 of 94 digits; Kent 1987). Most *Ctenophorus clayi* have lost one phalanx of the same digit (Greer 1987b), to give a pes formula equal to that of the manus. Over most of its range, *Moloch horridus*, has a much reduced phalangeal formula of 2.2.3.3.2 for both manus and pes (Cogger 1961). However, the more primitive formula of 2.3.4.4.3 is found in a population from central Western Australia (Greer 1989). This loss of only three phalanges instead of the more widespread 11 is remarkable. It is not yet known whether the two populations are distinct species or whether there is a gradual change between populations with the different formulae (Greer 1989).

Locomotion

Most agamids move by quadrupedal walking or running, but some species typically adopt a bipedal gait at high speed. *Chlamydosaurus kingii* tucks its front legs against its chest in bipedal movement, with the great frill covering its chest (Fig. 29.6). *Moloch horridus* moves with a deliberate action, in which the body rocks back and forth as the animal makes slow forward progress.

Little work has been done on the relative speeds of locomotion in Australian lizards. The relative lengths of limbs varies widely among the Australian agamids, both interspecifically and during growth (Witten 1985b). Garland (1985) found that differences in sprint speed between individuals were not related to different limb proportions or sex in *Ctenophorus nuchalis*. The highest speed recorded was 13.5 km/h, achieved within 3 m of the start.

Feeding and Digestive System

Agamids are ‘sit-and-wait’, or ambush, predators. Some species will change position regularly, but they generally do not seek prey from within cover. When a prey item comes within range the lizard lunges forward and either grasps it with its jaws directly, or uses the tongue to pick up the prey.

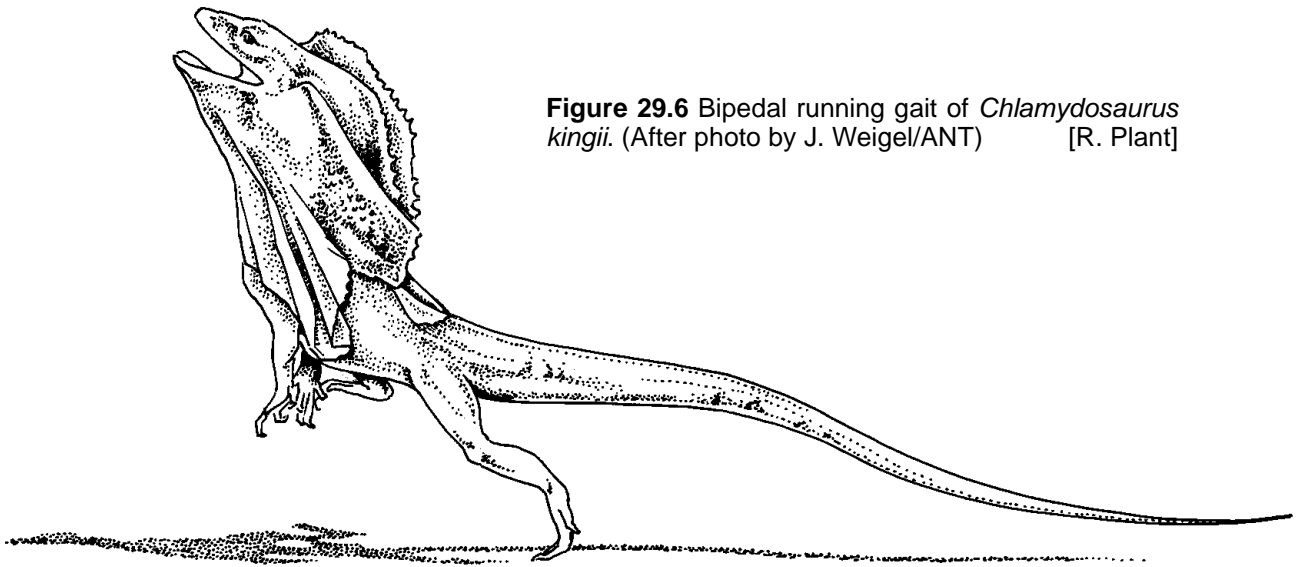


Figure 29.6 Bipedal running gait of *Chlamydosaurus kingii*. (After photo by J. Weigel/ANT) [R. Plant]

Dragons are probably opportunistic rather than selective feeders. They eat a large number of ants, especially in comparison with the members of other lizard families, but this probably reflects prey availability. Other lizards tend to avoid ants. Some of the larger species also eat plant material (Greer 1989).

Movements of the jaw and tongue ensure a secure hold on the prey and assist in moving it backward into the throat (see Chapter 24; Throckmorton & Clarke 1981). The alimentary tract has not been studied in any detail. The distinct stomach lies to the left of the midline. The pancreas lies to the left of the midline, as does the spleen. The pancreas extends from left to right across the peritoneum.

Circulatory System

The heart is typical of squamates, as described in Chapter 24 (see also Webb 1972). The heart itself is supplied by a single coronary artery and an apical artery (MacKinnon & Heatwole 1981). The coronary artery arises from the left systemic arch in *Pogona barbata* and *Amphibolurus muricatus*, but from the right systemic arch in *Physignathus lesueurii*. This difference in origin may be an adaptation to diving, as the right systemic arch normally receives more highly oxygenated blood. Agamids retain a gubernaculum cordis, a fibrous band joining the apex of the heart to the pericardium. An apical artery runs along this structure to reach the apex of the heart. The apical artery comes from the anterior epigastric artery, referred to inappropriately as the internal mammary by some authors (MacKinnon & Heatwole 1981).

Respiratory System

The lungs are two vascularised sacs occupying the thorax. The main area for respiratory exchange is arranged around the periphery of a large central cavity, and resembles a netting bag suspended within a balloon. Layers of tissue link the strands of netting to the outer wall of the lung, forming many parallel tubular cavities called faveoli (McGregor & Daniels 1990).

The relatively simple sac-like lungs of lizards are inflated by virtue of their attachment to the body wall of the thorax (McGregor pers. comm.). During inflation the faveoli are pulled open. The walls of the faveoli tend to collapse when the lungs are deflated, and are prevented from sticking to each other by large amounts of surfactant on the lung surface (McGregor & Daniels 1990).

Excretion

The kidney of reptiles produces urine which is not hyperosmotic. In agamids urine flows to the cloaca and then back into the colon. The wall of the colon extracts water and salts, thereby preventing excessive water loss. In *Ctenophorus ornatus* up to 98% of water may be reabsorbed before the urine is voided (Bradshaw 1975).

Sense Organs and Nervous System

Agamids rely heavily on sight for feeding and detection of predators. The retina of *Pogona* species has a well-defined central specialisation with some foveation (Rowe pers. comm.). This morphology is typical of an animal with acute vision. Whether it is typical of all agamids is not known. In the Asian genus *Calotes*, olfaction appears to play little, if any, role in prey detection (Cooper 1989). The same is probably true of Australian agamids, and indeed, possibly of the Iguania generally (Cooper 1989).

Endocrine and Exocrine Systems

Overall colour change has been demonstrated to be under the control of the hypophysis (pituitary gland). Removal of the hypophysis leads to a general paleness, presumably because of the absence of melanophore stimulating hormone (Rice & Bradshaw 1980). The mechanism of control of the second form of metachromatism in agamids, that of pattern changes, is unknown (Bradshaw & Main 1968).

The control of kidney function and the rate at which water is reabsorbed by the colon are influenced by hormones. The hypothalamus reacts to increased salt intake by reducing the rate at which urine is produced by the kidney. This is achieved by production of arginine vasotocin (AVT), which acts as an antidiuretic hormone (Bradshaw 1975). The control of colonic reabsorption is apparently influenced by adrenal corticosteroids in a way which is broadly parallel with the mechanism found in mammals. Bradshaw (1975) reported some dramatic differences between *Ctenophorus ornatus* and *C. nuchalis* in the levels of circulating corticosteroids. In *C. ornatus* the correlation between salt levels and corticosteroids was high when salt levels increased during dry weather. The same was not true of *C. nuchalis*, and adrenal failure was postulated as a causative factor in the high mortality rate of *C. nuchalis* (Bradshaw 1975).

The parietal organ has been implicated in the control of panting in *Amphibolurus muricatus* through its influence on the activity of the pineal gland (Firth & Heatwole 1976).

Most Australian agamids possess femoral glands. They are apparently a primitive feature of lizards, as they occur in a wide range of families, but their function is unclear. Cole (1966a) looked at the structure of femoral glands in iguanids, but was unable to demonstrate a clear function. He made the observation that they are more active in males, particularly in the breeding season, and on that basis suggested they might be used in territorial defence or marking. The same is true for Australian agamids, but the only evidence again is circumstantial. Cogger (1978) failed to find any volatile compound in the secretion which might have indicated a scent or pheromone function, and no

compounds were present in one sex but not the other. More recently Alberts (1991) noted intraspecific variation in two iguanid genera which may allow individual or sex recognition. She also found that the pores of males were active all season, but only unmated females had active pores.

The arrangement of femoral glands, as indicated by their external pores, is a useful taxonomic character. The primitive arrangement is that found in *Physignathus*. Femoral pores on the under side of the thigh extend medially into the preanal region in a continuous series (Fig. 29.7A). The widely separated left and right side pores (in the preanal region) is presumed to be the primitive condition because it is shared by *Leiolepis*, a primitive Asian agamid, as well as the more distantly related iguanid genera of the Americas (for example, *Sceloporus*; Cole 1983). A slightly different arrangement is found in most *Ctenophorus* (Fig. 29.7B–D), in which the preanal pores extend almost to the midline. A further minor modification is found in *C. isolepis* (Fig. 29.7D) and *C. scutulatus* where the medial end of the pore series arches strongly forward. The more primitive *Tympanocryptis* species, including *T. parviceps*, also have the primitive *Ctenophorus* arrangement. The more advanced *Tympanocryptis* have a reduced number of glands, with only two preanal and two femoral pores (Fig. 29.7E), or two preanal pores only.

Two other derived pore arrangements are present in Australian agamids. The fewer and more widely spaced pores of *Ctenophorus nuchalis* (Fig. 29.7G) form an arch, an arrangement shared by the genus *Pogona* (Witten 1982b). In the *Amphibolurus* group, there are separate preanal and femoral pore series. The more medial preanal pores are more posteriorly placed, usually on adjacent scales. The femoral series, where present, tends to be crowded onto the medial end of the thigh (Fig. 29.7H). The arrangement in *Chlamydosaurus* has similarities to both of these derived states. The preanal pores, although usually separate, are not always in the neat postero-medial series typical of *Lophognathus* (Fig. 29.7F).

Reproduction

There are two primary karyotypes in the Australian agamids. The large arid-adapted radiation has 12 metacentric macrochromosomes and 20 microchromosomes (King 1981; Witten 1983). *Physignathus* and *Hypsilurus* have 24 microchromosomes, but are otherwise similar to the arid-adapted species (Witten 1983). *Lophognathus gilberti* from northern New South Wales and from near Broome apparently have undergone fission of most of the macrochromosome complement (Witten 1983), resulting in a mixture of telocentric and metacentric macrochromosomes totalling 20. However, another population from the Gulf of Carpentaria retains the more common karyotype (King 1985).

All Australian agamids are oviparous. Clutch size is apparently related to body size, at least interspecifically (Fig. 25.6). The smaller species (for example, *Ctenophorus fordi*), lay as few as two eggs per clutch (Cogger 1978). The clutch may be as high as 35 in the larger *Pogona* (Fig. 29.8; Smith & Schwaner 1981). Most agamids lay between 4 and 10 eggs (Greer 1989).

Gonadal cycles of *Ctenophorus fordi* have been described in detail by Cogger (1978). Briefly, in males, spermatocytogenesis (proliferation of sperm-creating cells) begins in late autumn (May) and continues through winter into spring. By early September the testes are fully functional and continue to be so until early December. At this stage, testicular function may continue, or the testes diminish in size. In animals with regressing testes the inguinal fat bodies increase rapidly in size. Most males die in January; exceptions are those having regressed testes. Ovarian follicles begin to develop in September and ovulation occurs during October. Corpora lutea develop on the ovary at ovulation and remain until egg

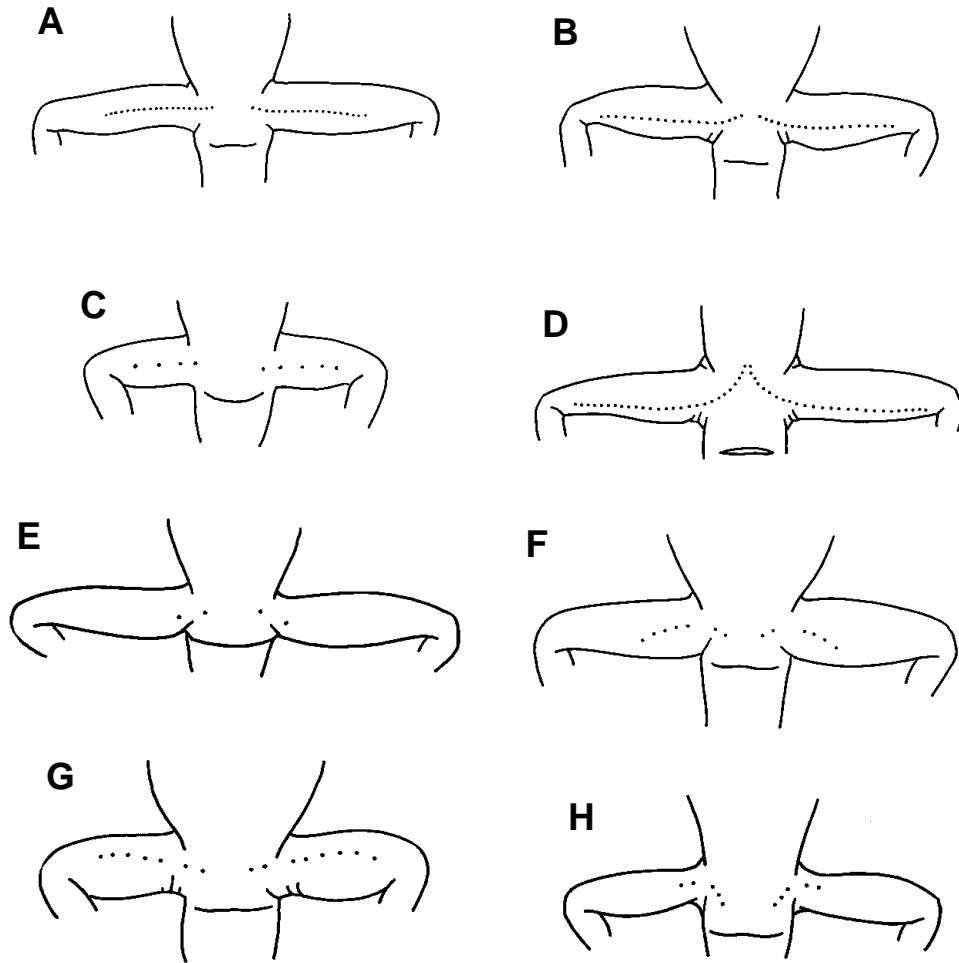


Figure 29.7 Femoral pore arrangements in agamids. **A**, *Physignathus lesueurii*; **B**, *Ctenophorus decresii*; **C**, *C. maculosus*; **D**, *C. isolepis*; **E**, *Tympanocryptis tetraporophora*; **F**, *Chlamydosaurus kingii*; **G**, *Ctenophorus nuchalis*; **H**, *Amphibolurus nobbi*. [R. Plant]

laying, which begins towards the end of October. Further follicular enlargement occurs commonly in females with oviducal eggs indicating that second clutches often occur. There is a minimum period of about six weeks between clutches, and a third clutch is theoretically possible. Females, like males, suffer high mortality at the end of December. Females still alive at the end of January also have enlarged inguinal fat bodies, and regressed ovaries. This general scheme fits well with the information available for other Australian agamids.

NATURAL HISTORY

Life History

Ctenophorus ornatus is associated with rock outcrops in Western Australia. Its life history has been well documented and, so far as is known, is typical of agamids.

Adult *C. ornatus* engage in mating behaviour in November. Each female lays two or three eggs during December. Some females may lay a second clutch as the first eggs hatch in January, so that hatchlings may continue to emerge until the end of March. Groups of juveniles are restricted to certain parts of the outcrop soon after their emergence. Apparently harassment by territorial males

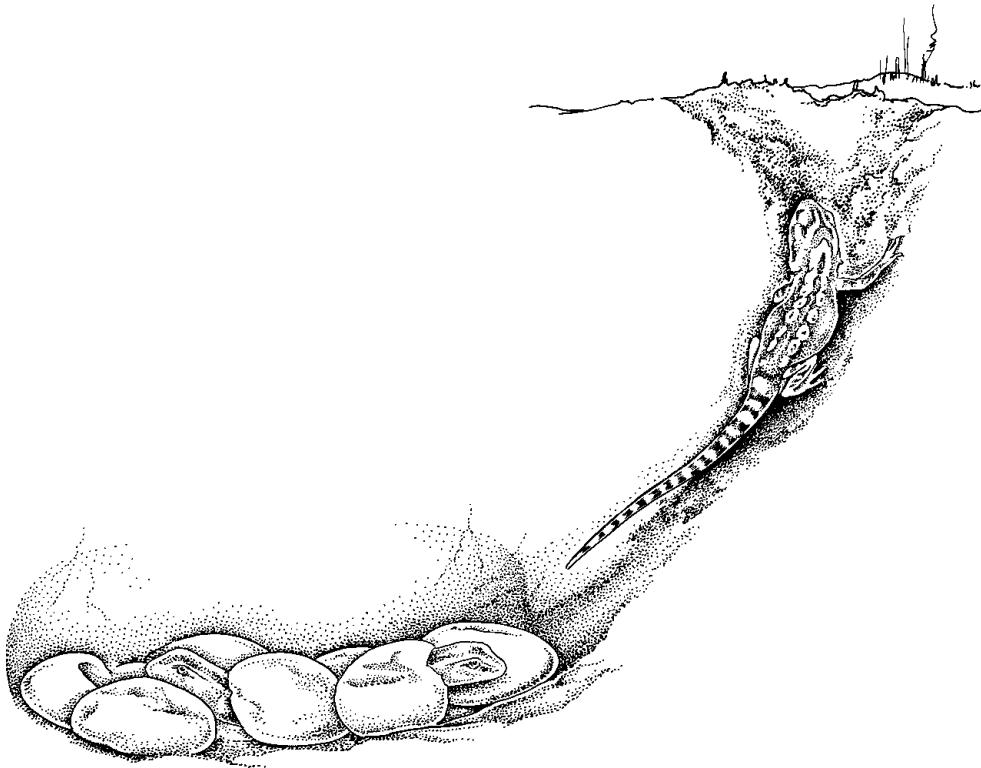


Figure 29.8 Young of *Pogona barbata* emerging from burrow. The young have to re-excavate the tunnel before they can emerge. (After photo by J. Weigel/ANT) [R. Plant]

is one factor that keeps the juveniles together. Harassment and the influx of adults from outlying areas drive most of the juveniles away from their hatching site to the marginal habitats from which the other adults have returned. Although *C. ornatus* is one of the larger species of *Ctenophorus*, some individuals achieve sexual maturity within their first year. Other individuals take two or three years to mature. Males become sexually mature at a snout-vent length (SVL) of 75 mm, and females at 69 mm (Bradshaw 1971).

Bradshaw (1971) classified individual *C. ornatus* as either fast or slow growers on the basis of the time it took them to reach sexual maturity. He found that slow growers were more resistant to drought, but more susceptible to severe winters. The resistance to drought is apparently due to a greater resistance to hypernatraemia (salt loading) in slow growing individuals. Hypernatraemia leads to increased urinary and evaporative heat loss which in turn causes loss of body weight (Baverstock 1975). Slow growers are susceptible to frost because they are forced to take refuge in less favourable retreats than larger animals (Baverstock 1978).

Many of the smaller *Ctenophorus* species are apparently 'annuals' (Storr 1965a, 1967a). There is variation in the timing and length of the breeding season, but it appears that for many populations very few if any adults survived to a second summer. It is possible for adults to be eliminated locally on an annual basis, with the species being represented only by eggs in the ground. Under conditions of low food availability, animals grow far more slowly and live much longer (Cogger 1974). The rapid growth typical of smaller species of *Ctenophorus* has also been recorded in one of the larger species, *C. nuchalis*. These relatively large animals reached sexual maturity in 9 or 10 months, and very few survive for a second summer (Bradshaw 1975).

Ecology

The smaller species of agamids are mainly insectivorous. This is probably more a result of insects being the most common prey available than any deliberate selection by the lizards. *Moloch horridus* eats small ants of the genus *Iridomyrmex* almost exclusively (Greer 1989). At least some of the larger species are omnivorous. *Pogona* species will eat dandelion flowers, and *Physignathus* are also omnivorous as adults (Greer 1989).

Only two Australian agamid genera inhabit forests. *Hypsilurus* is restricted to closed canopy forest, and *Physignathus* occurs along streams in a variety of vegetation communities. Most other species of agamids are found in arid parts of southern Australia. The few species found in the wetter parts of the continent are associated with heaths and open forests. Often these habitats are on poor soils where comparatively short periods without rain create effective desert conditions (Witten 1982b).

Amphibolurus nobbi nobbi in northern New South Wales is unusual in several aspects of its biology. Most individuals congregate in specific localities in autumn, where they hibernate. In spring males emerge first, as in *Ctenophorus maculosus* (Mitchell 1973). Females then emerge, mate and lay a clutch of eggs, after which all adults leave the breeding area. Hatchlings begin to emerge in January and disperse without pressure from larger individuals. Some females returning in autumn are gravid, and presumably lay an autumn clutch. Some hatchlings emerge in October, apparently from over-wintering eggs (Witten 1974).

Behaviour

Most agamids are territorial. Particularly in spring, males take up prominent positions from which they defend territories. The perching site varies between species and even within species. Species of *Lophognathus*, *Amphibolurus* and *Pogona* most commonly defend territories atop vegetation such as a shrub or small tree, or man-made perches such as fence posts and roadside dirt mounds. The more terrestrial species, such as small *Ctenophorus* and *Tympanocryptis*, tend to defend their territories from rocks or termite mounds. For example, on unsealed roads in central Queensland, a male *Tympanocryptis* may be seen every two or three metres sitting atop a dirt lump (pers. obs.).

The defence of territory is visually based in agamids. Use of colour and movement provide two very different methods of signalling to a rival.

Males in prominent positions are in full regalia. Male *Lophognathus gilberti*, for example, are commonly patterned in shades of grey but become black over most of their dorsal surface, with a brilliant contrast of white lips, and a light dorso-lateral stripe. Most males of the *Ctenophorus* group have permanent ventral patterns which are characteristic of the species. Some species become flushed with more spectacular colours. Male *Amphibolurus nobbi* are mainly grey with lemon dorso-lateral stripes and a red-tinted tail base for most of the year. In the breeding season the yellow and red colours become much more intense. The red-barred dragon *Ctenophorus vadrappa* (Pl. 5.4) takes its common name from a series of vertical red stripes on its lateral surface. This species combines brilliant colour with a complex display, which consists of three phases. The first involves orientation towards the intruder, so as to present a lateral view. The gular region is lowered, the trunk laterally compressed, and usually the front leg of either side is circumducted (rotated around in an overarm movement, but with the elbow bent). The second phase consists of a number of hind leg push-ups, during which the tail is coiled and the nuchal and vertebral crests raised. Coiling

of the tail may be associated with showing the red or orange ventral surface to the rival, as this colour intensifies during the display. The third phase consists of a head-bobbing sequence (Gibbons 1979).

Circumduction is part of the behavioural repertoire of many agamids. *Lophognathus gilberti* do it so regularly that people interpret the display as bidding farewell, an impression accentuated because circumduction often follows a short sprint. At least some species of *Diporiphora* include circumduction in displays. *Ctenophorus fordi* also circumducts, often after running, but in this species it is not obviously related to territorial or social behaviour (Cogger 1978). Circumduction in *Ctenophorus maculosus* was interpreted by Mitchell (1973) as a deterrent to males by unreceptive females.

Many lizards communicate by head-bobbing. This display is apparently useful in species recognition, as the speed and timing of the display is different for most species. Analysis of these displays has led to the definition of a 'display action pattern' which can be used to characterise a particular species (Carpenter 1967). Head-bobbing was elicited in *C. fordi* by the presence of other dragons but it did not respond to skinks in the same manner (Cogger 1978). Head-bobbing may be combined with front leg push-ups. Raising of the anterior part of the body displays the ventral surface of the lizard to a rival or prospective mate. The permanent ventral patterns of some species may be used in this way for species identification.

Copulation, where known, is relatively brief. The male grasps the female by the neck and one hemipenis is inserted for less than half a minute (12 to 23 seconds in *Ctenophorus fordi*; Cogger 1978; about 25 seconds in *C. maculosus*; Mitchell 1973). Copulation was not preceded by any display in *C. fordi* (Cogger 1978). In *C. maculosus* an approaching male 'undertakes a series of energetic head-bobs' (Mitchell 1973).

Ctenophorus fordi performs an extraordinary behavioural act after the main mating season (Cogger 1978). Between October and December, a female responds to the presence of a male by raising her hindquarters to present the cloacal region to the male. The male either ignores her or approaches and 'tastes' her hindquarters (Fig. 29.9), before both lizards move off. This

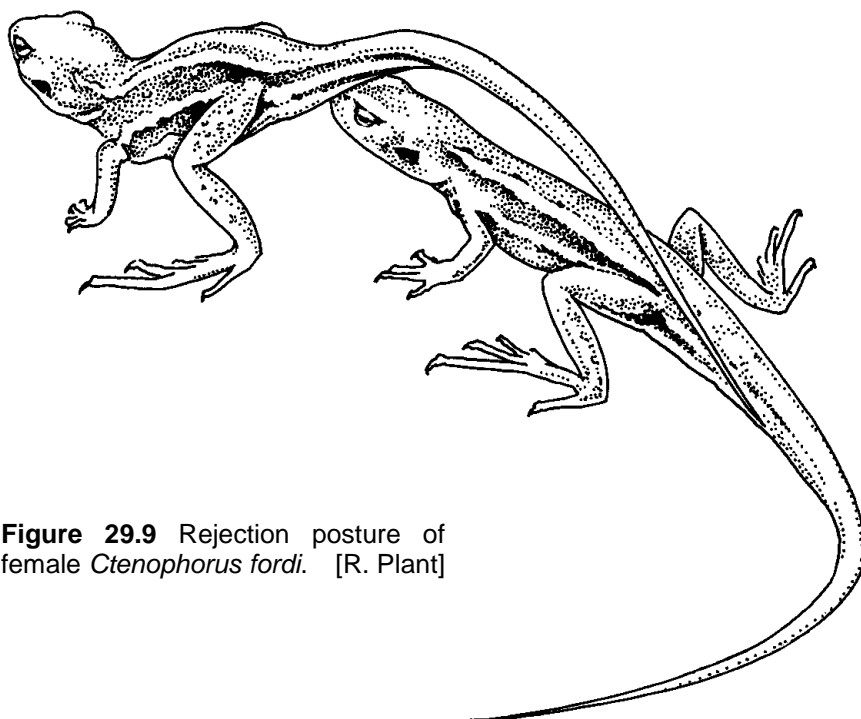


Figure 29.9 Rejection posture of female *Ctenophorus fordi*. [R. Plant]

behaviour is apparently not courtship, as mating has never been observed after this interaction. It could constitute a 'rejection posture', signalling to the male that she is not receptive (Cogger 1978). Another 'rejection posture' has been reported in *Ctenophorus maculosus*. In this species the female simply rolls onto her back (Mitchell 1973).

Two agamids apparently lack territorial behaviour—*Ctenophorus fordi* (Cogger 1978) and *Amphibolurus nobbi nobbi* (Witten 1974). Both are smaller than their nearest relatives, and their lack of territoriality may be a neotenic condition (Cogger 1978).

Agamids generally rely on crypsis to escape detection by predators (Pl. 5.1). Once detected, however, they may flee or display aggressively. *Pogona barbata*, for example, opens the mouth to expose its yellow lining and erects the gular region as a 'beard' (Pl. 5.8; Throckmorton, De Bavay, Chaffey, Merrotsky, Noske & Noske 1985). A similar display is given by *Pogona vitticeps* when under attack by a snake (Fig. 29.10).

Most lizards when active maintain a relatively constant temperature. Most Australian agamids are heliotherms, deriving their heat primarily from the sun. Given the opportunity, as in a laboratory thermal gradient, they will maintain a temperature within a narrow range, and the mean is referred to as the preferred temperature. That of Australian agamids falls in the range 35.5° to 38.2°C (Fig. 25.4), except for *Physignathus*, which is only 30.1°C (Heatwole & Taylor 1987). Preferred temperatures are often a useful indicator of phylogeny (Bogert 1949), so the result for *Physignathus* is remarkable. *Hypsilurus* species are also exceptional. Observations on *H. spinipes* in the field suggest that it makes little or no attempt to regulate its temperature, and field temperatures ranged between 15.5° and 25.1°C (Manning & Ehmann 1991).

In the field, conditions often will not allow regulation of body temperature at the preferred level, so it is more realistic to look at a temperature range over which the animals are normally active. This varies considerably between species, and even within species at different times. For example, Cogger (1974) found that even mild starvation caused *Ctenophorus fordi* to operate at lower activity temperatures.

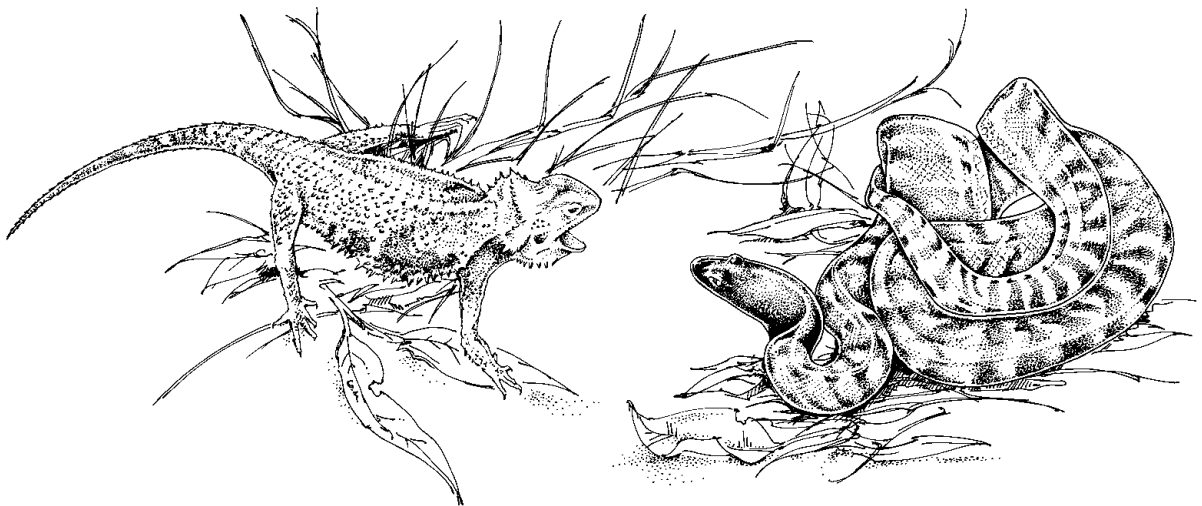


Figure 29.10 Threat display of *Pogona vitticeps*, in response to threatened attack by *Aspidites melanocephalus*. (After photo by D. Stammer) [R. Plant]

Different temperatures may also be acceptable under differing physiological conditions. Most preferred temperature determinations have been carried out using animals that have not fed recently. The preferred temperature is higher following feeding, and may be depressed for a variety of reasons apart from starvation (Witten & Heatwole 1978).

Daily activity patterns have been well documented for a number of arid-adapted Australian dragons (Bradshaw & Main 1968; *Ctenophorus nuchalis*, Heatwole 1970; *Ctenophorus fordi*, Cogger 1974; Fig. 24.15), and many features are common to the behaviour of these species. Before commencing normal activity, the lizards bask. During this phase the skin is darker, the body is dorso-ventrally flattened, and is oriented towards the sun thereby facilitating heat uptake. Once warm enough, the lizards begin normal activities, such as foraging or territorial defence. In deserts, temperatures in the middle of the day usually exceed those tolerated by lizards, and different behavioural patterns appear in response to rising temperatures. At first the lizards orient their bodies toward the sun thereby reducing heat uptake, and they seek shade intermittently. If temperatures continue to rise, shelter is sought, often in a burrow or vegetation. As temperatures begin to fall in the afternoon, activity is resumed. Lizards often press their bodies against a warm substrate as the sun recedes and prolong the period of elevated temperature.

One heat avoidance behaviour seen in desert species is 'stilting' (Bradshaw & Main 1968) in which the body is raised as high above the substrate as possible and is supported only on the front toes and the heels of the feet.

In the laboratory, lizards heated to above their preferred range will gape or pant. This behaviour has been observed in the field (Pl. 5.4), but is not common (Heatwole 1970). The level at which panting begins is raised in *Pogona* species by dehydration, but not in *Amphibolurus* (Parmenter & Heatwole 1975).

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Agamids occur in much of the Old World with major centres of diversity in Australia and Asia. Of 33 agamid genera listed by Wermuth (1967) many are endemic to India and Sri Lanka (nine) and the northern part of the Indo-Australian archipelago (five). Others are more widespread in Asia, with a few genera extending westwards into the Middle East. Though two genera extend into Africa (Wermuth 1967), no genus is endemic there.

The areas of highest agamid species diversity are in the southern part of the central Australian deserts and an area of the central coast of Western Australia (Witten 1982b). The wetter areas in the south-west of Western Australia and along the eastern coast have relatively few agamid species. This distributional pattern demonstrates the arid-adapted nature of most Australian agamid genera. A few species from arid genera have penetrated the wetter areas, but these are restricted to habitats with poor soils supporting heaths or open forests. Tasmania has only one agamid species, *Tympanocryptis diemensis*.

Physignathus lesueurii (Pl. 5.3) is riparian in habit, occurring near streams along the entire east coast. Another species occurs in South-East Asia. Presumably the ancestors of *Physignathus* have been displaced in the intervening islands by the related, but more derived, *Hydrosaurus*. *Hypsilurus* has at least two species in Australia, and a further 12 species in New Guinea (Moody 1980). The Australian species are restricted to forests of the east coast.

Affinities with other Groups

The Agamidae, Iguanidae and Chamaeleonidae form the infraorder Iguania (Camp, 1923). The Iguania is apparently the first 'branch' on the squamate evolutionary 'tree', with all other lizards placed in the Scleroglossa (Estes *et al.* 1988), and almost certainly contains the most primitive extant lizards (Camp 1923). It is clearly Gondwanan (Cracraft 1974), as it is not represented in Laurasian fossils until just before the Cainozoic. The iguanids arose in South America (Estes 1983b), although some species in Madagascar may represent a separate Gondwanan relict (Moody 1980). The Chamaeleonidae evolved in Africa and are still largely restricted to that continent and Madagascar. Only one species occurs on the Indian subcontinent (Welch, Cooke & Wright 1990), and another extends into southern Europe. Agamids are apparently the East Gondwanan representatives of the Iguania. This land mass split to form the modern Antarctica, Australia and the Indian subcontinent (Powell, Johnson & Veevers 1980). The latter two land masses still retain large endemic agamid radiations.

Evidence confirming this hypothesis comes from the fossil record of Europe and Asia. Agamids do not appear in this fossil record until the late Cretaceous or early Cainozoic (see below). Many other lizard fossils are present before this, and all are assignable to families belonging to more derived groups than agamids (Estes 1983b). Presumably agamids had been evolving elsewhere, and invaded Europe and Asia, as there are no obvious ancestors in earlier Laurasian fossils. They almost certainly were passengers on Greater India, a tectonic plate from part of Gondwana. Unfortunately the Gondwanan fossil record for the entire Mesozoic is poor, and the absence of lizard fossils for the period is not surprising.

The Chamaeleonidae are usually assumed to have been derived from the Agamidae (Camp 1923). This has been so widely accepted that Frost & Hillis (1990) used the Agamidae as an example of a paraphyletic group because the Agamidae continues to be recognised as a separate family while presumed descendants (chameleons) are recognised at the same taxonomic level. It is clear that the chameleons arose in Africa (Estes 1983b). The agamids now in Africa are recent immigrants (Moody 1980); there is no genus of agamid endemic to Africa. If the agamids gave rise to the chameleons then they probably did so from a Gondwanan source. Most modern families were in existence by the late Cretaceous (Estes 1983b). The agamids and chameleons belong to the most primitive subdivision of lizards (Iguania), and are assumed to have developed before more derived lizard families. Faunal exchange between Africa and Laurasian land masses would not have occurred early enough to allow the evolution of chameleons from Asian agamids.

A different opinion of agamid origins was recently published by Greer (1989). He suggested that agamids arose 'on the northern landmass and entered southern continents ... relatively late in their history'. He wrote this before Early Miocene *Physignathus* was described (Covacevich, Couper, Molnar, Witten & Young 1990), and would find the statement more difficult to justify now. Moody (1980) also favoured this origin for Australian agamids. He discarded a number of characters because they 'influenced the prediction of common ancestry of the highly derived Australian agamids (*Moloch* and *Chelosania*) and the terrestrial and saxicolous agamid radiation of Africa and Asia'. Moody thus disregarded data which did not fit the accepted Asian origin for agamids and retained data which did. Preliminary biochemical data indicates the Australian radiation is closer to the terrestrial agamids of Asia and Africa than to the arboreal South-East Asian agamids that Moody and Greer considered to be ancestral to the Australian agamids (Baverstock & Donnellan 1990). This is possibly the result of a faster rate of biochemical evolution in the Asian arboreal radiation (Joger

1991). However, chromosome morphology of Asian *Gonocephalus* (Ota, Matsui, Hikida & Mori 1992) indicates that these are unrelated to Australian lizards once placed in the same genus, and confirms the biochemical data.

The proposal to include the Agamidae within the Chamaeleonidae by Frost & Etheridge (1989) is rejected here for three reasons. First, the main feature linking the two groups is their dentition, with both families possessing acrodont teeth (Camp 1923). However, the nearest relative of the Squamata, the Sphenodontida represented by the tuatara *Sphenodon* of New Zealand (Gauthier, Estes & de Queiroz 1988), also possesses acrodont teeth (Robinson 1976) and therefore the character may prove to be ancestral and no more diagnostic of close relationship than any other feature shared by early lepidosaurs. There are fossil sphenodontids with dentition essentially identical to agamids, including the possession of anterior pleurodont teeth (Whiteside 1986). While *Sphenodon* has anterior successional teeth (Robinson 1976), these are no longer pleurodont 'except perhaps for the premaxillary teeth ... where the distinction of pleurodonty and acrodonty becomes somewhat blurred' (Rieppel 1992). It is probable that the first lizards had a similar dentition. This suggestion is not new. Cope (1900) considered acrodont dentition primitive (*vide* Camp 1923). The alternative, that agamids evolved a dentition identical to one already in existence, is much less plausible. If the ancestor of the Iguania had agamid-like dentition then the evolution of the three modern families is simplified. Agamids retained the ancestral condition (29.1B), chameleons lost the pleurodont teeth (29.1C), while the iguanids lost the acrodonts (Fig. 29.1A).

Other differences between the dentition of agamids and chameleons include: the lack of anterior pleurodont teeth in the chameleons (Fig. 29.1C) but presence in at least juveniles of all extant agamids; a gap between adjacent teeth and a smooth lingual tooth in chameleons surface, unlike the swollen inner surface of agamid teeth; and the teeth of chameleons firmly ankylosed to the outer margin of the tooth-bearing bone, not slightly on the inner surface (Moody & Rocek 1980).

Further, even if Agamidae and Chamaeleonidae are shown to be monophyletic, they differ in so many other features that their continued recognition as full families is easy to justify. Estes *et al* (1988) list 85 apomorphies for the Chamaeleonidae, yet only three features unique to the combined taxon 'Acrodonta'. Finally, taxonomists have a responsibility to maintain a stable nomenclature. Changes, particularly at higher levels should only be made with overwhelming evidence. Chamaeleonidae and Agamidae are long established and well-defined groups, and there is simply not enough evidence to overturn them. For the same reason the counter suggestion of Lazell (1992) to include the Agamidae within the Iguanidae is rejected.

Apart from dentition, several characters indicate a closer relationship between the agamids and chameleons than with the rest of the Iguania. One is the meeting of the maxillae between the premaxillae and vomers in the palate (Borsuk-Bialynicka & Moody 1984). Again, 'it is difficult to say if [it is] symplesiomorphic or homoplastic' (=separately derived) (Borsuk-Bialynicka & Moody 1984). This shared character does not appear to be plesiomorphic for lizards as the maxillae in sphenodontids are separated anteriorly by the premaxilla (Gauthier *et al.* 1988). In chameleons the premaxilla is reduced in size, and this reduction, rather than an expansion of the maxillae, may have resulted in the anterior meeting of the maxillae. The explanation for this reduction is logical. Chameleons have lost pleurodont teeth. Premaxillary teeth in both agamids and sphenodontids are pleurodont, and as the ancestors of modern chameleons reduced, then lost, their pleurodont teeth the premaxilla may have been reduced in the process.

The possession of reticular papillae on the tongue is another possible character linking agamids and chameleons (Schwenk 1988). This feature is shared with anoles, and its strength as a phylogenetic indicator is unknown. However, anoles have a similar microstructure of the scales and mechanoreceptors to chameleons (Peterson 1984; Ananjeva, Dilmuchamedov & Matveyeva 1991), but not to agamids or most other iguanids. The phylogeny of the anoles, then, is also uncertain. The honeycomb micro-ornamentation of agamid scales is shared with some iguanids, probably indicating common ancestry (Peterson 1984). Some evidence therefore indicates that agamids may be closer to some iguanids than to chameleons.

Affinities within the Agamidae

The most primitive agamids include *Physignathus* and the Asian genera *Leiolepis* and *Uromastyx* (Moody 1980). The latter two genera have been placed in a separate family, the Uromastycidae, by some (for example, Moody 1983), but more recently have been placed within the Agamidae as a subfamily (Borsuk-Bialynicka & Moody 1984). These genera, including *Physignathus*, have femoral glands in the primitive arrangement with pores opening on the posterior margin of a scale. They possess small tubercular scales which overlap little if at all, and tend to form transverse whorls around the tail. They have smooth labial scales. These genera also possess only lentiform epidermal sensors, a character shared with all Australian agamids, but not other agamids, which have scale sensors with 'hairs' (Ananjeva *et al.* 1991). Another character suggesting this group may form a phyletic group is the possession of a straight ventral suture between the maxilla and palatine bone, parallel to the tooth row; the same suture is angled sharply antero-medially in the main Asian agamid radiation (Moody 1980). If the subfamily Uromastycinae (or Leiolepidinae; Frost & Etheridge 1989) is recognised it should include the Australian agamids as well as *Uromastyx* and *Leiolepis*.

Australian agamids form two distinct groups: the mesic-adapted *Physignathus* and *Hypsilurus* in one, and the larger radiation of arid-adapted species including the large genus *Ctenophorus*. *Ctenophorus* is more derived than *Physignathus* only in the absence of a lacrimal bone. *Chelosania* is not clearly related to either group, but is discussed below with the mesic-adapted group.

Mesic-adapted agamids. *Physignathus* is the most primitive member of this group. With certainty only two other genera, *Hypsilurus* and *Hydrosaurus*, belong in the group. *Hypsilurus* is best represented in New Guinea; only two species occur in Australia. *Hydrosaurus* is restricted to Indonesia and the Philippines. The neural processes of the trunk vertebrae of all members are elongate, enlarge ontogenetically and are better developed in adult males than adult females.

Biochemical data indicate that *Hypsilurus* and *Physignathus* may be more distantly related to the arid-adapted radiation than is *Physignathus* (Baverstock & Donnellan 1990). This is not reflected in the morphology. Morphological features shared by *Physignathus* and *Hypsilurus* could have been present in the common ancestor of all Australian agamids and lost in the arid-adapted radiation. Alternatively, *Hypsilurus* could have undergone more rapid biochemical change since its divergence from *Physignathus*. More data are needed to decide which is more likely. However, *Physignathus* has changed little since the Miocene (Covacevich *et al.* 1990), so the biochemical data could be seen as uncovering old differences masked by morphological conservatism.

The riparian genus *Physignathus* has one Australian species and another in Asia. The lacrimal bone is retained and femoral glands are in the primitive arrangement. The dorso-lateral scales are small, tubercular, and tend to form transverse series, although their keels are aligned in postero-medial series. There

are scattered enlarged tubercles which also tend to align in transverse series. The trailing edges of toes have a series of flattened scales which may assist the animal when swimming. This feature is shared with *Hydrosaurus*, in which the scales have developed into a distinct 'web'.

For most of this century *Hypsilurus* was considered part of the Asian genus, *Gonocephalus*. Recent evidence suggests it may be more closely related to all other agamids than to the group containing *Gonocephalus* (Baverstock & Donnellan 1990; Ota *et al.* 1992). It was placed in *Gonocephalus* on the basis of characters developed as arboreal adaptations. The body is laterally compressed, and there are distinctive nuchal and gular skin folds used as visual signalling devices. Femoral glands have been lost, but the lacrimal bone is retained, as it has been in the Asian *Gonocephalus*. The enlarged neural spines of trunk and proximal caudal vertebrae support spectacular crests in some species. This feature is shared with *Physignathus* and *Hydrosaurus*, but not *Gonocephalus* (Moody 1980). The labial scales are smooth and dramatically enlarged in some species, including the Australian *Hypsilurus boydii* (Pl. 5.7), which also has other enlarged flattened scales on its cheeks.

Chelosania is a monotypic genus confined to northern and north-western Australia. The lacrimal bone is retained, but is smaller than in *Physignathus*. The genus lacks the enlarged neural spines of *Physignathus* and *Hypsilurus*, but the body is laterally compressed. There are five or six skin folds behind the tympanum, each with a row of tubercular scales. The primitive tubercular scales of the trunk are arranged in postero-lateral rows. Nuchal and vertebral scale ridges are present, but femoral glands are lacking. Though very distinctive, its relationships are unclear.

Arid-adapted agamids. These are characterised as a group by the loss of the lacrimal bone (Cogger 1961), and a karyotype with only 20 microchromosomes (Witten 1983). In the absence of a lacrimal, the palatine bone of some species has extended into the lower margin of the orbit where the lower posterior part of the lacrimal would be expected. In some *Pogona* and *Chlamydosaurus* skulls this lateral process of the palatine contributes very little to the orbital margin, if at all. In other genera it contributes an obvious elongate piece of bone. This has been well illustrated by Greer (1989, Fig. 9) for '*Amphibolurus*' *temporalis* though identified there as the lacrimal. If this is a separate bone, it is likely to have been formed from the palatine process, as *Lophognathus* is apparently highly derived among Australian agamids (see below). As well as the 20 microchromosomes, most members of the group have 12 macrochromosomes. Only some populations of *Lophognathus gilberti* have 20 macrochromosomes (Witten 1983).

Australian arid-adapted agamids form three groups: a large group containing *Ctenophorus* and a number of derived genera; the *Tympanocryptis* group; and the monotypic *Moloch*. The following discussion of phylogenetic relationships is based on a comparison of morphological characters. The group has not been subjected to a formal phylogenetic analysis.

Ctenophorus and derived genera: *Ctenophorus*, containing a number of species groups, includes the least derived species in the arid-adapted group. Perhaps the least specialised species group in *Ctenophorus* is formed by *C. cristatus* and the closely related *C. caudicinctus*. The two species are quite dissimilar in habit. *C. cristatus* is a widespread inhabitant of the mallee across the southern part of the continent. It depends on extreme speed to avoid predation. *Ctenophorus caudicinctus* is a rock-dweller of the northern half of the continent which, while also a rapid runner, retreats to rocky outcrops for shelter. Both species have relatively large, somewhat heterogeneous dorsal scalation, rather than the primitive tubercular form. There is a tendency towards interscalar pores in both species, and the relative proportions of limbs and tail in both are similar, despite

the disparate ecological niches occupied by the two species. Most individuals of both species retain the nuchal and vertebral scale ridges. However, the nuchal scale ridge of *C. cristatus* is both distinctive and unique among the terrestrial Australian agamids. A similar nuchal crest is found in some *Hypsilurus*. In juveniles of both genera a discontinuous nuchal scale row becomes contiguous in adults.

The rock-dwelling *C. decresii* and its relatives are depressed as an adaptation to living beneath rocks; two species are burrowers (*C. pictus* and *C. salinarum*). Most are very brightly coloured animals with pronounced sexual dichromatism. The species-group is probably relatively primitive within the genus. The vertebral scale series is retained in most species, at least in some individuals, and the scales are small and tubercular. The lower eyelid has a denticulate appearance.

Most of the running lizards of the *C. isolepis* group are associated with sandy deserts. The nuchal and vertebral scale ridges are retained and prominent in some species, but have been totally lost in some others. There is pronounced sexual dichromatism in most species, and most males have permanent black ventral markings.

The burrowing *C. reticulatus* group have stout limbs, a relatively deep head and body, and a denticulate fringe on the lower eyelid. Some members of the group have derived pore arrangements. *C. maculosus* has a reduced number of pores, which tend to be concentrated on the medial part of the thigh (Fig. 29.7G). *C. nuchalis* has another derived pore arrangement where the femoral pores arch forward on the thigh. *C. clayi* has a similar arrangement, but the number of pores is reduced. Permanent black markings of males are retained in most members of the group.

Cryptagama contains one small species originally described in the genus *Tympanocryptis* because of its similarity to *Tympanocryptis cephalus* (Pl. 5.1). These similarities are almost certainly independently derived in adapting to a ground-hugging cryptozoic habit. *Cryptagama* retains the primitive arrangement of femoral glands, although the number is reduced. The scales are much smaller in this species than in all other Australian agamids, with the possible exception of *C. clayi*. *Cryptagama* has clear affinities with *Ctenophorus* (Witten 1984).

Pogona shares a derived pore arrangement with *Ctenophorus nuchalis*, as well as the eyelid fringe, and is clearly related to the *C. reticulatus* species group (Witten 1982b). It includes five species referred to as bearded dragons. All species have an expanded gular pouch, and most have some indication of a series of spinose scales across the throat which forms a 'beard'. One or more rows of spinose scales occur along the side of the trunk. All species have strongly heterogeneous dorsal scalation which tends to break up the outline of the lizard and contribute to camouflage. The vertebral scale row has been lost.

Some specimens of *P. minor* from the west of the continent have a pore arrangement similar to that of *Amphibolurus*, with the more medial preanal pores more posteriorly placed, and an inguinal gap in the pore series. It seems probable that both *Chlamydosaurus* and the *Amphibolurus* group share an ancestor with *Pogona*.

Four genera form the *Amphibolurus* group: *Amphibolurus*, *Diporiphora*, *Caimanops* and *Lophognathus*. They are not strongly differentiated, and further study may lead to the species within these genera being included in *Amphibolurus*. The *Amphibolurus* group has lost the primitive gland arrangement; all members have the medial preanal glands more posteriorly placed, and the femoral glands, if present, form a separate series. The group also has ridged labials, presumably a derived feature. No member of the group has retained transverse whorls of scales on the tail. The phylogeny within the group is not clear. Presumably *Diporiphora*, the largest genus of the group, is the most

derived because most species have lost femoral pores and the midline scale ridge. *Lophognathus* is distinguished by a brilliant white lip stripe and is more arboreal than most other arid-adapted agamids. *Caimanops* lacks femoral pores, which leaves *Amphibolurus* as the least derived genus of the group.

Diporiphora superba (Pl. 5.5) deserves special comment as the single truly arboreal species of the arid-adapted radiation of Australian agamids. It is green in colour and is so slender it gives the impression of being badly emaciated. It also has an extraordinarily long tail, sometimes in excess of four times the snout-vent length. A species of *Diporiphora* is the most heat resistant Australian dragon recorded (Bradshaw & Main 1968).

The frilled lizard *Chlamydosaurus* has usually been placed within the *Amphibolurus* group (Cogger 1961; Witten 1982a, 1982b). The arrangement of preanal glands is similar, but the condition is not as regular as in the other genera of the group. Other characters shared with the *Amphibolurus* group such as a relatively long tail may represent adaptations to an arboreal habit. *Chlamydosaurus* and *Pogona* share a narrow premaxilla and an expanded gular pouch, features not present in *Amphibolurus*, and both have lost a vertebral scale ridge. It is likely that *Chlamydosaurus* and *Amphibolurus* both descended from a *Pogona*-like ancestor, but independently.

Tympanocryptis group: members of this group are all small cryptic terrestrial species, typified by the possession of interscalar pores and heterogeneous dorsal scales. Some members retain the primitive gland arrangement, but the scalation of all members is modified from the presumed primitive condition. All members possess ridged labials, which is probably another derived condition. Ridged labials occur in the *Amphibolurus* group, but no member of that group retains the primitive pore arrangement. The *Tympanocryptis* group is therefore not closely related to any other member of the arid-adapted group. However, the phylogeny within this group is clear. *Tympanocryptis adelaidensis* and *T. diemensis* are the most primitive members of the genus. Each has a tympanic membrane and has prominent spines on the base of the tail. The arrangement of preanal and femoral glands is also primitive. Both species often have a nuchal scale ridge. *Tympanocryptis parviceps* is intermediate between the *T. adelaidensis* species group and the *T. lineata* species group. This species retains the primitive arrangement of their preanal and femoral glands, but has lost a functional tympanum. One phalanx from the pes is variable in occurrence, being present in some individuals (Moody 1980), but lost in most (Greer 1987a). The advanced *Tympanocryptis* have lost a functional tympanum and one phalanx of the pes. The number of preanal and femoral glands is reduced to either two or four. Because of the interscalar emergence of these pores they are often not visible in small specimens or females, but reflection of the skin allows the glands to be seen clearly.

Moloch: the single species in this genus is the most dramatically modified Australian agamid (Pl. 5.6). It is extremely spiny, with even the ventral surface having some strongly spinose scales. There is a distinctive nuchal hump on the neck which may serve as a decoy to distract predators from the diminutive head. The digits are very short, the number of phalanges being reduced relative to other Australian agamids. All scales are tubercular, abutting adjacent scales without overlapping. Femoral glands are absent. The acrodont teeth are oblique and the pleurodont teeth have been lost. Despite the extreme morphological changes, biochemical data suggest *Moloch* is a relatively recent derivative from within the arid-adapted radiation (Baverstock & Donnellan 1990).

Fossil Record

The earliest agamid fossils are from the upper Cretaceous of Mongolia, and have been placed in the subfamily Priscagaminae (Borsuk-Bialynicka & Moody 1984). This group includes the genera (*Priscagama* and *Pleurodontagama*) and *Mimeosaurus crassus*. Originally *M. crassus* was referred to the Chamaeleonidae (Gilmore 1943). The Priscagaminae comes from a deposit containing many fossils originally referred to the Agamidae but later transferred to other families. Gilmore (1943) described *Macrocephalosaurus* and *Conicodontosaurus* as agamids. *Macrocephalosaurus* was later transferred to its own family, the Macrocephalosauridae (Sulimski 1975), and Moody (1980) considered that *Conicodontosaurus* belonged in the same family within the Scincomorpha. Sulimski (1972) described *Adamisaurus* in the Agamidae, but later (1978) transferred it to its own family. These fossils have a dentition which resembles the acrodont condition, but is, in fact, a pleurodont dentition modified so that the teeth are placed higher on the tooth-bearing bone (Sulimski, 1978). *Pleurodontagama* lacks the most diagnostic characteristic of agamids. The inclusion of the Priscagaminae in the Agamidae may prove correct, but should be carefully assessed in the light of its associated fauna.

When describing *Pleurodontagama*, Borsuk-Bialynicka & Moody (1984) suggested it may be one of the last agamids to retain an all pleurodont dentition. As modern agamids retain anterior pleurodont teeth it could equally be argued that *Pleurodontagama* has lost the ancestral mixed dentition. Carroll's (1988b) argument that streptostyly may have favoured pleurodont dentition in most lizards supports the latter idea.

The earliest undoubted fossil agamid, *Tinosaurus*, is common in Eocene deposits of both North America and Asia (Hecht 1959; Hoffstetter 1962). *Palaeochamaeleo* of the late Eocene of Europe is referable to the modern genus *Uromastyx* (Moody 1980; Estes 1983b). Agamids, some of them relatively modern, thus make a sudden appearance in the Eocene.

Until the last few years all agamid fossils reported from Australia were relatively recent, from the Pliocene or later (Molnar 1982a). Research on the extensive Riversleigh fauna has yielded several agamids from the Miocene including apparently modern *Physignathus* (Covacevich *et al.* 1990). Another genus from Riversleigh, *Sulcatidens*, is now extinct.

The Riversleigh fauna is mainly of Miocene age, with a few deposits extending back into the late Oligocene (Tyler, Hand & Ward 1990). Miocene *Physignathus* has so far only been identified from jaw bones, both upper and lower, which carry the distinctive acrodont teeth of agamids. *Sulcatidens* takes its name from its modified dentition. The four posterior teeth of the maxilla are notched anteriorly so that the tooth in front is partly enclosed. Such posterior teeth are almost square in shape, and distinct from the triangular shape of most other agamids. Apart from *Physignathus* and *Sulcatidens*, other agamid fragments have not been assigned to any genus (Covacevich *et al.* 1990). These fragments suggest quite an extensive agamid fauna present in the Miocene, and may well represent ancestors of the large modern arid-adapted radiation. The presence of Miocene *Physignathus* which are very similar to the modern form should not be surprising, since it is one of the world's most primitive lizards.

The existence of modern genera in the Australian Miocene and the European Eocene (*Uromastyx*: Moody 1980; Estes 1983b) highlights the extraordinary conservatism of agamids as a group. This is further emphasised by the fact that *Uromastyx*, which almost certainly evolved on the Indian tectonic plate, has its centre of greatest diversity in north-western India (Moody 1980).