



FAUNA
of
AUSTRALIA



27. FAMILY GEKKONIDAE

Max King & Paul Horner



Pl. 4.1. *Nephurus wheeleri* (Gekkonidae): in this genus, the tail ends in a rounded sensory knob; these geckos are found among shrub and in stone fields in the arid central west. [G. Shea]



Pl. 4.2. *Nactus eboracensis* (Gekkonidae): usually found under ground debris in forests and woodlands of Cape York. [H. Cogger]



Pl. 4.3. *Pseudothecadactylus lindneri* (Gekkonidae): inhabits sandstone caves or crevices in far north-western Australia. [J. Wombey]



Pl. 4.4. *Oedura castelnaui* (Gekkonidae): a gecko with a moderately depressed tail; lives arboreally under bark and debris, Cape York. [H. Cogger]



Pl. 4.5. *Diplodactylus ciliaris* (Gekkonidae): ranges from coastal forests of north-western Australia to the arid interior. [H. Cogger]



Pl. 4.6. *Gehyra pilbara* (Gekkonidae): hides during the day in the crevices and tunnels of termite mounds in north-western Australia. [J. Wombey]



Pl. 4.7. *Phyllurus cornutus* (Gekkonidae): has a strongly flattened leaf-like tail which assists to camouflage the lizard against an appropriate background. [H. Cogger]



Pl. 4.8. *Phyllurus cornutus* (Gekkonidae):: spines and other skin structures also assist in camouflage (see also Pl. 4.7); the species is found in wet forests from Cape York to the central east coast. [H. Cogger]

DEFINITION AND GENERAL DESCRIPTION

Most members of the family Gekkonidae are distinguished from other lizards by the presence of large eyes which have a fixed transparent spectacle, or brille, and a pupil which appears as a narrow vertical slit (Fig. 27.1). The body is covered by a loose-fitting velvety skin which has small, juxtaposed scales on the dorsal surface.

The Gekkonidae comprises some 800 species, and is one of the largest vertebrate groups. The family is distributed circumglobally and species occupy an extensive array of habitat types; the variety of form and degree of specialisation of its members reflect a diversity of niches. Two of the four subfamilies of the Gekkonidae, the Diplodactylinae and Gekkoninae, occur in Australia. The Eublepharinae and Sphaerodactylinae are not found in this region.

Geckos of the subfamily Diplodactylinae are distinguished from other gekkonids by derived characters—an 'O'-shaped muscle that closes the external auditory meatus, and a thickened mid-portion of the tectorial membrane of the ear (Kluge 1987). The Diplodactylinae is subdivided into two tribes, the Carphodactylini and Diplodactylini. Males of the former tribe are distinguished by the presence of a large patch of pre-anal pores, which are usually arranged in multiple rows. This character has been modified secondarily in two of the genera, *Nephrurus* and *Phyllurus*, according to Bauer (1990), who also noted that co-ossification of the dermis with the underlying bones of the skull occurred in the Carphodactylini, but not in the Diplodactylini. The short, wide nasal process of the premaxilla in the Carphodactylini is diagnostic, as are the presence of an inner ceratohyoid process and the absence of autotomy planes in some caudal vertebrae (Kluge 1987). The Diplodactylini generally possess paired terminal toe pads, except in *Diplodactylus damaeus* where these may have been lost secondarily.

Fourteen genera of Diplodactylinae are recognised. Those in the tribe Diplodactylini (*Diplodactylus*, *Strophurus*, *Rhynchoedura* and *Crenadactylus*), are found only in Australia. Five of the ten genera of Carphodactylini occur in Australia (*Carphodactylus*, *Rhacodactylus* (including *Pseudothecadactylus*), *Oedura*, *Phyllurus* and *Nephrurus*; Pl. 4.1, 4.3, 4.4, 4.5). *Naultinus*, *Hoplodactylus* and *Heteropholis* occur in New Zealand, and *Bavayia*, *Rhacodactylus* and *Eurydactylodes* occur in New Caledonia and the Loyalty Islands. This taxonomy emphasises the link between Australian and Pacific forms.

The subfamily Gekkoninae, which comprises 58 genera, is distinguished from other geckos by having a single centre of ossification in the ontogeny of the premaxilla. Two centres are present in the Eublepharinae and Diplodactylinae. Gekkonines have a pliable, calcium-shelled egg which hardens on exposure to air, unlike the parchment-shelled egg of diplodactylines, and the egg is more elliptical than those of other subfamilies. The endolymphatic system is expanded into a large sac on each side of the neck, in which calcium for egg shell formation is stored. Gekkonine autotomy planes occur along the length of the tail, whereas they are concentrated in the base of the tail in the Diplodactylinae (Greer 1989).

Only seven gekkonine genera are represented in Australia: *Gehyra*, *Heteronotia*, *Hemidactylus*, *Lepidodactylus*, *Cyrtodactylus*, *Nactus* and *Phyllodactylus* (Pl. 4.2, 4.6). Of these, certain species of *Lepidodactylus* and *Hemidactylus* appear to be recent introductions from Asia (Cogger 1992).

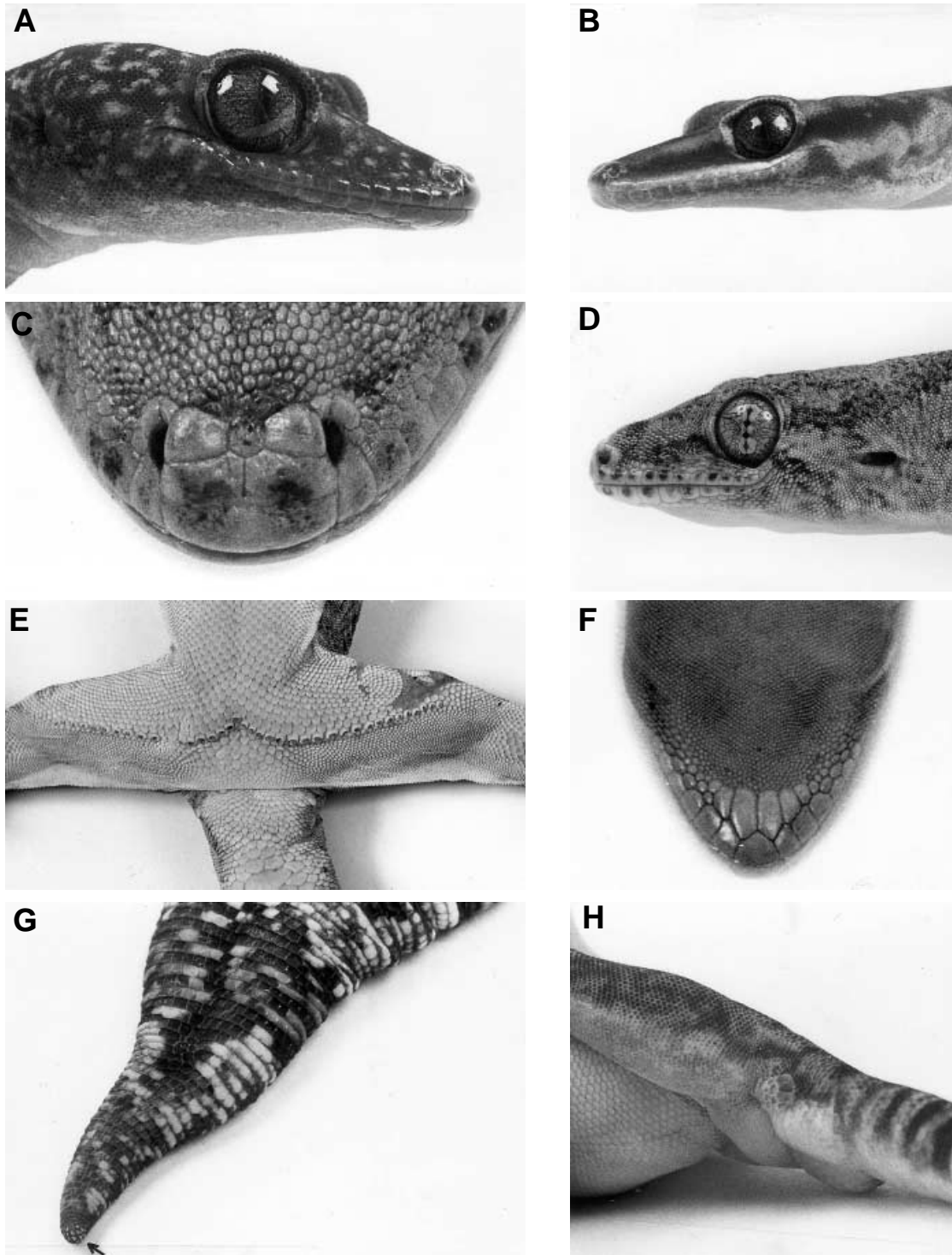


Figure 27.1 Selected morphological features of the Gekkonidae. **A**, head of *Oedura filicipoda* showing the large eye and shiny mouth scales; **B**, the depressed head, large elevated eyes and long snout of *Oedura gracilis*; **C**, scalation around nasal apertures and snout of *Gehyra membranacruralis*; **D**, lateral view of the robust head of *Gehyra membranacruralis*, showing the position of the ear aperture, and pupil shape; **E**, ventral view of the hind limbs of *Gehyra membranacruralis*, showing the distinct row of femoral pores and the skin folds on the back legs; **F**, glossy chin shields of *Gehyra australis*, in ventral view; **G**, spinose scales on the tip of the tail of *Oedura filicipoda* which permit the tail to operate as a 'fifth limb'; **H**, postero-lateral view of a male *Oedura gracilis* showing the enlarged hemipenial sacs and post-anal tubercles. [Photos by M. King & P. Horner]

HISTORY OF DISCOVERY

The history of discovery of the Australian Gekkonidae can be divided broadly into five areas of exploration, systematic research, or technical application: the voyages of discovery and the analysis of specimens from Australia in British, French and other European museums, from 1790 to 1850; the expeditions to the interior between 1850 and 1920; modern systematics and museum exploration, from 1920 onwards; and the use of genetic and morphological analysis after 1970.

Intensive biological collecting accompanied the early British settlements at Sydney Cove in New South Wales (1788), and the subsequent isolated outposts of Fort Dundas on Melville Island (1824), at Raffles Bay (1827) and at Port Essington (1838) on Cobourg Peninsula in the Northern Territory. Most of this material was sent to Britain for analysis. The French government despatched the corvettes *Le Géographe*, *Le Naturaliste* and the goulette *Le Casuarina*, from which extensive collections were made in Western Australia between 1800 and 1804 and to a lesser extent along the eastern Australian coastline. Surprisingly, very few gekkonid species were described during this initial period, although *Phyllurus platurus* (White 1790) provided an interesting exception.

This burst of biological collecting provided the source material for the second period of activity which centred on the British Museum of Natural History in London and the Muséum National d'Histoire Naturelle in Paris. Eight of the major gekkonid genera were defined by J.E. Gray in London between 1825 and 1845 (*Hemidactylus*, *Cyrtodactylus*, *Phyllodactylus*, *Diplodactylus*, *Gehyra*, *Oedura*, *Crenadactylus* and *Heteronota*). Gray also described a suite of species, some of which have survived the rigours of synonymy (Cogger, Cameron & Cogger 1983a). In Paris, A.M.C. Duméril and G. Bibron described a series of species, many of which were collected at Shark Bay in Western Australia by French voyagers.

Expeditions throughout the interior and to the more remote areas of Australia in the mid to late 19th and early 20th century made significant collections of herpetological material. They included the *Chevert* expedition in 1877, the Horn Expedition to central Australia of 1896, the Elder exploring expedition in 1893 and Dr E. Mjöberg's Swedish Scientific expedition of 1910 to 1913. British maritime expeditions continued to be of significance, for example, those of HMS *Flying Fish* at Christmas Island, and of HMS *Erebus* and *Terror*. All added to the great number of specimens in British, European and more recently the Australian museums.

The British Museum continued to contribute to gekkonid systematics, and G.A. Boulenger and A. Günther described 13 Australian species between them from 1867 to 1897. A number of European taxonomists (Peters, Steindachner, Weigmann, Girard, Werner, Thominot, Lönnberg and Anderson) also contributed to the Australian faunal list before 1914. In the same period, an increasing number of Australian herpetologists, centred in each of the Australian state museums, were active in describing the Australian gekkonid fauna. They included C. de Vis (Queensland Museum), D. Fry (Western Australian Museum), A.H.S. Lucas and C. Frost (Museum of Victoria), J.D. Ogilby (Australian Museum) and E.C. Stirling and A. Zeitz (South Australian Museum).

From the 1960s, Australian systematists, largely museum-based, and international scientists interested in particular Australian gekkonid groups, made significant advances in describing this fauna. By far the greatest contribution was made by G. Storr of the Western Australian Museum who described 16 gecko species between 1963 and 1989. While working in Australia in 1962 and 1963, A.G. Kluge made a significant contribution to the higher taxonomy of the

Diplodactylinae, and also described and reinstated a number of species. More recently, museum and university-based taxonomists have described some 17 species from remote regions in the north and interior of Australia.

In the 1970s population cytogenetics was introduced as a tool for analysing those species that are morphologically variable and taxonomically uncertain, and generally have very broad geographic distributions. Following chromosomal analysis of the *Diplodactylus vittatus* complex (King 1977a), *Diplodactylus polyopthalmus*, *D. furcosus* and *D. ornatus* were resurrected as species and *D. granariensis* was described (Storr 1979b). The chromosomal races described in the *Phyllodactylus marmoratus* complex (King & Rofe 1976; King & King 1977) led to the description of *P. marmoratus alexanderiz*, and those in the *Gehyra variegata-punctata* species complex (King 1979) resulted in the description of *G. minuta* and *G. montium*. A similar analysis of the *G. australis* species complex (King 1982b, 1983a) resulted in the resurrection of *G. dubia*, and the description of *G. pamela*, *G. borroloola*, *G. robusta* and *G. occidentalis*. Additional chromosomally distinct forms of *Gehyra* remain to be described.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Australian gekkonid species range from 25 mm to 130 mm snout-vent length and generally have a depressed body. However, some exceptional species show lateral compression. The body may have distinct lateral skin folds (Fig. 27.1E). Many species have loose, velvety skin made up of minute granular scales, whereas others have a dorsal surface with clusters of pronounced tubercles surrounded by smaller scales. Abdominal scales are often large, plate-like and imbricate. Geckos have well-developed, pentadactylic limbs with complex modifications to toe shape. Some rock-dwelling and arboreal species have pad-like toes with complex subdigital lamellae, although others retain primitive claw-like toes without laterally expanded pads. Some terrestrial forms also share lamellar specialisation, whereas others have simple toes. The individual lamellae are actually compound pads made up of microscopic projections or setae which take hold on the substratum (see Locomotion).

The tail is generally thick, but varies in its degree of specialisation and size. In rock-dwelling, and sometimes arboreal, species, such as *Rhacodactylus* (*Pseudothecadactylus*) *lindneri* (Pl. 4.3), the long tail, round in section, and with specialised pinose lamellae on the tip, is prehensile and is used as a fifth limb (Fig. 27.1G). The compound ejaculatory tail glands of members of the *Strophurus ciliaris* complex can be used as a defence mechanism to squirt an irritant at predators. Many species can autotomise their tails along structural breakpoints when attacked. The writhing, distracting tail squirms on the ground, while the animal either lies motionless, slowly sneaks away, or flees. The tail regrows in time. Tails may also be large and function as fat reservoirs, as the round plug of a burrow entrance, as in *Diplodactylus conspicillatus*, or as leaf-like camouflage, as in most *Phyllurus* species (Fig. 27.2A; Pl. 4.7, 4.8). In the genus *Nephrurus*, most species have a tiny sensory ball on the end of a heart-shaped and otherwise pointed tail (Fig. 27.2B; Pl. 4.1; Russell & Bauer 1987).

The gekkonid head is generally robust, depressed and diamond-shaped and the snout is short and blunt (Fig. 27.1A, B, D). The large eyes are set laterally on a sloping forehead. Auditory openings are generally round to oval in shape. Large, hard, shiny nasal and chin shields cover the margins of the jaws and nasal area and contrast markedly with the dull and velvety head and body scales. The

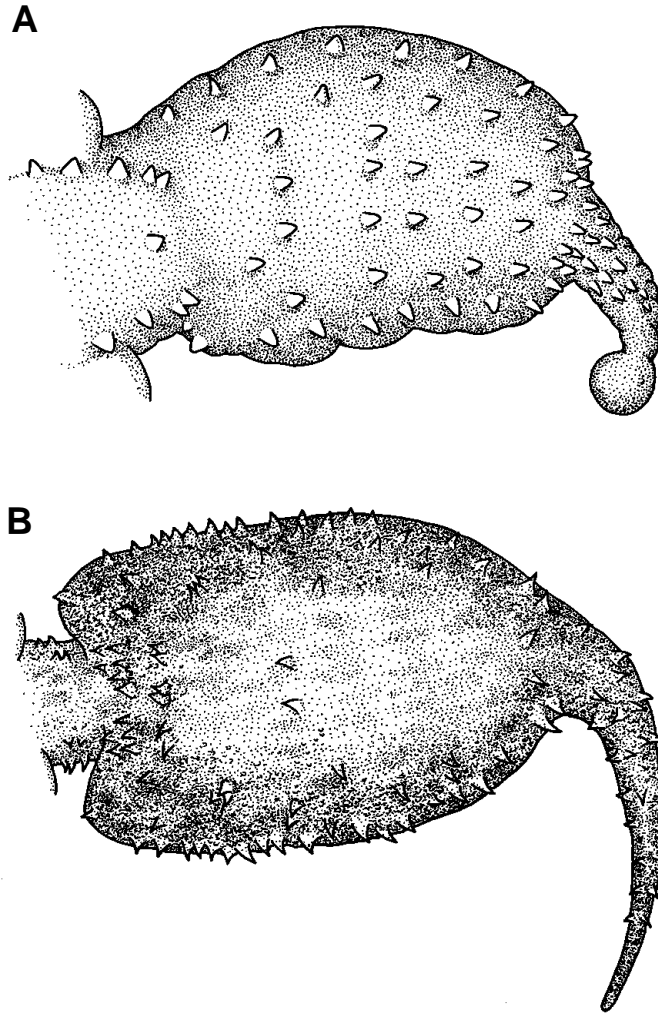


Figure 27.2 Tail shape in geckos. **A**, a knob-tailed gecko, *Nephurus levis*; **B**, the southern leaf-tailed gecko, *Phyllurus platurus*. [M. Cilento]

powerful jaws bear dorsal and ventral rows of uniformly short, peg-like teeth. The wide, flat tongue has a notch in its leading edge and is frequently used by the animal for licking its face and eyes (Fig. 27.3).

The back pattern colouration of geckos is often striking. *Strophurus elderi* has a grey-black background colouration with occasional raised tubercles which appear as white spots. *Oedura gemmata* has a velvet black back with lemon yellow spots and a white-banded black tail (see also Pl. 4.4). Heavily camouflaged species often have intricate back patterns of grey, brown, black, and buff. Some groups are able to change their skin colour from almost translucent pink to a marked pattern (for example, *Gehyra borroloola*), by the action of chromatophores in the cells of the skin. Longitudinal stripes on both the back and abdomen of some species which live in spinifex (for example, *Strophurus michaelsoni*) provide camouflage.

The post-anal region of males is enlarged, to form two sac-like pouches at the base of the tail. These pouches appear to be associated with the internal housing of the twin hemipenes (Fig. 27.1H), and bear clusters of large caudal spurs on their postero-lateral surface.

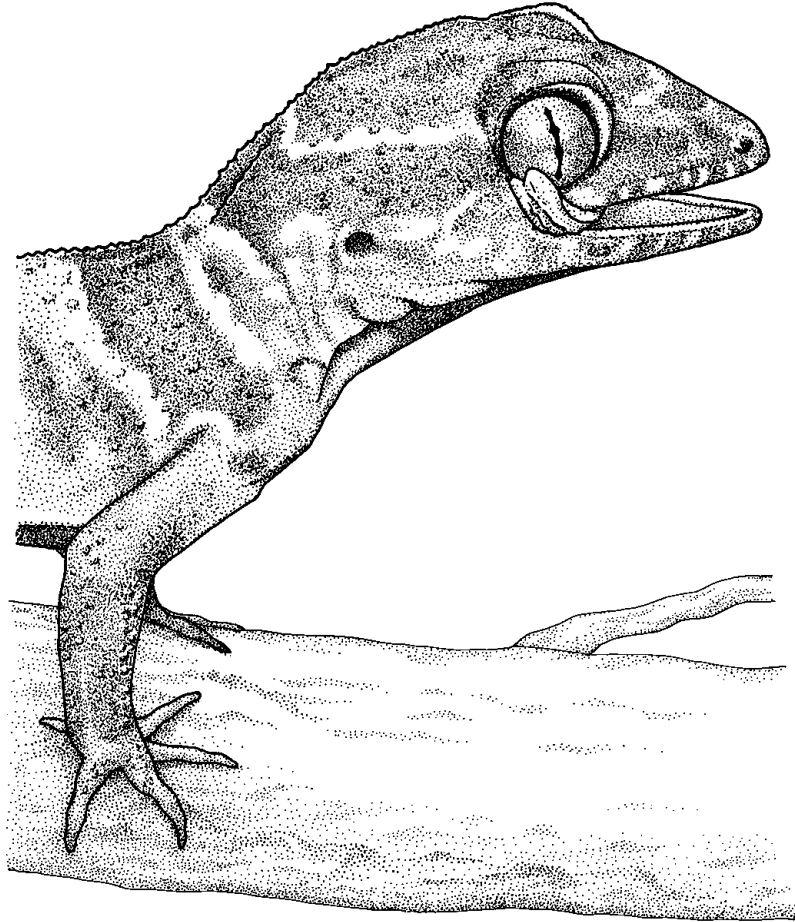


Figure 27.3 *Cyrtodactylus louisianensis* using its tongue to wipe its face, a behaviour peculiar to the Gekkonidae and Pygopodidae. (After photo by Frithphoto/ANT) [M. Cilento]

Skeletal System

The Gekkota are amongst the oldest of the squamate groups. As such they have numerous ancestral characteristics, but also some specialised structural characteristics when compared to other squamate groups. The following is general description of the basic gekkonid skeletal system derived from Romer (1956) and Bauer (1990).

The skull is depressed and broad, and the dermal bones are thin. The pterygoid flange is well developed. The dentition is typically pleurodont and the teeth are numerous. Occasionally the stapes is perforated for the stapedia artery. The hyoid apparatus is usually nearly complete, but may be completely developed in some species. The hyoid and second epibranchial frequently make contact with the skull.

The typical gekkonid skull has several derived characters, including loss of the supratemporal arch and reduction of the jugal, which produces an incomplete post-orbital arch. A reduction in the bracing structures contributes to the internal mobility of the skull (Bauer 1990). Kluge (1967a) identified two patterns in the ontogeny of the premaxilla in the Gekkonidae which are most apparent at the egg-tooth stage. The Diplodactylinae and Eublepharinae have paired centres of ossification, whereas the Gekkoninae and Sphaerodactylinae have a single centre. In the Diplodactylinae, the premaxillae remain partially paired early in ontogeny, although in the Carphodactylini they fuse in the midline at the time of

hatching in some genera, but remain paired throughout life in others (Bauer 1990). Co-ossification of the dermis to the underlying skull bone occurs in the Carphodactylini but not in the Diplodactylini (Bauer 1990). Moreover, the short wide basal process of the premaxilla in the Carphodactylini is a derived condition.

Gekkonid teeth are small, conical, homodont and pleurodont and occur on the dentary, maxilla and premaxilla. The anterior teeth are generally larger than the posterior teeth. Palatine teeth are absent. Bauer (1990) distinguished between tiny, extremely numerous teeth found in the carphodactyline genera *Nephrurus*, *Carphodactylus* and *Phyllurus*, and the moderately sized, blunt and distally compressed teeth found in other diplodactylines, and primitively in gekkonine and eublepharine geckos.

The hyoid apparatus of geckos is primitive, wherein all three cornua of the hyoid apparatus are well-developed as long slender structures. The hyoid and second epibranchial cornua frequently attach to the paraoccipital process dorsally, and the lingual process is long and slender. The epibranchial cartilage of the last arch is continuous with the second ceratobranchial beneath it.

A series of detailed comparative analyses has been made on the structure of the hyoid apparatus in gekkonids. Kluge (1983) distinguished a group of gekkonine genera, termed the Ptyodactylini, by the absence of the second ceratobranchial arch. Within the Diplodactylinae, certain carphodactyline genera share uniquely derived characters of hyoid structure, such as an inner proximal ceratohyal projection in *Nephrurus*, *Phyllurus*, *Naultinus* and *Carphodactylus* (Kluge 1967b). This projection is absent in the Diplodactylini.

There are usually 23 to 29 presacral vertebrae and up to 47 caudal vertebrae. Within the Diplodactylini there are 25 to 27 presacral vertebrae (Holder 1960), and from 24 to 27 in the Carphodactylini. Generally the vertebrae are amphicoelous (in which the intervertebral surface of each centrum is biconcave) with a continuous notochord and with small, free trunk intercentra, but are procoelous (in which the centra are concave anteriorly and convex posteriorly), with small condyles, in a few genera. Septa are present in caudal centra and the tail is short and fragile.

Amphicoely is peculiar to the Gekkonidae. It is regarded as a secondarily derived condition, and has generated considerable debate on its evolution and phylogenetic significance (Kluge 1987). Both amphicoely and procoely are encountered in the geckos and the difficulty of attributing a derived or ancestral polarity to this condition remains. Kluge concluded that the primitive state of procoely was attained several times among gekkonoids and that amphicoely with a continuous notochordal canal, may have been acquired by paedomorphosis in early gekkotans (Gauthier 1981). Bauer (1990) viewed amphicoely as a primitive character within the Carphodactylinae and considered that procoely, which is found in certain species, is derived.

The eight cervical vertebrae of carphodactyline geckos are typically gekkonid and characterised by an association with persistent intercentra that lie ventral to the intervertebral discs, or with a persistent notochord (Bauer 1990). The intercentra are enlarged with ventral hypopophyses. The cervical intercentra are narrow. However, species of *Rhacodactylus* had broad intercentra with posteriorly directed hypopophyses.

The trunk vertebrae are relatively uniform. Bauer (1990) interpreted the high neural spines found in certain Carphodactylini as a derived character. In the Carphodactylini and Diplodactylini, one to three lumbar vertebrae (pre-sacral vertebrae which do not bear ribs) are typical; gekkonines have a single lumbar vertebra. Most geckos have two sacral vertebrae, although some carphodactylines have three or four (Bauer 1990). In the latter group, other vertebrae have been modified and included in the sacral complex (Fig. 27.4E).

Moffat (1973) reported the absence of a sacral pleurapophyseal process in the Diplodactylinae. Her interpretation of this as a loss, and therefore a derived condition has been disputed by Bauer (1990) and Kluge (1987).

Not surprisingly, the geckos have a highly variable number of caudal vertebrae, a feature associated with the extreme variation in tail morphology. The number of caudal vertebrae ranges from 22 to 47 in the Carphodactylini (Bauer 1990). There is not always a direct correlation between caudal number and tail length, and *Phyllurus*, *Nephrurus* and *Carphodactylus* have greatly shortened centra compared to those of other Carphodactylini. Bauer (1990) regarded this as a derived state. In this group, many vertebrae are fused and all have reduced, or lack, transverse processes on the post-pygial caudal vertebrae (autotomising septum-bearing vertebrae). Tail autotomy is common throughout the Gekkonidae and is possible through any post-pygial vertebra in most Gekkoninae. While autotomy may be restricted to one or several autotomy planes in the Diplodactylini, only one or two vertebrae have autotomising septa in the Carphodactylini. *Nephrurus asper* lacks them altogether. The reduced number of autotomy sites is correlated with a loss of transverse processes, or caudal vertebra. The commonest site of the first autotomy plane is in the sixth caudal vertebra in both the Diplodactylinae and Gekkoninae (Bauer 1990) (also see Behaviour).

Ribs may be present on both cervical and trunk vertebrae (Fig. 27.4A, D, E). Each of the thoracic ribs consists of a vertebrocostal element, which is always present, an intermediate element composed of cartilage, and a sternal or mesosternal component. Abdominal ribs lack intermediate or mesosternal elements. Thoracic ribs may have a direct sternal attachment, or may be attached to a narrow band of cartilage which runs postero-ventrally from the sternum, termed the mesosternum (Fig. 27.4C). Parathoracic ribs, or parasternalia, which are posterior to the thoracic ribs, curve anteriorly, then fuse at the midline. Within the Carphodactylini, Bauer (1990) found between two and three sternal and mesosternal ribs and from none to seven parathoracic ribs. Kluge (1967b) proposed that an increased number of parathoracic ribs is correlated with arboreality in the genus *Diplodactylus* (which at that time included *Strophurus* species). Bauer (1990) found the same correlation in the Carphodactylini.

The sternum is a short, broad plate lying in a midventral position, posterior to the coracoids and superficially overlapped by the interclavicles. Sternal fontanelles are absent and a parasternum is sometimes present. Most carphodactyline species have a long and broad sternum, whereas in *Nephrurus* it is short and narrow (Bauer 1990). In *Naultinus*, the sternum remains unossified throughout ontogeny, thus recapitulating the primitive form.

In modern geckos the pectoral girdle lacks paired cleithra. The lower end of the clavicle is broadened and is either hook-shaped or perforated. It does not overlap with the interclavicle head. The interclavicle may be T-shaped, cruciform or rod-shaped (Romer 1956). The primitive clavicles in the Carphodactylini are longer than wide and bear a pair of laterally directed coracoid extensions. The interclavicle is primitively imperforate, although fenestrae are present in some genera. The primitive clavicle in this tribe is broadly expanded and fenestrated medially. Size and number of fenestrae vary within and between genera. They are absent in *Carphodactylus* and *Phyllurus*, whereas very large fenestrae occur in *Nephrurus* (Bauer 1990).

The second portion of the pectoral girdle, the scapulocoracoid, is an endochondral formation. The scapulocoracoids are paired and articulate with the leg bones. The scapula and coracoid form a compound element in which each component joins at right angles. Usually all four scapulocoracoid fenestrae are well developed and the two upper ones are emarginate. In the Carphodactylini, the primitive scapula is a broad, stout blade at its border with the suprascapula.

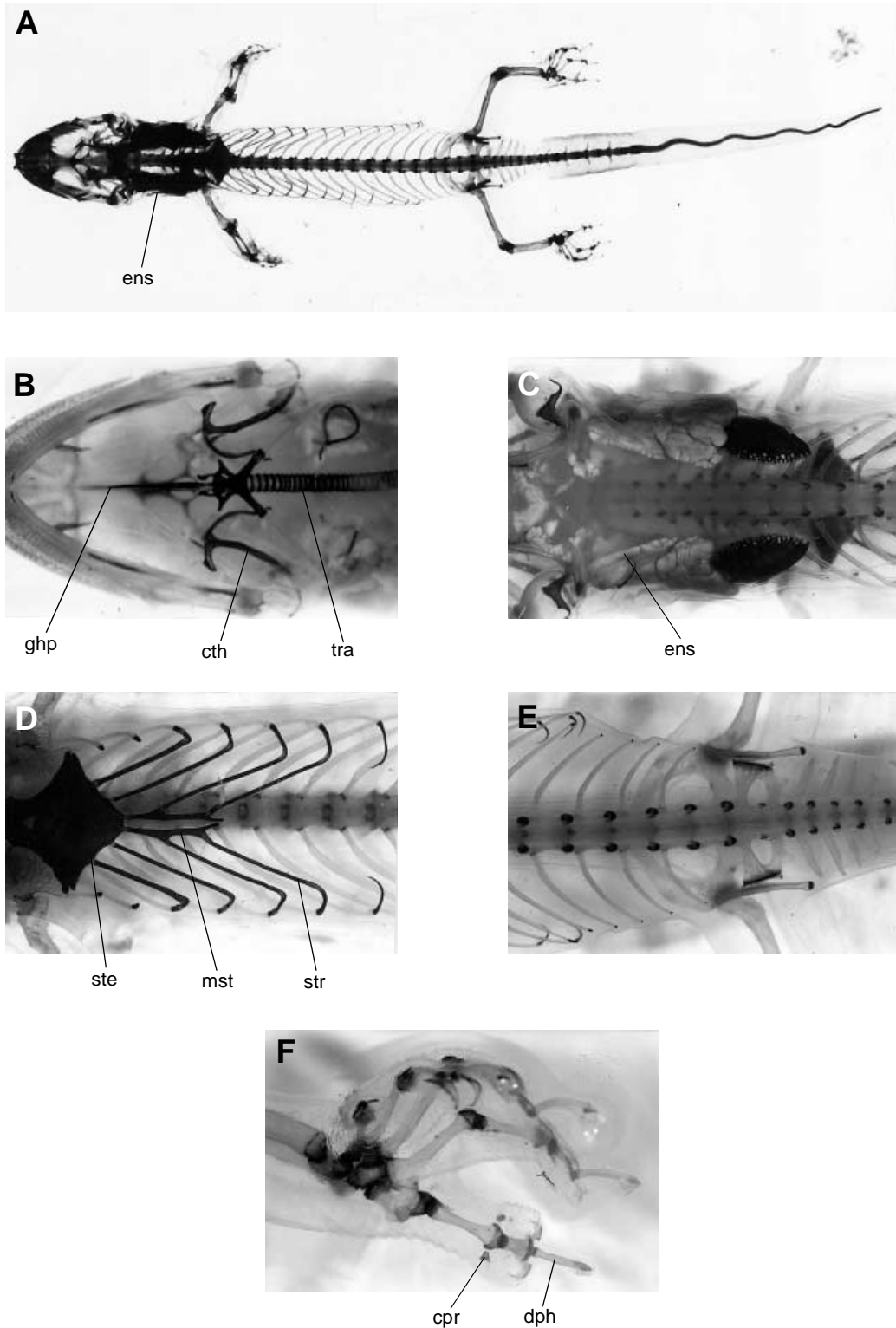


Figure 27.4 Alizarin preparation of an adult specimen of *Hemidactylus frenatus* showing the skeletal morphology of a typical gekkonid. Bone appears as grey material, except in the tail where the tissue is still visible, and cartilaginous tissue is black. **A**, dorsal aspect of the whole animal; **B**, ventral view of the hyoid apparatus, which is predominantly cartilaginous; **C**, dorsal view of the endolymphatic sacs anterior to the clavicles; **D**, ventral view of the sternum and sternal ribs; **E**, dorsal view of the pelvic girdle; **F**, foot. **cpr**, cartilaginous processes supporting the toe pad; **cth**, ceratohyal arch; **dph**, distal phalange with associated claw; **ens**, endolymphatic sacs; **ghp**, glossohyal process; **mst**, mesosternum; **ste**, sternum; **str**, sternal ribs; **tra**, trachea. [Photos by M. King & P. Horner]

It is narrow at its midpoint and expanded ventrally at the coracoid suture. However, the scapula of *Nephrurus* has a narrow shaft and an elongate blade (Bauer 1990).

The basic structure of the forelimb consists of a humerus, ulna, radius, carpals, metacarpals and phalanges. There is considerable variation in foot and toe structure, which has been accompanied by osteological divergence. Bauer (1990) found variation between carphodactylinae genera in the size of the metacarpals and in phalangeal formula, and considerable phalangeal reduction in the Diplodactylini. The significance of the variation in toe structure is dealt with more extensively in the following section.

The pelvic girdle differs from the pectoral girdle in that it is an endochondral structure. The pubic bones of geckos are separated by a substantial epipubic cartilage (Romer 1956). The pubis is relatively narrow in most geckos and a pectineal tubercle is present. *Phyllurus* has a typically broad and robust pubis (Bauer 1990). The blade-like metischial process on each ischium is narrowly separated from the other in the Diplodactylini and New Zealand and New Caledonian Carphodactylini, whereas in the remaining Carphodactylini these processes are expanded postero-laterally and widely separated from each other. Geckos have a dagger-shaped hypischium, which extends posteriorly to the metischial process. It is of variable length and form in different genera.

Overall, hind limb structure is relatively uniform within the Gekkonidae. As with the front limbs, considerable variation occurs in structure of the metatarsals and phalanges associated with highly derived foot and toe structure (Fig. 27.4F). Metatarsals are shortest in the Diplodactylini. Bauer (1990) recognised three groups of genera in the Carphodactylini which share a common pattern of metatarsal length (from shortest to longest): *Nephrurus* and *Naultinus*; *Phyllurus* and *Carphodactylus*; and the remaining Carphodactylini. The fifth metatarsal is short and broad, and medially receives a projecting spine from the fourth metatarsal (Romer 1956). The fifth metatarsal is strongly hooked in the genera with expanded toe pads, but only slightly hooked in the padless Australian genera. This structure permits the foot to grip the substrate and is analogous to the heel. Many of the characteristics of toe structure are also reflected in the osteology of gekkonid digits. Paraphalangeal elements are frequently present in the toes of species having adhesive pads.

Bauer & Russell (1989) described the ossified anal bones and other minor ossifications such as the supraorbital scales.

Locomotion

As in primitive reptiles, the Gekkonidae generally have larger hindlimbs than forelimbs. The body lies flat on the substratum at rest, but is cleared a short distance from the ground during movement. The limbs provide a wide trackway (Fig. 27.5).

Modifications in skeletal structure permit adjustment between the position of the tibia and tarsus to provide a laterally projecting hind foot, as is also true of the forearm and manus of the front foot. Such adaptations are important in the gekkonids with their highly specialised foot structures and surface attachment mechanisms, and permit geckos to run at great speed on a range of surfaces. King (1984a) observed a galloping gait in the diplodactylinae, *Oedura filicipoda*.

Perhaps the most spectacular example of multiple convergence in form and function in the Gekkoninae, is the evolution of seven major patterns of foot morphology in response to selection for a more efficient climbing foot (Russell 1976) (Fig. 27.6). Similar patterns have evolved independently in the Diplodactylinae (Russell 1979). In both subfamilies, the shift in adaptive zone from terrestriality to arboreality has provided the selective medium in which

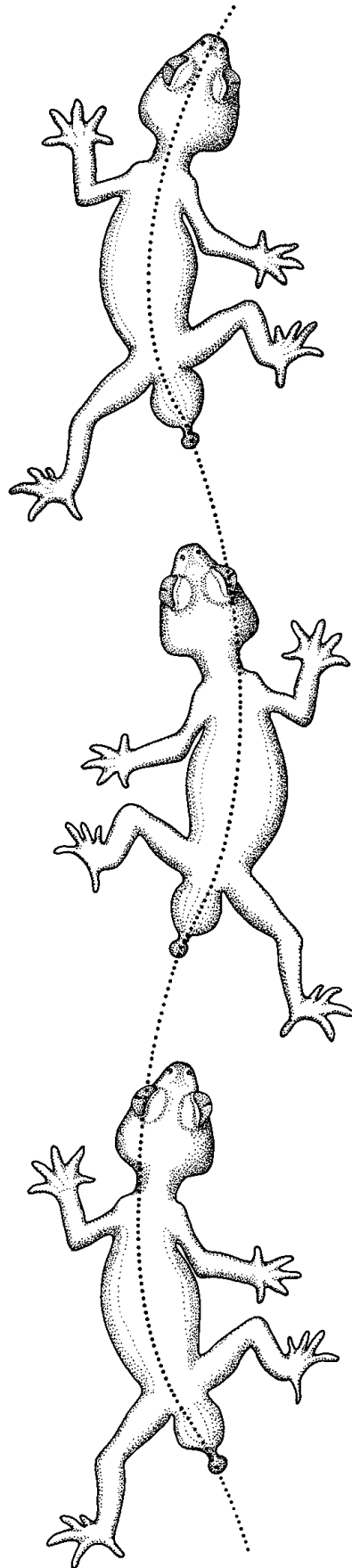


Figure 27.5 Locomotory movement in the Gekkonidae. The dotted line emphasizes the swimming motion of the spine. [M. Cilento]

these mechanisms have evolved. Russell (1979) proposed that each shift towards the development of adhesive subdigital pads from the primitive foot design, has been accompanied by restructuring of the foot. That the same pattern of change has arisen independently in a number of lineages is attributed to the similarity of selective pressures and the channelling of change in morphological complexity in a particular direction. Indeed, the integrated control mechanisms required for the efficient operation of a subdigital pad have arisen on several independent occasions and the structural differences between these mechanisms are a product of their different ancestry. There are many examples of the evolution of climbing feet from terrestrial ones and vice versa.

Primitive padless digits are found in both the Gekkoninae and Diplodactylinae (Fig. 27.6F). Russell (1979) identified three key features, as exemplified by the carphodactyline, *Carphodactylus laevis*. The double bellied extensor muscle to each digit gives rise to a single stout tendon which is tightly bound to all interphalangeal joints by strong ligaments. Secondly, the flexor musculature is simple and the flexor tendon traverses the phalanges mid-ventrally in a synovial sheath and inserts in the claw-bearing phalanx with a particularly high mechanical advantage. Lastly, the phalangeal formula is primitive and the joints between the phalanges overlap strongly both dorsally and ventrally, thus preventing hyperflexion or hyperextension of the digits.

These features permit grasping and climbing on rough surfaces, or trees, but pads or hyperextension are lacking (Fig. 27.6F; Russell 1979). Extensive radiations of primitive, padless *Nephrurus* (Carphodactylini) have abandoned rock-dwelling, or arboreal habits and demonstrate purely terrestrial adaptations of the primitive foot. These include adaptations of toe structure for life in a sandy environment, such as puffy feet with pinose scales, a reduction in size of the digits, and reduced phalangeal formula (Bauer & Russell 1991).

In the primitive foot pattern of the Gekkoninae, muscle masses do not traverse any of the phalanges on the dorsal surface of the toes and the phalanges articulate with double-headed joints which prevent hyperextension (Russell 1976). The genus *Cyrtodactylus* is typical of this type, but also demonstrates an evolutionary series in which pad formation has occurred in some species. Most species have long slender digits which exhibit a slight kink, beneath which are large, subdigital scales with microscopic hook-like outgrowths 2 to 3.5 mm long. These outgrowths are probably precursors of the microscopic hook-like setae which form adhesive toepads. Russell (1976) demonstrated an enlargement of subdigital scales associated with this kink in some *Cyrtodactylus* species, which include a lateral expansion of the scales into pads. These changes are accompanied by modification of the articulation of the phalanges that permits hyperextension. The dorsal musculature and tendons have also extended dorsally along the toe surfaces. Thus, there has been development of muscle, bone and tendons associated with toepads and setae.

Hyperextension is basic to the function of adhesive pads in the Gekkonidae. The thousands of microscopic setae present on the adhesive subdigital lamellae of the toes of geckos, can engage microscopic irregularities on the surface on which the animal is climbing, such that a pad makes contact and effectively hooks on to a surface. To remove the pad, the gecko must detach the pad in the opposite direction to which it was applied. To achieve release, blood is forced into sinuses within the toes, the muscles dilate and the phalanges disarticulate, thus changing the position of the setae. The toes can be curled back as the setae are effectively disengaged. This obligatory locomotory mode permits the gecko to walk on and adhere to smooth, vertical surfaces and even hang on the lower side of horizontal surfaces. It is noteworthy that the positioning of the feet obliquely to the body, plus the radiation of the toes on each foot, spanning over 200° of arc, provides all-round support for the animal and thus consolidates an otherwise precarious attachment.

Multiple evolutionary pathways of toepad form and function are evident within the different gekkonid lineages. Thus, while the genera *Gehyra*, *Hemidactylus* and *Lepidodactylus* of the Gekkoninae have very large toepads with multiple scansors and adhesive properties, in other genera only particular pads may be adhesive (Figs 24.2; 27.6A, B). In species of *Phyllodactylus*, *Diplodactylus*, *Crenadactylus* and *Rhynchoedura* only the paired, large terminal pads on each toe are adhesive.

The shift from terrestriality to arboreality has been considered to be the driving force in the specialisation and development of adhesive toe pads (Russell 1976). However, numerous species in different lineages have either secondarily lost these pads because of a new direction in habitat specialisation, or have acquired quite different morphological specialisation with other adaptations. While modification in toe structure from padless to padded may provide for a transposition to an arboreal habitat, it also allows sufficient plasticity to enable species to specialise secondarily in a rock-dwelling lifestyle, as has occurred in some Australian *Gehyra* (King 1984c), without the necessity for any substantial change in toepad structure. This is not true for those geckos which have reverted to a purely terrestrial existence, living on or in different soil types.

Russell (1979) proposed that pads were acquired once within the Diplodactylinae, and that the Carphodactylini and Diplodactylini exploited them in different ways. Since he regarded terminal pads as primitive and argued that they were associated with arboreality (as in the Gekkoninae), secondary terrestriality developed in association with the invasion of the Eremean floristic zone. Supporting evidence for this view comes from the presence of mechanisms for hyperextension in terrestrial Diplodactylini which have very small pads, or no pads at all, and which do not hyperextend their toes (Fig. 27.6E). Terminal pads have been lost completely in *Diplodactylus damaeus* and yet musculature, sinuses and osteology associated with hyperextension remain. Other adaptations to a sandy substrate include the reduction in size of digital scales and their development into a spinose form (Bauer & Russell 1991).

A substantially different evolutionary course from most Diplodactylini (excluding *Strophurus*), has occurred in the Carphodactylini, in that basal, as well as terminal, adhesive toepads have developed. The arboreal and rock-dwelling *Strophurus* show this same development (Fig. 27.6C, D). In the Carphodactylini, the pair of terminal pads which characterise the Diplodactylini have been much reduced or lost in most groups. An exception is the genus *Oedura*, in which the terminal pads and the intermediate scales are enlarged. Highly developed basal toepads have also evolved in the Gekkoninae (for example, *Hemidactylus*), although by different pathways (Russell 1979). Operation of the toepads in the Carphodactylini involves a simpler internal mechanism than that of advanced gekkonines.

Complex locomotory adaptations resulting in complete changes in foot structure in terrestrial and arboreal species have been accompanied by a number of additional locomotory adaptations. Parallel adaptations to an arboreal existence are seen in the Carphodactylini and Gekkonini. Thus, *Gehyra membranacruralis* has a prehensile tail with a pinose scale tip, which it uses as a 'fifth limb' to hang from foliage. Species of the carphodactyline genera *Naultinus* (see Bauer 1990, Fig. 52) and *Rhacodactylus* have similar prehensile tails, although in *Rhacodactylus (Pseudothecadactylus) lindneri* the tail tip has a series of pinose scales (presumably with setae), which may act as an adhesive pad. Remarkably, the cavernicolous carphodactyline, *Oedura filicipoda*, has a similar prehensile tail with pinose scales on the tip (Fig. 27.1G), even though its tail is also used as a fat storage area.

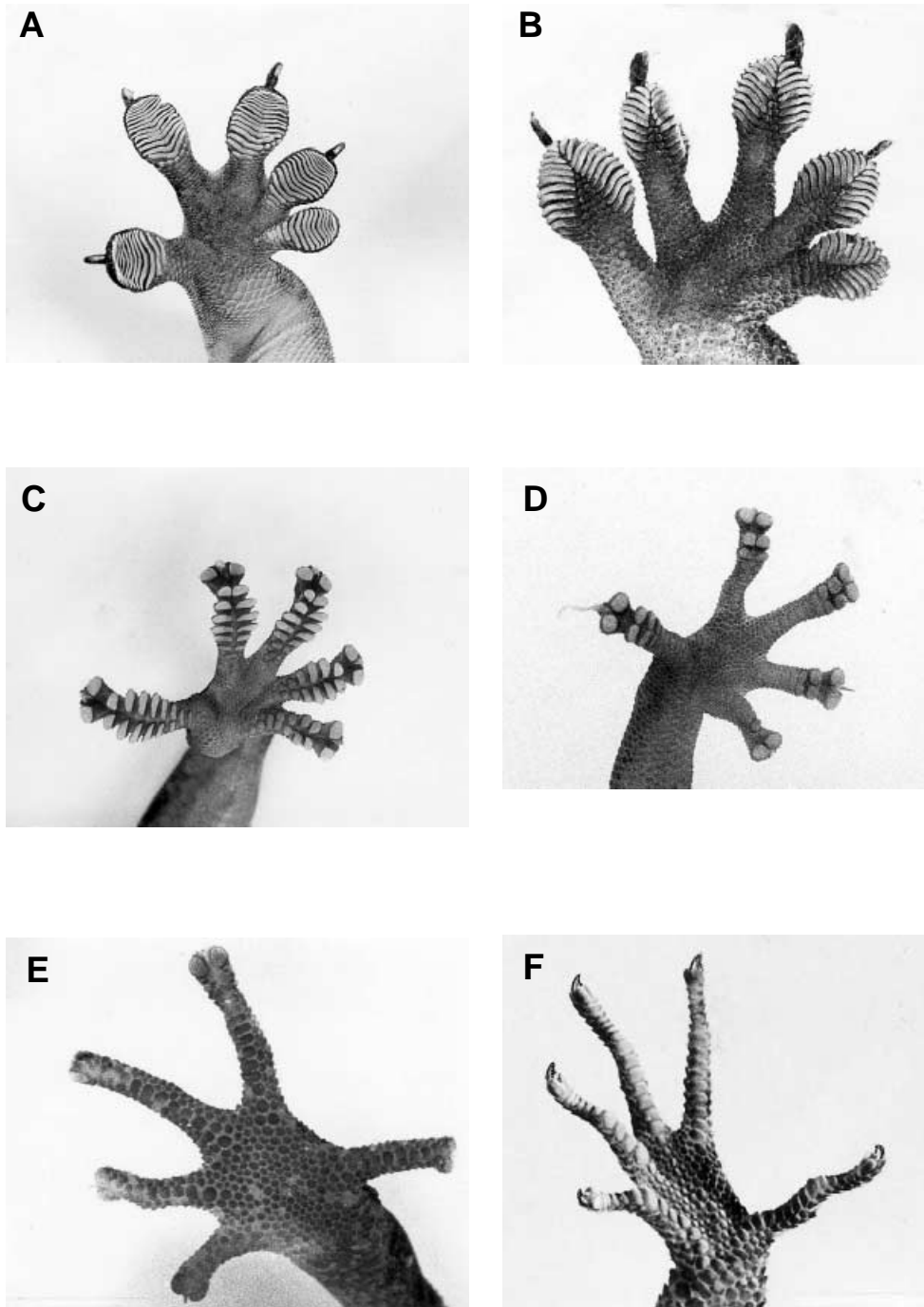


Figure 27.6 Ventral view of the hind feet of selected gekkonid species. **A**, dilated toepads and numerous subdigital lamellae of *Gehyra membranacruralis*, in which the claw on the fifth toe is absent; **B**, the wedge shaped group of rounded scales dividing the toepads increases the opposing angle between lamellae in *Gehyra xenopus* and large claws are present on digits 1 to 4; **C**, the large pair of terminal toepads and the very enlarged intermediate pads form each toe of *Oedura filicipoda* into one laterally divided adhesive surface; **D**, the enlarged pair of terminal toepads and two pairs of subterminal pads of *Oedura gracilis* are typical of this genus; **E**, the terminal adhesive toepads and other subterminal pads of *Diplodactylus occultus* are reduced in relation to toe length; **F**, adhesive pads are lacking in the primitive gekkonine condition shown by *Heteronotia binoei*
 [Photos by M. King & P. Horner]

Feeding and Digestive System

Three aspects of ingestive behaviour are considered: licking food, drinking water, and preying on other animals. Free-ranging and captive geckos use the same technique to lick food as they use for drinking. *Rhacodactylus lindneri* and *Phyllodactylus guentheri* lick nectar from blossoms on trees and *Gehyra australis* licks decaying, or pulpy fruit. Gekkonids generally lick water from the surface of leaves or rocks, but on occasion, captive *Gehyra* species have been observed drinking water from a glass petri dish. This involved partial submersion of the head and continuation of the lapping motion.

Geckos can be voracious predators and will actively pursue and kill their prey. Generally they attack moths and arthropods by running up to the animal, biting down on it and then beating the prey on the ground by shaking the head laterally. The geckos' head size governs the size of large insects which can be eaten. The prey is orientated longitudinally in the gecko's mouth, so that protrusions, such as an insect's legs, fold back, thus avoiding obstruction. The prey is swallowed with assistance from the tongue, muscular contractions in the neck and body, and by progressive biting and swallowing.

Sense Organs and Nervous System

Sensilla of supposed mechanoreceptive function are widespread among geckos, although their presence in Australian species has been poorly studied. They have been reported in a number of gekkonines, and are principally associated either with scales bordering the subdigital lamellae, with the labial scales, or with the body scales (Russell & Bauer 1987).

The possible function of the terminal caudal knob, which is characteristic of most members of *Nephrurus*, has long intrigued herpetologists (Fig. 27.2B; Pl. 4.1). This hard, rigid integumentary structure is richly supplied with vascular tissue and has numerous, regularly arranged sensilla on each of its surface scales (Russell & Bauer 1987). The caudal peduncle supporting the knob is well-muscled, permitting the knob to be moved freely, thereby suggesting that it may play an active role in sensory reception. Surface sensilla on the caudal knob probably monitor disturbance impinging directly on their exposed surfaces. Compared with other geckos, frequency of tail autotomy in *Nephrurus* is generally low (Bauer 1986a) and *N. asper* is the only gecko unable to autotomise any portion of its tail (Holder 1960). Russell & Bauer (1987) postulated that, apart from the mechanoreceptive function of the knob, its extensive vascularisation may also be an advantage in thermoregulation and heat exchange. They noted that the carphodactyline genus *Carphodactylus* has a similar, but much smaller, terminal knob on its tail.

Taste buds occur in the oral and pharyngeal epithelia of most vertebrates, but are generally considered to be unimportant to lizards (Schwenk 1985). Schwenk found that geckos have numerous taste buds in the oral epithelium, but virtually none on the tongue. However, Nonoyama (1936) recorded numerous taste buds on the tongue of *Gekko japonicus*, suggesting that taste bud numbers and distribution may be variable within the family; concomitantly, the reliance placed on this chemosensory mode may also differ.

Endocrine and Exocrine Systems

Little is known of endocrine systems in Australian gekkonids, although endolymphatic sacs have been examined. In most lower vertebrates, the endolymphatic sacs are part of a calcium-filled system associated with the ear or organs of balance. In many gekkonine and sphaerodactyline species, the sacs are greatly enlarged and protrude from the cranial vault to lie along the surface of the peripheral lateral neck musculature (Fig. 27.4A, D; Kluge 1967a).

The function of the endolymphatic sacs in geckos is still unclear. The endolymphatic system may regulate pressure in the labyrinth by removing the endolymphatic fluid from the sacculus, thus aiding the transmission of sound waves from the skull into the ear, and also it may be a source of calcareous material for bone growth (Whiteside 1922). Additionally, as the paired endolymphatic sacs are larger in females (Greer 1989) and the size and density of the sacs increases before egg-laying, the system could provide calcium for egg shell production (Bustard 1968e). In support of this hypothesis, gekkonine species have a hard, relatively impermeable, calcareous shelled egg (Bustard 1968e) and possess prominent endolymphatic sacs, whilst the diplodactylines have relatively pliable, permeable egg shells (Greer 1989), and apparently lack enlarged endolymphatic sacs. Lymphatic sacs filled with calcium carbonate have not been detected in Eublepharinae, or in most Diplodactylinae. However, Bauer (1990) found aragonite accretions in sacs in the nuchal area of *Eurydactylodes* species. He concluded also that the accumulation of calcium carbonate is related to calcium stress in reproductive females.

Exocrine structures in geckos include 'escutcheon' scales and pre-anal organs. The latter are present in the males of most lizard groups. Pre-anal organs are tubular evaginations of the epidermis (Fig. 27.1E) and include femoral glands and similar structures in the posterior abdominal region (Kluge 1967b). Their external apertures, pre-anal pores, occur either in the centre of a scale, or at its posterior edge. Homologous scales in females are occasionally indented in a pattern that suggests the male pore arrangement. The pre-anal organs secrete an odourless, cellular material, or 'secretion plug', that arises from the basal layer of germinal cells, passes into the lumen and differentiates as it travels distally towards the pore (Cole 1966b; Maderson 1972); their function remains unclear (Cole 1966b; Kluge 1967b). Pre-anal organs are most heavily swollen with waxy cellular material during certain seasons, which are seemingly correlated with the sexual cycle (Kluge 1967b). Greenberg (1943) suggested that they function in some prelude to copulation in the gekkonid, *Coleonyx*, in which males were observed rubbing the wax cones from the pores transversely across the tail of the female. She responded by elevating her tail. Pheromone dispersal may be another possible function, as the epidermal glands are well placed for transfer of products to the substrate during locomotion (Maderson 1970a, 1972).

'Escutcheon' scales, or generation glands, are restricted to sphaerodactylid geckos and thus not found in Australian gekkonids (Maderson & Chiu 1970). They are thought to have evolved from pre-anal organs (Kluge 1967b; Bauer 1990). They are specialised, unpigmented glandular scales located on the abdominal, femoral and post-cloacal regions (Taylor & Leonard 1956). They are more pronounced in males and increase in number with age (Kluge 1967b).

The caudal glands in the genus *Strophurus* are used in defence. They secrete a sticky, black, or pale yellow, substance which has a distinct musty odour (Rosenberg, Russell & Kapoor 1984). The caudal secretions of *S. ciliaris*, *S. rankini* and *S. strophurus* are mainly proteinaceous, with at least one glycoprotein component present in the secretion of *S. strophurus* (Rosenberg *et al.* 1984). In active *Strophurus* species, the secretion can be ejected explosively from the dorsal surface of the tail to a distance of 300 mm or more (Bustard 1970b; Morrison 1950, 1951). Considerable quantities may be extruded, and the secretion can be directed by an appropriate curvature of the gecko's tail. Apart from being irritating to eyes (Morrison 1951), the secretion is non-toxic, at least to chicks (Rosenberg & Russell 1980) or rats (Richardson & Hinchliffe 1983), and the extreme stickiness of this exudate may be its most effective defensive property (Rosenberg *et al.* 1984). The gecko itself is not irritated by the secretion, as has been shown by observations of an individual licking residual secretion from its tail (Russell & Rosenberg 1981).

In *Strophurus*, the defensive glands are a longitudinal, paired series of caudal chambers that secrete and store the glandular products (Rosenberg & Russell 1980). They are located deep within the caudal musculature, adjacent to the caudal vertebrae, and muscular contraction ejects the secretion. The fluid leaves the tail through a mid-dorsal epidermal rupture zone located anteriorly in each caudal segment (Russell & Rosenberg 1981). Regenerated tails contain elongate unsegmented glands. Therefore individuals with regenerated tails retain the ability to extrude the defensive secretion, and ejection of the secretion occurs either at the junction of the old and new tail, or in rupture zones contained in any remaining segments of the original tail (Russell & Rosenberg 1981).

Reproduction

Like most other reptiles, gekkonids are generally bisexual, except for a few parthenogenetic forms. Several different reproductive strategies have been established. Generally the Gekkoninae and Sphaerodactylinae lay one or two calcium-shelled eggs per clutch, and the Diplodactylinae and Eublepharinae usually lay two parchment-shelled eggs. All Australian taxa are oviparous. However, species of the New Zealand genera *Naultinus* and *Hoplodactylus* are live bearers (viviparous), as is the New Caledonian *Rhacodactylus trachyrhynchus* (Bauer 1990). Other species of *Rhacodactylus* are oviparous. Viviparity has been derived independently in these temperate and tropical species. Apparently, viviparity is not necessarily a low temperature adaptation, but may be associated with the provision of an energy reservoir enhancing the survival of juveniles. Much foetal nourishment in live-bearing carphodactylines is derived from yolk. The choriovitelline placenta is used for food absorption (Bauer 1990). Viviparous species are generally slow-moving animals and the yolk may be a nutritional buffer for young which may not have immediate hunting success.

Calcium-shelled eggs of the Gekkoninae and Sphaerodactylinae are soft when first laid, but harden after exposure to air. The egg shells are made of calcite and provide resistance to desiccation. They are capable of withstanding exposure to sea water for prolonged periods while still remaining viable (Brown & Alcala 1957). In contrast, diplodactyline and eublepharine eggs fail to show any mineralisation and are sensitive to aridity and humidity changes (Kluge 1987).

Male gekkonids have a bilaterally symmetrical reproductive system. The testes are located deep within the body cavity and are attached by mesenteries to the dorsal peritoneal lining on either side of the spine. In certain spiny tailed diplodactylini (*Strophurus* spp.), which are active during daylight hours and exposed to the sun, the peritoneal lining and the tunica of the testes are black; this may be a means of reducing the mutagenic effects of solar radiation. Testes undergo substantial changes in size, as much as ten-fold, as a prelude to sperm production. The seasonality of these changes is dependent on the reproductive strategy adopted by the species. For example, in *Phyllodactylus marmoratus*, testis weights are at their greatest in January and February and decline during the less active winter months. Meiotic activity commences in the spring, reaches a peak in November and extends to February.

Female reproductive systems are also bilaterally symmetrical, and the pair of ovaries lies in the dorsal midline in a similar position to the testes. Because of the great size of gekkonid eggs (up to 30% of the body weight), substantial anatomical and physiological changes are associated with egg production. The uterine area of the oviduct is relatively compact in the non-breeding season. However, before ovulation the oviducts become massively enlarged and distorted. Fat is mobilised and converted to yolk and fat bodies are substantially reduced in size, particularly those of the tail. Thus, in *Gehyra variegata*, loss of the tail in a female can prevent egg production (Henle 1990b).

Reproductive strategies adopted by Australian gekkonids may be grouped into four categories, three of which occur in southern forms. Females of species such as *Heteronotia binoei* (southern populations) are inseminated by males during the spring and early summer (Bustard 1968d), and lay a clutch of two eggs between late November and early December. These hatch between late February and March. A second strategy has been adopted by *Gehyra variegata*, as shown for populations in the Pilliga scrub and at Kinchega, New South Wales (Bustard 1969d; Henle 1990b). Mating occurs from September to December. Females produce two single-egg clutches per year, the first in late November and early December, the second in early January. A first wave of hatchlings appears in February and a second in March.

The third strategy is seen in *Phyllodactylus marmoratus*. In this cold-adapted species, mating occurs in autumn after egg laying is completed (King 1977b). Sperm are stored in oviducal lamellae throughout the winter months and are available for immediate fertilisation when ovulation occurs. This strategy allows very early fertilisation when males may be less active because of lower temperatures. Early egg-laying and hatching ensure that the hatchlings will have an opportunity to accrue adequate food reserves before winter. A similar reproductive strategy is apparent in *Phyllurus platurus* (Green 1973).

In the tropical regions of Australia a fourth strategy appears to operate. Hatchlings of *Hemidactylus*, *Oedura* and *Gehyra* are commonly observed in the wet season when there is an abundance of insect life. *Hemidactylus frenatus* can breed throughout the year in other tropical environments. More southerly species of these genera have been observed to lay eggs in the dry season. Greer (1989) suggested that this may be because of poor egg survival in the wet season.

Morphologically distinguishable sex chromosomes are rare in the Gekkonidae, although they have been found in the gekkonines, *Phyllodactylus marmoratus* (King & Rofe 1976), *Gehyra australis* (King 1977c) and *Gehyra purpurascens* (Moritz 1984). Female heterogamety has been reported in all of these. Sex chromosomes are unknown in the Diplodactylinae. Parthenogenesis has been reported in *Lepidodactylus lugubris*, *Nactus pelagicus* and *Heteronotia binoei* (Moritz & King 1985).

Chromosomal variation within the Gekkonidae is extreme. The most recent summary was published by King (1987a, 1987b). In all groups, the ancestral karyotype is acrocentric. In the Diplodactylinae, the ancestral number is $2n=38$. In the polyphyletic Gekkoninae, clusters of species have different acrocentric numbers ranging from $2n=32$ to $2n=46$. In both subfamilies, individual species often have extensive karyotypic modifications as a result of structural rearrangements (also see Affinities with other Groups; Affinities within the Taxon).

NATURAL HISTORY

Life History

Little information is available on the longevity of gekkonids. Most accounts are drawn from captive animals. Personal observations suggests that geckos can be particularly long-lived. A specimen of *Oedura gemmata* which had been captured from the wild in 1980 and maintained in the laboratory, died in 1991 (King & Horner pers. obs.). This animal was an adult when captured and remained much the same size over the 11 years of its confinement. One of the few reports of longevity in the wild is for a New Zealand carphodactyline, *Hoplodactylus maculatus*, which had been monitored for 17 years (Anastasiadis & Whitaker 1987).

Other aspects of gekkonid life history support the view that these are long-lived species. Sexual maturity in *Gehyra variegata* occurs at two years and egg production commences when females are three years old (Henle 1990b). The same pattern was observed in *Oedura monilis* (Bustard 1971). In *Strophurus ciliaris*, sexual maturity occurs at three years, whereas female *S. spinigerus* are mature at 20 months (How, Dell & Wellington 1986). How & Kitchener (1983) found that *Oedura reticulata* females were reproductively mature after 4 years. Moreover, in most instances geckos only produce two eggs per annum, indicating a very low reproductive rate and suggesting that longevity is an important component of reproductive success.

Henle (1990b) calculated a life expectancy of 6.5 years for *Gehyra variegata* after the attainment of sexual maturity at 2 years in females. Mortality was particularly low for adults and there were no differences between males and females, or between adults and subadults. However, juveniles showed a considerably higher mortality. Similar results were obtained by Bustard (1969d) in his examination of *G. variegata* in the Pilliga scrub, although he did find a female-biased sex ratio. It is noteworthy that the arboreal preference of *G. variegata* is correlated with a low number of potential predators.

Ecology

Most geckos are dietary generalists which prey on various arthropods and occasionally small vertebrates, and eat some plant material. Pianka & Pianka (1976) determined that at least three Australian desert species, *Diplodactylus conspicillatus*, *D. pulcher* and *Rhynchoedura ornata*, are dietary specialists which feed almost exclusively on termites.

Behaviour

Of all reptiles, gekkonids appear to be the most vocal. Calls usually take two forms. In the first of these, gekkonine and diplodactyline geckos produce defensive or distress calls when threatened. In the Gekkoninae, these may be a simple chirp, or scream, such as heard in species of *Gehyra*, *Hemidactylus* and *Phyllodactylus* (Daniels, Flaherty & Simbotwe 1986). In the Diplodactylini, aggressive threat calls may be accompanied by back-arching, leg-extension and mouth-opening. Numerous instances of these calls have been described for *Phyllurus* and *Nephrurus* (Bauer 1990) and one of us (King pers. obs.) has observed this in *Diplodactylus byrnei*. Calls of the second form are associated with contact in territoriality or mate attraction. These contact calls consist of multiple chirps and are known from a number of gekkonine genera including *Hemidactylus*, *Gekko*, *Phyllodactylus*, *Ptenopus*, *Ptychozoon*, *Cyrtopodion*, *Ptyodactylus* and *Thecadactylus* (Kluge 1987). Bustard (1969c) suggested that *Strophurus* species also make contact calls.

Three types of call were detected in Mexican populations of *Hemidactylus frenatus* (Marcellini 1977, 1978). A single chirp is given under stress. A multiple chirp call is made by both sexes, but more generally males, associated with feeding, defaecation, mating, or fighting between males. The third type of call consists of a very rapid burst of short chirps, made when males are preparing to fight.

Diplodactyline and gekkonine geckos have developed a series of unusual defensive mechanisms, in addition to vocalisation and defensive posture (Fig. 27.7). Some of the most spectacular of these adaptations are found in the Diplodactylinae. In *Strophurus*, the fourteen species are characterised by ejaculatory tail glands. The tail may be curled over the animal's back and aimed at a potential predator. A stream of sticky, viscous and irritating liquid is then fired at the target from one of the tail glands.

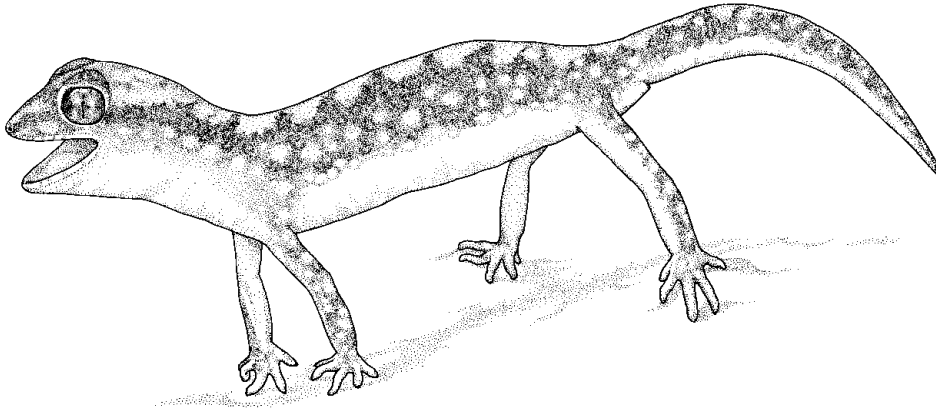


Figure 27.7 Defensive posture of *Diplodactylus damaemi*. (After photo by O. Rogge/ANT) [M. Cilento]

One of the more bizarre aspects of display adopted by members of *Strophurus*, involves flash colouration and is associated with typical defensive posture. *Strophurus spinigerus*, *S. intemedius*, *S. rankini*, *S. williamsi*, *S. strophurus* and certain populations of *S. ciliaris* have a bright blue mouth lining. This is revealed as part of their defensive posture, which involves stiffening the legs and arching the back. *Strophurus spinigerus* bulges its bright yellow eyeballs at the same time.

Diplodactyline and gekkonine geckos are able to drop their tails as a defensive strategy. This is used as a last resort, as it involves the loss of perhaps a third of the body weight, including valuable stored fat. Its loss may render females incapable of breeding in the following egg-laying season. While gekkonines are apparently able to economise in the degree of tail loss, since they have more numerous sheer points, diplodactyline tend to lose the whole tail. Generally, tail autotomy follows physical grasping of the tail by a predator. However, there is evidence to suggest that autotomy can occur as a result of shock alone (Greer 1989).

When geckos adopt their defensive posture, they often lash the tail from side to side. *Nephrurus* species temptingly sway the ball on the tail tip. Both behaviours may attract a potential attacker to the tail as a prelude to tail autotomy. However, in *Hemidactylus* and *Gehyra*, such tail lashing appears to be associated with aggression and territorial fighting.

Most Australian geckos are nocturnal, and avoid the extreme heat of the day by living either in spider holes or similar burrows. Some shelter under rock exfoliations, or under the bark of trees. Nevertheless, many of the arid-adapted gekkonine species are unable to avoid extreme temperatures in their particular habitat. *Gehyra variegata* remain active even when night-time temperatures reach 45°C (Henle 1990b). The critical thermal maximum for this species is 43.8°C (Spellerberg 1972a). Cloacal temperature was found to be more closely correlated with substrate temperature than with air temperature. Nevertheless, this does illustrate the very high temperatures these organisms can tolerate.

At Kinchega, New South Wales, *Gehyra variegata* are active at temperatures ranging from 7.5° to 45°C, during September to May (Henle 1990b). During the colder months, *Gehyra variegata* attempt to elevate body temperature by moving under the bark of trees or to the sunny side of fence posts (Bustard 1967a). From June until August, *Gehyra variegata* remain inactive and do not feed. They are unable to digest food at the lower temperatures.

In most geckos that have been studied, there is a differential activity pattern during the night. At sunset they become active and start to hunt, but as the ambient temperature drops they reduce their activity and remain inactive until warmed by the morning sun. During the daylight hours they shelter from the heat, but are capable of making forays from their sheltered position to take prey. Certain species of *Strophurus* may actively bask in the sun to achieve their optimal operating temperature (Greer 1989). However, this behaviour is unusual and even atypical for that genus.

When stressed by temperatures approaching their critical thermal maximum, geckos open their mouths and pant. Heatwole, Firth & Stoddart (1975) also observed fluttering of the gular area, presumably increasing air flow and evaporative cooling efficiency. Nevertheless, most terrestrial diplodactylines attempt to avoid thermal stress by sheltering in burrows and only emerge in the cool of the evening.

Areas of gekkonid reproductive behaviour for which some data are available are copulation and communal egg-laying. A male *Hemidactylus frenatus* grasps the neck of the female from the back while holding her chest with his front feet. The pair then twist their bodies around so that one of the hemipenes enters the female laterally. After copulation, the pair repeat the procedure using the other hemipenis. This behaviour has been reported for a number of gekkonid species (Greer 1989). Communal egg-laying is common in species of *Phyllodactylus*, *Heteronotia*, *Lepidodactylus*, *Phyllurus* and *Oedura* (Greer 1989). King (pers. obs.) has observed communal sites containing up to thirty eggs of *Phyllodactylus marmoratus*, often in areas where there was an absence of sheltered sites, and where all females might lay their eggs under one log. In areas where adequate cover was available, communal egg-laying was not generally observed, at least in *P. marmoratus*.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

The Gekkonidae are distributed throughout the mainland of Australia, except for the very south of Victoria, the Bass Strait islands and Tasmania. The seven genera of Gekkoninae within Australia can be subdivided into two groups. One group comprises genera that contain one or more endemic species: *Gehyra*, *Phyllodactylus*, *Heteronotia*, *Nactus* and *Cyrtodactylus*. The second contains the recently introduced Asian genera *Lepidodactylus* and *Hemidactylus*. Of the former group, *Gehyra* and *Heteronotia* are distributed throughout mainland Australia. *Cyrtodactylus* and *Nactus* occur as relic populations on Cape York Peninsula, presumably reflecting a Papua/New Guinean connection, whereas *Phyllodactylus* occurs in the far south of eastern and western Australia and on the Norfolk and Lord Howe island complexes. Both *Gehyra* and *Phyllodactylus* are well represented in other countries. *Gehyra* species occur in Madagascar, India, South-East Asia and the islands of the Pacific basin. *Phyllodactylus* is thought to be polyphyletic and occurs in Africa, South and North America and southern Europe. The Australian representatives of this genus have uncertain affinities. The genus *Cyrtodactylus* is one of the most successful and widespread gekkonines, and is found throughout south-eastern Europe, southern Asia and the Indo-Malayan Archipelago. *Heteronotia* is endemic to Australia and is morphologically very similar to *Cyrtodactylus* and *Nactus*.

The majority of gekkonine species are concentrated in the arid interior of the continent and in northern Australia. Generally, species within a genus are distributed allopatrically and occupy particular geographic regions defined by

belts of mountain ranges, river systems, soil types or deserts. In some instances, species are distributed parapatrically and sympatry can occur between species which usually occupy different niches.

The Diplodactylini (*Diplodactylus*, *Rhynchoedura*, *Strophurus* and *Crenadactylus*) are Australian endemics. Some genera in the Carphodactylini are found only in Australia (*Carphodactylus*, *Oedura*, *Nephrurus* and *Phyllurus*), some which are shared between Australia and other countries (*Rhacodactylus*, including *Pseudothecadactylus*, in Australia and in New Caledonia), and some which are found only in New Caledonia and the Loyalty Islands (*Eurydactylodes*, *Bavayia*) and New Zealand (*Naultinus*, *Hoplodactylus* and *Heteropholis*).

Within the Diplodactylini, species of *Diplodactylus* are generally distributed allopatrically in relation to their closest relatives, and if not, are sympatric but isolated in specific habitat types, or specialised niches. The monotypic genus *Crenadactylus* is found in the western half of the continent, and *Rhynchoedura* occurs in the arid areas of Australia.

Species within the Carphodactylini are divided into two morphological groups. One group includes the tropical rainforest specialist, *Carphodactylus* and the northern rock-dwelling genus *Rhacodactylus* (*Pseudothecadactylus*), which occur across the tropical north of Australia. The arboreal, or rock-dwelling, members of *Oedura* also belong to this group and are generally found throughout the northern two thirds of Australia, although southern species are known. The second group comprises members of *Phyllurus* and *Nephrurus*. The leaf-tailed *Phyllurus* are found in a narrow belt along the eastern coast of Australia, where they live in the lush forests and associated ranges, on rock outcrops or on trees. *Nephrurus* (including *Underwoodisaurus*), encompasses a variety of burrowing terrestrial species which inhabit most of arid Australia and generally occur on the western side of the Great Dividing Range.

Affinities with Other Groups

The Gekkonidae is closely related to the Pygopodidae and there is considerable support for a sister group relationship between the Pygopodidae and the gekkonid subfamily Diplodactylinae (Chapters 26, 28). Indeed, chromosomal data suggest that the Pygopodidae diverged from the Carphodactylini (King & Mengden 1990).

Affinities within the Taxon

Because of the extensive and complex distributional patterns of the gekkonid subfamilies (Fig. 27.8), the phylogenetic origins and relationships between them have proved contentious. The Sphaerodactylinae occurs in Central America, whereas the Diplodactylinae is found in Australia, New Zealand, New Caledonia and the Loyalty Islands, and thus represent regionally intact distributions. In contrast, the Eublepharinae is found in western North America, pockets occur in eastern and western Africa, the Middle East, India, a Japanese/Chinese isolate and a small area in South-East Asia. The Gekkoninae occurs circumglobally. However, this tends to be misleading, since much of this distribution is occupied by a few, highly successful genera and many of the more primitive genera are restricted to Africa. Such a distribution, with independent lineages occurring in different zoogeographic regions, could support the polyphyletic nature of this taxon.

Numerous complex arguments have been used to explain the subfamilial distribution pattern, including rafting and substantial migrations and extinctions. However, the most reasonable explanation for the present day distribution is a Gondwanan origin (Cracraft 1974; King 1987c) (for an alternate view, see Greer

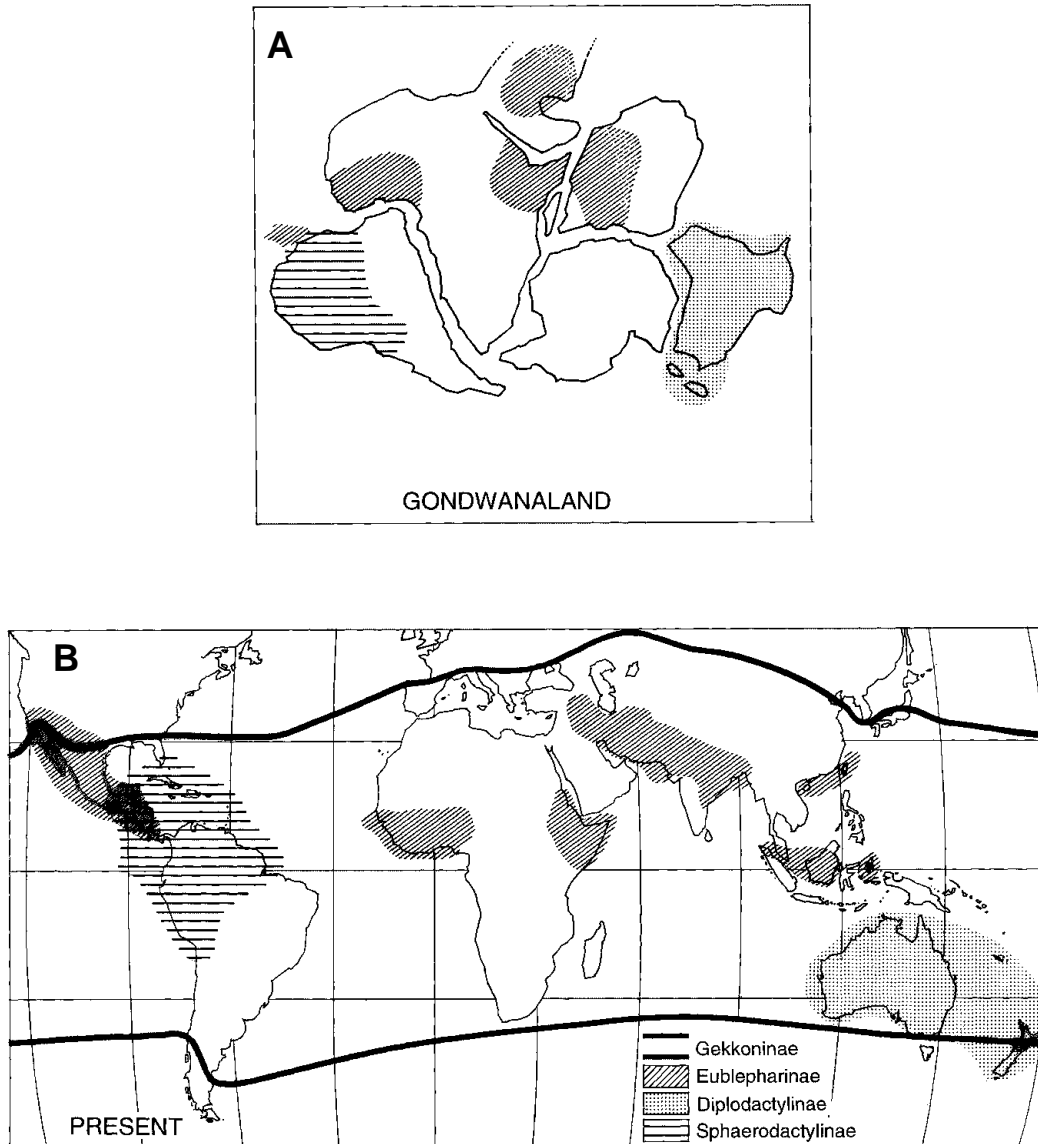


Figure 27.8 Distribution of the Gekkonidae. **A**, the presumptive Gondwanan distributions; **B**, present distributions. [W. Mumford]

1989). All of the higher taxa are present on the components of the ancient supercontinent including the primitive Gekkoninae, the Diplodactylinae (in a unified land mass), the Eublepharinae (in a series of isolates), and most of the Sphaerodactylinae. The non-Gondwanan components, such as the North American Eublepharinae and Sphaerodactylinae, can be accounted for by colonising radiations after contact between North and South America. This may equally apply to the Middle Eastern and Asian Sphaerodactylinae, which were probably established from colonising radiations of species subsequent to the contact of the Indian plate with the Asian land mass. This same argument could account for the distribution of the Gekkoninae in Europe and Asia after the contact of Africa with that region. Much of the world has been colonised by Kluge's (1967a) 'modern expanding dominants' such as the gekkonine genera *Gehyra*, *Hemidactylus*, *Cyrtodactylus* and *Lepidodactylus*. It is probable that the ranges of these species were expanded over much of their distribution by association with man's activities, rafting, or simply migration (Vanzolini 1968).

Storr's (1964a) view that *Gehyra* radiated throughout Australia from an Asian introduction, may be tempered by the highly complex distribution pattern of *Gehyra* within Australia, South-East Asia, the Pacific basin, India and Madagascar. Indeed, the greatest morphological and species diversity in this genus occurs within Australia and relatively few species of *Gehyra* are found in the other regions (King 1979, 1983a, 1984c; King & Horner 1989; Moritz 1986). The distributional evidence suggests that the ancestral *Gehyra* had a broad Australian distribution, before they were reduced to a series of relictual populations. Subsequent internal radiations of *Gehyra* recolonised the continent.

Similar arguments can be applied to *Cyrtodactylus*, *Heteronotia*, and *Phyllodactylus*. Thus, although *Phyllodactylus* is probably an artificial assemblage, it is worth considering that its distribution includes southern Africa, south-western North America, Central America and Norfolk Island. This distribution accords with a Gondwanan origin. Morphological similarity between Australian and Asian species of *Cyrtodactylus* and *Heteronotia* suggests a direct biogeographical relationship. The widespread Australian distribution of the complex clones of *Heteronotia*, and the considerable time required to establish these, suggests that this genus, too, may be a Gondwanan relict.

Chromosomal comparisons of the Gekkoninae (King 1987a) indicate that eight distinct chromosomal lineages are present in the 74 karyotyped species. Ancestral numbers in each group are $2n = 32, 34, 36, 38, 40, 42, 44$ and 46 respectively. These data suggest that the Gekkoninae is a polyphyletic assemblage and group comparisons reveal some agreement with the morphogroups, based on toe structure, proposed by Russell (1976). The species found within Australia have evolved from four independent ancestral karyomorph groups (King 1987a): *Hemidactylus* $2n = 46$, *Gehyra* and *Lepidodactylus* $2n = 44$, *Cyrtodactylus*, *Nactus* and *Heteronotia* $2n = 42$ and *Phyllodactylus* $2n = 40$, indicating a series of distinct evolutionary lineages within Australia. The division of the Gekkoninae into the tribes Gekkonini and Pytyodactylini on the basis of the presence or absence of a second ceratobranchial arch by Kluge (1987), cuts across the eight chromosomal groups of King (1987a) and the seven morphogroups which were defined on toe structure by Russell (1976, 1979), and adds weight to the inference that the Gekkoninae is polyphyletic.

The absence of Australian fossil material has precluded the confirmation of pre-Miocene Gekkoninae in this continent, although specimens dating back to the Cretaceous have been found in other regions (Estes 1970).

A Gondwanan origin for the Diplodactylinae has been confirmed by two types of evidence. First, a chromosomal analysis of the Diplodactylinae indicates that a highly derived karyomorph which has 19 fixed inversion differences is shared by members of the Carphodactylini in Australia (*Rhacodactylus*, including *Pseudothecadactylus*, and *Oedura*), in New Caledonia (*Rhacodactylus* and *Bavayia*), and New Zealand (*Hoplodactylus*). King (1987a, 1987c) argued that the most logical means by which the derived karyomorph could have established such an unusual distribution was when Australia, New Zealand and New Caledonia were in contact through Antarctica in the Gondwanan supercontinent 80 million years ago. Albumin immunological distances between species of *Phyllurus*, *Nephrurus*, *Oedura*, *Crenadactylus* and *Diplodactylus* also support a Gondwanan origin. The length of separation between the last three genera was estimated to be at least 66 million years (King 1987c), which predates the separation of Australia from Antarctica, and may be greater, but is beyond the resolution of the technique. The Diplodactylinae was thus established in Australia when it was part of the Gondwanan supercontinent (King 1987c).

Current understanding of the lower taxonomic categories of Australian Gekkonidae has been modified by analyses of population cytogenetics. A number of widely distributed and morphologically variable species have been recognised as species-complexes within the Gekkoninae and Diplodactylinae, although the impact has been far greater within the former.

Seven distinct chromosome races have been detected in the gekkonine species complex of *Gehyra australis* of northern and eastern Australia (Fig. 27.9; King 1983a, 1984c), four of which have been described as new species. A similar situation applies to the *Gehyra variegata-punctata* species-complex which is distributed throughout Australia. Twelve chromosome races have been detected (Fig. 27.9A; King 1979, 1984c; Moritz 1986). Many of these have been described as new species and some remain undescribed. These studies indicate that the earlier proposal by Storr (1964a) that *Gehyra* radiated through Australia after a relatively recent introduction from Asia is no longer appropriate, and that a Gondwanan origin is more likely.

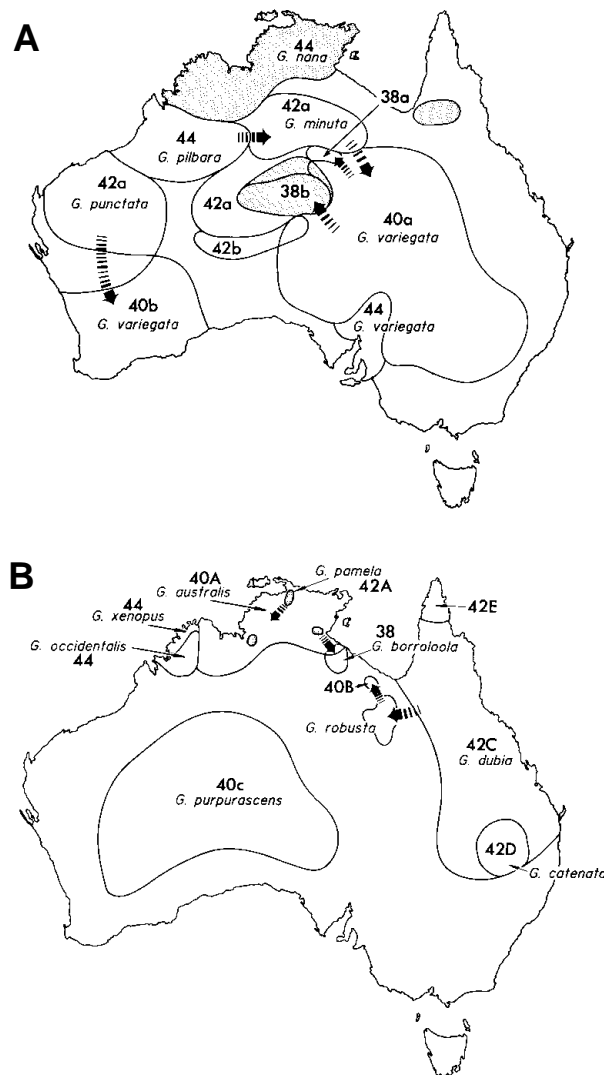


Figure 27.9 Distribution of chromosome races in *Gehyra*. **A**, the *Gehyra variegata-punctata* species complex: arrows indicate the probable direction of colonising radiations during speciation, and shading indicates the three regional distributions of *G. nana*; **B**, *Gehyra purpurascens*, and species and chromosome races of the *Gehyra australis* species complex. The three small shaded areas in the north refer to isolated populations of the $2n=42A$ chromosome race. [W. Mumford]

Gehyra species with the ancestral $2n=44$ karyomorph have a disjunct distribution. Isolated relictual populations of *G. nana* are found in central, north-western and north-eastern Australia (Fig. 27.9A). Although separated by thousands of kilometres, these are morphologically, chromosomally and electrophoretically indistinguishable (King 1984c; Moritz 1986). To have such a widespread distribution, the species must at one time have been distributed continuously. In addition, a form of *G. variegata* with $2n=44$ occurs as an isolate in the Flinders ranges of South Australia. A number of species which share the ancestral karyomorph are found in the north-west of Western Australia (Fig. 27.9A, B). King (1984c) argued that this high density of species with $2n=44$ in the north, together with their relictual populations in central and southern Australia, reflect a once continuous $2n=44$ Australian distribution, which was broken up into a series of isolates (Fig. 27.9A). Species with lower chromosome numbers ($2n=42$) appear to have colonised areas to the south of the northern $2n=44$ stronghold, whereas more recent radiations of $2n=40$ and $2n=38$ forms colonised areas further to the south, or had occupied particular mountain ranges in central Australia, thus recolonising most of the continent. A shift in habitat occurred away from the purely rock-dwelling $2n=44$ species, to arboreal forms and habitat generalists. In some instances, recently derived races have reverted back to specialist rock dwellers. No biochemical, molecular, or fossil data are available to provide an full perspective on the evolution of Australian *Gehyra*.

Phyllodactylus marmoratus is also a complex of chromosome races (King & Rofe 1976; King & King 1977). These include $2n=36$ ZZ/ZW, $2n=36$, $2n=34$ and $2n=32$ races which appear to have radiated into Western Australia from the east. Sequential chromosome fusions were established during the colonisation of Western Australia. The two Australian representatives of *Cyrtodactylus* are restricted in their distribution to Christmas Island and the northern area of Cape York Peninsula. Since two of the species are also found in New Guinea, these forms appear to be relics of population movements between New Guinea and Australia, which occurred when there was a land-bridge connection.

Species of *Heteronotia* are most similar in their morphology to *Cyrtodactylus* and *Nactus*, but are only found within Australia. Chromosomal, mitochondrial DNA and electrophoretic investigations of the *Heteronotia binoei* complex have revealed the presence of bisexual diploid chromosome races as well as triploid parthenogenetic forms (Moritz 1983; Moritz, Donnellan, Adams & Baverstock 1989a; Moritz, Brown, Densmore, Wright, Vyas, Donnellan *et al.* 1989b). Three $2n=42$ diploid chromosome races were recognised in bisexual populations and were regarded as biological species. These could be further subdivided into eight karyomorph groups by comparing their chromosome banding patterns. The parthenogenetic triploid species ($2n=63$) had 17 separate karyotypes, most of which were in three geographically widespread chromosomal forms. These were postulated to be the products of hybridisations between bisexuals. Two of the three parthenogens have very large central and western Australian distributions and appear to have actively colonised the area. The complexity of the situation is highlighted by the fact that 52 different genotypes are recognised within the triploid parthenogens (Moritz *et al.* 1989a).

The situation within the monophyletic Diplodactylinae contrasts with that in the gekkonine genera. Within the tribe Diplodactylini, Russell & Rosenberg (1981) separated a cluster of species groups in *Diplodactylus* (the *strophurus*, *michaelseni* and *elderi* groups) into the subgenus *Strophurus* on the basis of shared caudal-gland systems and the absence of certain osteological characters. This subgenus was elevated to generic status by Greer (1989). King (1987a) showed that the spiny-tailed members of *Strophurus* (*strophurus*, *ciliaris*, *intermedius*, *williamsi*, *taenicauda* and *spinigerus*) form a distinct cluster of chromosomally derived forms, distinguished by five pericentric inversions from

the ancestral diplodactyline karyomorph. However, *S. elderi* is chromosomally divergent from this complex. The chromosomes of the *S. michaelsoni* group are unknown. The members of *Strophurus* are generally arboreal species which are distributed allopatrically over the arid and tropical areas of Australia. Species of the *S. elderi* and *S. michaelsoni* complexes are specialised for living in spinifex clumps (*Triodia* sp.).

The genus *Diplodactylus* includes a widely distributed group of purely terrestrial species which are found throughout Australia in a range of habitat types. They shelter either under rocks or in burrows. Their distributions are regionally restricted and are associated with deserts, or belts of particular soil or vegetation types. They are chromosomally similar and share an ancestral acrocentric $2n=38$ karyotype, although some minor differences have been detected between species (King 1987a). An exception is the *Diplodactylus vittatus* complex which, like *Gehyra* and *Phyllodactylus*, was thought to be a widely distributed, morphologically variable species until King (1977a, 1987a) and Storr (1979b) identified a species complex, comprised of five allopatric chromosome races, some of which were subsequently described as species. *Rhynchoedura ornata* and *Crenadactylus ocellatus* are widely distributed, arid-adapted species. It is probable that *C. ocellatus* is a species complex, since it appears to occupy different habitat types in various parts of its range.

Generic subdivisions and radiations of the Carphodactylini appear to have occurred over a considerable time span. Bauer (1990) proposed that the subdivision of the Carphodactylini into *Carphodactylus*, *Nephrurus*, and *Phyllurus* was associated with the orogenic activities which produced the Great Dividing Range some 53 million years ago, isolating the different ancestral forms in eastern and western Australia. Thus Eocene desertification was associated with speciation in the arid-adapted, knob-tailed *Nephrurus*; the knobless *N. milii* and *N. sphyrurus* evolved independently, with the former attaining its extensive western distribution in the Miocene. Bauer (1990) reasoned that *Nephrurus* was isolated into northern and southern lineages by the central Australian continental lake system, which restricted *N. asper* and *N. wheeleri* to central, northern and north-western Australia. The smooth-skinned southern lineage of *Nephrurus* subsequently invaded the entire arid region of Australia.

Division of the *Phyllurus* and *Carphodactylus* lineages has been attributed to Pleistocene vegetational changes and the remnants of the continental lake system (Bauer 1990). The subdivision of *Phyllurus* species into a series of linear isolates is also attributed to post-Pleistocene changes in sea level and rain forest fragmentation.

The northern Australian *Rhacodactylus* (*Pseudothecadactylus*) provide some areas of contention. Bauer (1990) argued that these forms could not have been found in Australia before the opening of the Tasman sea (at least 80 million years ago), because they appear to be amongst the most recently derived forms in his cladistic analysis. He invoked the colonisation of northern Australia by late Tertiary rafting from New Caledonia to explain their presence in Australia. Bauer supposed that the subdivision of the Carphodactylini into padless and padded groups was associated with enforced isolation associated with the Tasman Sea. This is unnecessary if the padded Carphodactylini had radiated throughout Australia, New Zealand and New Caledonia when they were still a part of the Gondwanan supercontinent (Fig. 27.8). Moreover, the paucity of padded Carphodactylini within Australia can be explained by the fact that *Oedura* are in reality carphodactylines. Such an action reconciles the shared derived chromosomal similarity between *Oedura* species and *Rhacodactylus*, *Bavayia* and *Hoplodactylus* (King 1987a). It explains also the great similarity in osteology, musculature and form of the toepads in *Rhacodactylus*, *Oedura*, and *Bavayia* (Russell 1979). Kluge (1967a) separated the Carphodactylini from Diplodactylini by the presence of numerous rows of pre-anal pores in certain

Carphodactylini. These have been extensively modified in *Nephrurus*, *Phyllurus* and *Bavayia sauvagei* (Bauer 1990), and cannot be construed as a reliable character. Indeed, they may have been lost secondarily in *Oedura*.

The genus *Oedura* comprises thirteen species and is distributed throughout Australia in discrete allopatric units. This genus has been placed in the Carphodactylini because of its great morphological and chromosomal similarity to the highly derived *Rhacodactylus* (*Pseudothecadactylus*). Species are either saxicoline or arboreal, and *O. filicipoda* is thought to be cavernicoline. If sympatric, *Oedura* species are generally separated by habitat specialisation. Kluge (1967b) suggested that *Oedura* was derived from a *Diplodactylus*-like terrestrial ancestor because of the similarity of digit structure. However, Russell (1979) argued that there is little justification for this claim, since the lamellae on the proximal portions of the digits are controlled by different mechanisms from those in *Diplodactylus*, suggesting an arboreal ancestor.