



# FAUNA *of* AUSTRALIA



## 31. FAMILY SCINCIDAE

**Mark N. Hutchinson**



Pl. 6.1. *Trachydosaurus rugosus* (Scincidae): very common and easily recognisable by its short, rounded tail and large, coarse scales; dry habitats in southern and eastern Australia. [H. Cogger]



Pl. 6.3. *Cyclodomorphus gerrardii* (Scincidae): a nocturnal insectivore, found mainly in wet temperate to tropical forests in eastern Australia. [H. Cogger]





Pl. 6.4. *Tiliqua occipitalis* (Scincidae): found in a variety of dry habitats in southern Australia from New South Wales to the west coast. [J. Wombey]



Pl. 6.5. *Egernia stokesii* (Scincidae): seen singly here, this species typically forms 'family' groups of all ages; among rocks and boulders in central and western Australia. [H. Cogger]



Pl. 6.6. *Gnypetoscincus queenslandiae* (Scincidae): a nocturnal species that hides under rotting logs during the day; endemic to the wet tropics.  
[H. Cogger]

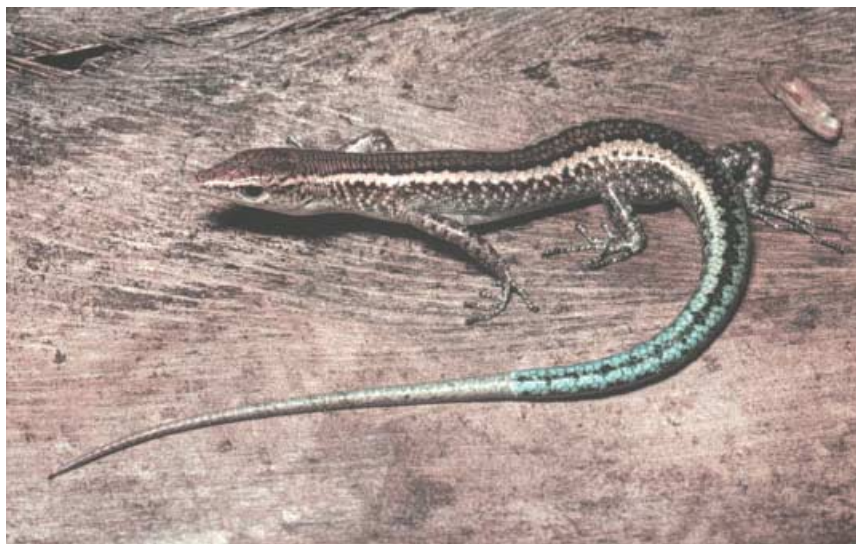


Pl. 6.7. *Carlia rhomboidalis* (Scincidae): occurs in rainforest, stream margins and in similar moist habitats in north-eastern Queensland.  
[J. Wombey]





Pl. 6.8. *Glaphyromorphus nigricaudis* (Scincidae): a nocturnal species, found in coastal dunes to marginal rainforest in Cape York and Torres Strait Islands.  
[H. Cogger]



Pl. 6.9. *Cryptoblepharus egeriae* (Scincidae): an arboreal species that forages in the ground litter; endemic to Christmas Island, Indian Ocean.  
[H. Cogger]



Pl. 6.10. *Morethia ruficauda* (Scincidae): uses its bright tail to distract predators; found in dry to arid areas near streams and water-holes in central and north-western Australia. [H. Cogger]



Pl. 6.11. *Ctenotus taeniolatus* (Scincidae): an eastern Australian species ranging from coastal heathland to montane forests. [J. Wombey]





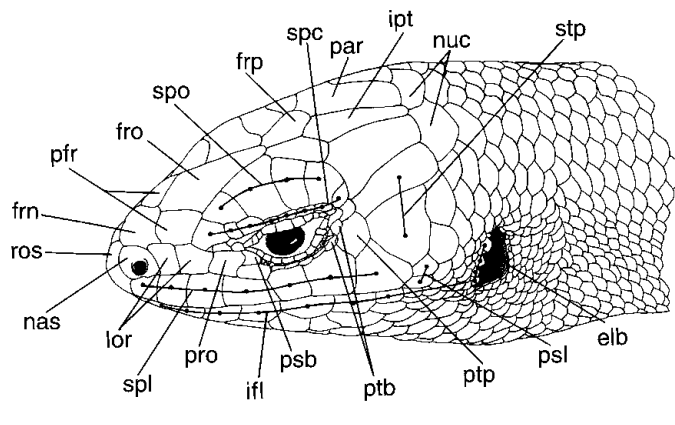
Pl. 6.12. *Lerista punctatovittata* (Scincidae): lacks forelimbs and has reduced hindlimbs; burrows in dry, open forests, inland south-eastern Australia.  
[H. Cogger]



Pl. 6.13. *Anomalopus verreauxi* (Scincidae): the paler of two colour morphs; a species with strongly reduced forelimbs and tiny, styliform hindlimbs; occurs in a pale and found in humid coastal and montane habitats, central east coast.  
[J. Wombey]

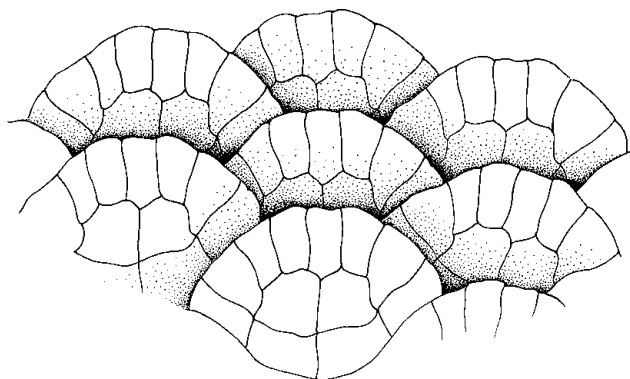
## DEFINITION AND GENERAL DESCRIPTION

The family Scincidae is the largest of the sixteen or so families of lizards. Scincids (skinks) belong to the infraorder Scincomorpha, a monophyletic group of families whose members tend to be elongate and have relatively long-snouted and somewhat flattened skulls, in which the upper temporal opening is usually reduced or lost. The head is usually covered with enlarged plates, termed head shields (Fig. 31.1), and osteoderms are frequently present in some or all scales.



**Figure 31.1** Head of a skink, *Egernia whitii*, showing the enlarged shields and their nomenclature. **elb**, ear lobules; **frn**, frontonasal; **fro**, frontal; **frp**, frontoparietal; **ifl**, infralabials; **ipt**, interparietal; **lor**, loreals; **nas**, nasal; **nuc**, nuchals; **par**, parietal; **pfr**, prefrontals; **pro**, preocular; **psb**, presubocular; **psl**, postsupralabials; **ptb**, postsubocular; **ptp**, primary temporal; **ros**, rostral; **spc**, supraciliaries; **spl**, supralabials; **spo**, supraoculars; **stp**, secondary temporals. [J. Thurmer]

Typically scincids are slightly to markedly elongate lizards with moderate to short limbs and glossy cycloid scales, reinforced by characteristic compound osteoderms (Fig. 31.2). The partially to well-developed secondary palate is a distinctive feature of the skull. It is formed primarily by development of a novel lamina of the palatine bone on each side, which together essentially floor and prolong the choanal passage. In some species the palatal rami of the pterygoids extend the secondary palate posteriorly to about the level of the back of the tongue. Other osteological characteristics include paired premaxillae, descending processes from the parietals which meet the epipterygoids and an enlarged labial coronoid process of the dentary.



**Figure 31.2** Osteoderms from the dorsal scales of *Eremiascincus fasciolatus* showing the compound structure characteristic of skinks. [J. Thurmer]



The inner ear has an accessory inertial body, the culmen (Wever 1978), which modulates hair cell sensitivity, and largely replaces the tectorial membrane, which is vestigial in skinks. Preanal and femoral pores are absent. The tail is usually long and tapering and, except for a very few species, can be shed and regenerated. The tongue is broad, has an arrowhead-shaped tip and is covered with serrated scales (Schwenk 1988). Many species have reduced limbs, sometimes accompanied by a loss of digits; nine Australian species are completely limbless.

Skinks are typically diurnal, terrestrial and active on the surface of the ground or low perches; a significant number are secretive to fossorial, carrying out most activities within leaf litter or underground. Some species are climbers, living in trees or on rocks. Skinks are found in all terrestrial ecosystems, from tropical forests to desert sand dunes and alpine habitats. A few are semiaquatic, able to swim and hide under water to escape predators (Daniels 1990), and some species inhabit the intertidal zone, on rocky shores, beaches or mangroves.

Though the family is cosmopolitan, it has centres of diversity in the Australian, Ethiopian and Oriental Regions and is relatively poorly represented in the Neotropic and Holarctic Regions. The family is still expanding, as new species are described. Halliday & Adler (1986) provided an estimate of 1275 species in 85 genera, although recent generic rearrangements have increased the latter figure. In Australia and its external territories there are 325 species in about 32 genera (as of 12 December 1990). The Australian genera form three monophyletic assemblages, informally termed the *Egernia* Group, the *Eugongylus* Group and the *Sphenomorphus* Group (Greer 1979b). The taxa comprising these groups are shown in Table 31.1.

## HISTORY OF DISCOVERY

The first Australian skinks to be described scientifically were among the animals treated by White (1790). White gave descriptions of two species that he placed in the Linnaean genus *Lacerta*, the genus which included all fully limbed, non-gliding lizards. These two species are now known as *Tiliqua scincoides*, the eastern bluetongue, and *Ctenotus taeniolatus*, the coppertail skink.

British and French collectors (notably the 1800–1804 Baudin expedition; Bonnemains, Forsyth & Smith 1988), and the European museum taxonomists who described the collections, steadily increased the number of species known from Australia. Twenty-one species of Australian skinks were listed by Duméril & Bibron (1839), representing twelve modern genera. At this time the concept of a family Scincidae began to emerge, although Duméril and Bibron also placed other degenerate-limbed and skink-like taxa (amphisbaenians and diploglossine anguids for example) with their ‘Scincoidiens’. In those pre-Darwinian times, much taxonomic weight was placed on easy-to-score external features, such as degree of limb degeneration; thus the three species of *Lerista* known at the time (*L. bougainvillii*, *L. lineata* and *L. praepedita*) were placed in three separate genera and two different subfamilies.

The century’s most significant work on reptiles was George Boulenger’s British Museum catalogues, published in three volumes between 1885 and 1887. In Volume III (Boulenger 1887), 78 species of Australian skinks were listed. These species, mostly still valid, represent 23 of the genera currently recognised. Boulenger’s family and generic definitions were relatively broadly based on combinations of both internal and external anatomical features, and easily accommodated additional species as they became known. As a result, Boulenger’s scheme became widely accepted for the next fifty years, and was still in use in modified form long afterwards, for example, in Eric Worrell’s (1963b) *Reptiles of Australia*.

**Table 31.1** Distribution of skinks in the Australian zoogeographic subregions. In addition, the genera *Lygosoma* and *Oligosoma* occur on Christmas Island and Lord Howe Island respectively.

Genera	Number of species	Torresian	Eyrean	Bassian
<i>Egernia</i> Group				
<i>Cyclodomorphus</i>	4	2	2	2
<i>Egernia</i>	29	6	12	10
<i>Tiliqua</i>	10	1	4	5
<i>Eugongylus</i> Group				
<i>Bartleia</i>	1	1	–	–
<i>Bassiana</i>	3	–	–	3
<i>Carlia</i>	21	22	2	2
<i>Cautula</i>	1	1	–	–
<i>Cryptoblepharus</i>	7	6	4	2
<i>Emoia</i>	2	2	–	–
<i>Eugongylus</i>	1	1	–	–
<i>Lampropholis</i>	11	9	–	4
<i>Lygisaurus</i>	5	5	–	1
<i>Menetia</i>	6	5	3	1
<i>Morethia</i>	8	3	6	4
<i>Nannoscincus</i>	1	–	–	1
<i>Niveoscincus</i>	8	–	–	8
<i>Proablepharus</i>	3	1	3	–
<i>Pseudemoia</i>	4	–	1	4
<i>Sphenomorphus</i> Group				
<i>Anomalopus</i>	7	6	–	4
<i>Calypotis</i>	5	4	–	1
<i>Coeranoscincus</i>	2	2	–	–
<i>Ctenotus</i>	86	30	55	8
<i>Eremiascincus</i>	2	2	2	–
<i>Eulamprus</i>	10	6	–	5
<i>Glaphyromorphus</i>	11	12	–	1
<i>Gnypetoscincus</i>	1	1	–	–
<i>Hemiergis</i>	5	–	3	5
<i>Lerista</i>	62	12	54	6
<i>Notoscincus</i>	3	1	2	–
<i>Ophioscincus</i>	3	3	–	–
<i>Saiphos</i>	1	1	–	1



So successful was Boulenger's taxonomy that systematic studies of Australian skinks slowed post-Boulenger. Research on skinks worldwide tended to shift towards anatomical studies, taking a stable taxonomy for granted. Notable amongst these were several on osteology (Siebenrock 1892, 1895; Kingman 1932; Haas 1936; El Toubi 1938; Brock 1941), embryology (Rice 1920) and palatal anatomy (Busch 1898). During the first half of the twentieth century, the major taxonomic advances centred on attempts to break down Boulenger's unwieldy genus *Lygosoma* into more natural genera (Smith 1937). The subfamilial and generic scheme which resulted (Mittleman 1952) was not widely or fully accepted, since many of the genera appeared to be based on trivial external features, so that in subsequent years various *ad hoc* combinations of Boulenger's, Smith's and Mittleman's taxonomic systems appeared in the literature.

A resurgence of interest in skink systematics in Australia began in the mid 1960s, with publications by Fuhn (1969) and Greer (1967; Greer & Parker 1968), which showed that the skink secondary palate was far more variable in its detailed osteology than had been realised and that these variations were useful in indicating phylogenetic relationships. At the same time, Storr (for example, Storr 1968b, 1969) began to revolutionise alpha taxonomy, showing that the Australian skink fauna is far richer in species than was indicated by the then current taxonomy. Storr (1964b) also provided a benchmark review on the biogeography of Australian skinks, summing up a view that followed from the taxonomy and static continent orthodoxy of the time.

Between 1965 and 1990, the number of skink genera recognised in Australia grew from about 14 to 32 and the number of species from approximately 140 to over 300. The fauna is now regarded as highly endemic, and characteristic not just of the Australian region but of the Australian continent. Few Australian genera extend beyond southern New Guinea, and most of the diversity seems to have developed *in situ*, rather than having derived from multiple invasions. The recent book by Greer (1989) summarised the state of knowledge for many aspects of the natural history and morphology of the Australian skinks, and reviewed the phylogenetic relationships of the fauna as seen by the most influential student of scincid relationships over the last twenty years.

## MORPHOLOGY AND PHYSIOLOGY

### External Characteristics

Australian skinks range in size from an adult snout-vent length of 35 mm in *Menetia* to over 350 mm in *Tiliqua* (maximum 371 mm for *T. scincoides intermedia*; Shea, in Greer 1989). Adult mass in these same genera ranges from 0.4 g to over 1000 g (Henle 1989a; Hutchinson pers. obs.).

Most skinks have a small head which is not delineated from the neck, a body square in cross-section with well-developed limbs bearing graduated toes ( $4 > 3 > 2 = 5 > 1$ ) and a long tapering tail (usually more than 120% of snout-vent length when original). Several major variations occur (Pl. 6). In fossorial, litter or sand-swimming species, the head becomes relatively smaller, narrower and wedge-shaped. Associated with this is elongation of the body and reduction of limb size and often digit number. Examples of this trend include members of the genera *Lerista* (Pl. 6.12; Greer 1987c, 1990a) and *Anomalopus* (Pl. 6.13; Greer & Cogger 1985). Although relatively few skinks are truly arboreal or saxicoline, those that are share a morphology which includes a broad and flattened head and body, and long, strong and sharply clawed limbs and toes used for climbing. Some species of *Egernia*, members of the *E. whitii* and *E. major* species groups, are unusually robust with a deep head, stocky body and muscular appendages.

Another group of giant skinks, the genus *Tiliqua*, has a peculiar body form which combines a large, heavily built head and bulky, flattened body with very short, seemingly weak limbs and a tail shorter than the body (Pl. 6.4).

Sexual dimorphism in size and proportions is usual in skinks, although often only subtly apparent (Hutchinson & Donnellan 1988, 1992; Hutchinson, Robertson & Rawlinson 1989; Simbotwe 1985; Yeatman 1988). In general, females have longer bodies than males, and proportionately narrower heads and shorter appendages. Often, especially in elongate species, females average higher presacral vertebral counts than males. Examples are *Lerista* (Greer 1987c), *Pseudemoia* (Hutchinson & Donnellan 1992), *Tiliqua* (Shea pers. comm.) and those in Greer (1989, Table 4).

Colour patterns are extremely variable. A trend is for longitudinal patterns in terrestrial species, especially grass-dwellers, while transverse barring is much rarer, usually in secretive shade or litter-dwelling species. A combination of grey-brown dorsum and blackish sides forms a common colour pattern for surface-dwelling woodland species (Greer 1989, Fig. 59). Climbing species, especially rock dwellers, are usually spotted or mottled, with little trace of linear pattern elements (Covacevich 1984). Burrowers or cryptozoic species tend to be weakly patterned but may have contrasting or bright colours on the tail, belly or head. Colour change as a result of melanocyte expansion/contraction as occurs in iguanian and gekkotan lizards is not present, although longer term (measured in days rather than minutes) changes in degree of pigmentation have been suggested to occur in *Lampropholis* (Greer 1989).

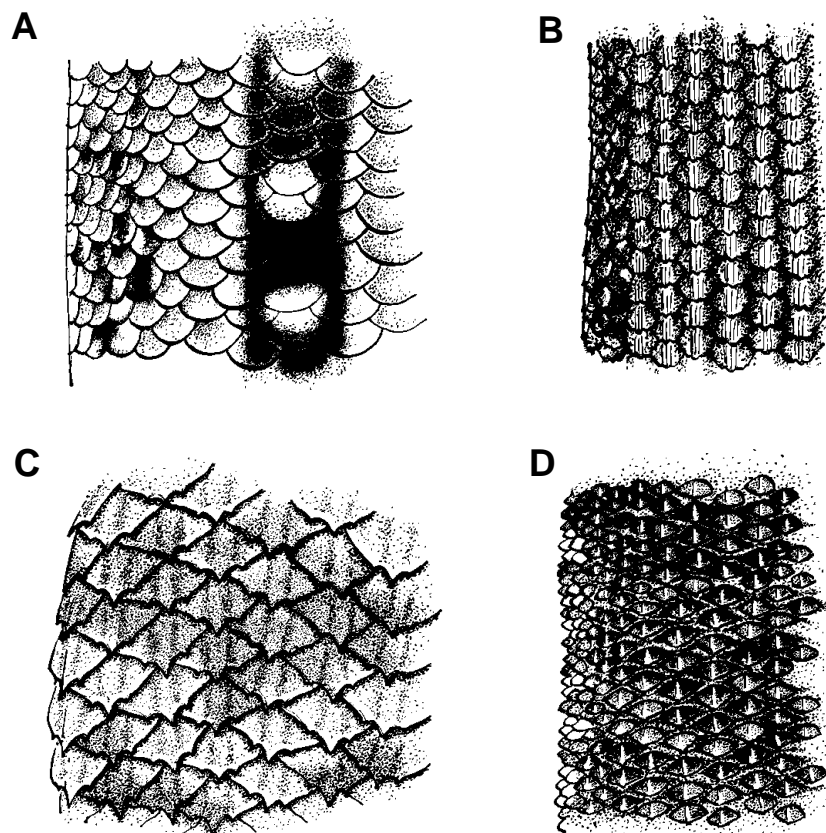
Sexual dichromatism is not generally a feature of Australian skinks, but does occur in some *Eugongylus* Group genera. The most striking dichromatism occurs in the genus *Carlia* (Covacevich & Ingram 1975; Ingram & Covacevich 1989) in which males of most species develop bright lateral colouring, usually red, green or blue (sometimes in combination), sometimes with black pigment patches on the neck or chin for further emphasis, while females retain the cryptic pattern of a dark, sometimes light-edged lateral stripe. Other genera exhibit dichromatism. Males of *Lygisaurus* develop a red flush on the tail (Ingram & Covacevich 1988). In *Bassiana*, *Morethia*, *Pseudemoia* and *Proablepharus*, males of most species develop red pigmentation on the throat or belly (Pl. 6.10; Donnellan & Hutchinson 1990; Greer 1980b, 1982; Hutchinson 1990a; Hutchinson, Donnellan, Baverstock, Krieg, Simms & Burgin 1990). Males of at least some species of *Menetia*, a genus in which relationships are obscure, develop bright yellow to orange ventral colouring (Greer 1989; pers. obs.). Populations of *Lampropholis delicata* from Queensland (Greer 1989) and Eyre Peninsula, South Australia (Hutchinson pers. obs.) show a pattern dimorphism, in which females have a white midlateral line which is absent in males.

### Body Wall

Scale size in skinks is relatively large, with generally fewer than 40 longitudinal rows of body scales. All scales are supported by compound osteoderms (Fig. 31.2), those on the head, especially the frontal, interparietal and parietals often becoming fused to underlying skull bones during postembryonic ontogeny.

The numbers of longitudinal rows of scales along the body are correlated to some extent with mode of life. Reduced-limbed species and litter- or grass-dwelling species tend to have relatively few rows (less than 28) of relatively large scales, while climbing species, especially rock dwellers, have increased numbers (often 34 or more rows) of small scales (Fig. 31.3). This may enhance, respectively, 'armour-plating' of the burrowing/litter dwelling species and softness and flexibility of the skin, facilitating entry into crevices, in the climbers.





**Figure 31.3** Scale variation in skinks. **A**, typical smooth cylcoid scales of *Egernia whitii*; **B**, keeled, or carinate, scales of *Carlia jarnoldae*; **C**, spiny scales of *Egernia depressa*; **D**, juxtaposed, tubercular scales of *Gnypetoscincus queenslandiae*.  
[K. Bowshall-Hill]

Macroscopically, scale surfaces of skinks are usually smooth, often with a matt surface dorsally but polished and highly glossy laterally and ventrally (and dorsally in cryptozoic taxa). Keels or striations are present in some taxa, often variably developed in congeneric species. In a few species, the keels are pronounced, such as in some *Carlia* (Ingram & Covacevich 1989). In the *Egernia cunninghami* species group (Horton 1972) they are extended into backward-facing spines which are longest and strongest on the tail. *Gnypetoscincus queenslandiae* has bizarre, pointed, juxtaposed scales, giving it a coarse, atypical skin texture. A second, somewhat similar, spiny-scaled skink taxon has been discovered recently in south-eastern Queensland (Covacevich pers. comm.). Scalation modified in a similar way is also found in some non-Australian genera (*Tribolonotus* and *Fojia*), both of which inhabit rainforest areas, either beside streams or within saturated rotting logs (Cogger 1972; Greer & Simon 1982; McCoy 1980). The shingleback, *Tiliqua rugosa*, has massive, ridged dorsal scales with thick osteoderms that effectively form an armoured shield (Pl. 6.1). A study of the micro-ornamentation of lizard scales by Renous & Gasc (1989) included a number of skinks and showed that the ornamentation varies according to the degree of contact between a region of the body surface and the substrate. Micro-ornamentation of the skin has been used in some reptiles as a phylogenetically informative character, but has not yet been used in skinks.

The structure of the dermis in squamates and the control of skin-shedding was reviewed by Maderson (1984). As in other squamates, skinks periodically shed a complete outer epidermal layer. It is shed in several large patches, and does not form a coherent 'ghost' as it does in snakes and gekkotan lizards.

The lining of the body wall is distinctively pigmented in a way which reflects habits and mode of thermoregulation. Diurnal, surface-active skinks have a black lining to the cranial and body cavities, but this is absent in nocturnal or fossorial species (Greer 1989). The black colouring has been explained by Porter (1967) as providing an internal shield blocking high energy ultra-violet radiation which is able to penetrate lizard skin and could cause tissue damage.

### Skeletal System

The typically scincomorphan skull is broad and flattened, with a reduced upper temporal opening and a relatively long snout. The family as a whole shows considerable variation, so this discussion will be confined to Australian taxa. King's (1964) study on *Eulamprus quoyii* is the only one which has attempted to describe the entire skeleton of an Australian skink. Partial descriptions, especially of the skull, of numerous species have been published, but no overall review of the trends and major patterns of variation is available for the Australian fauna.

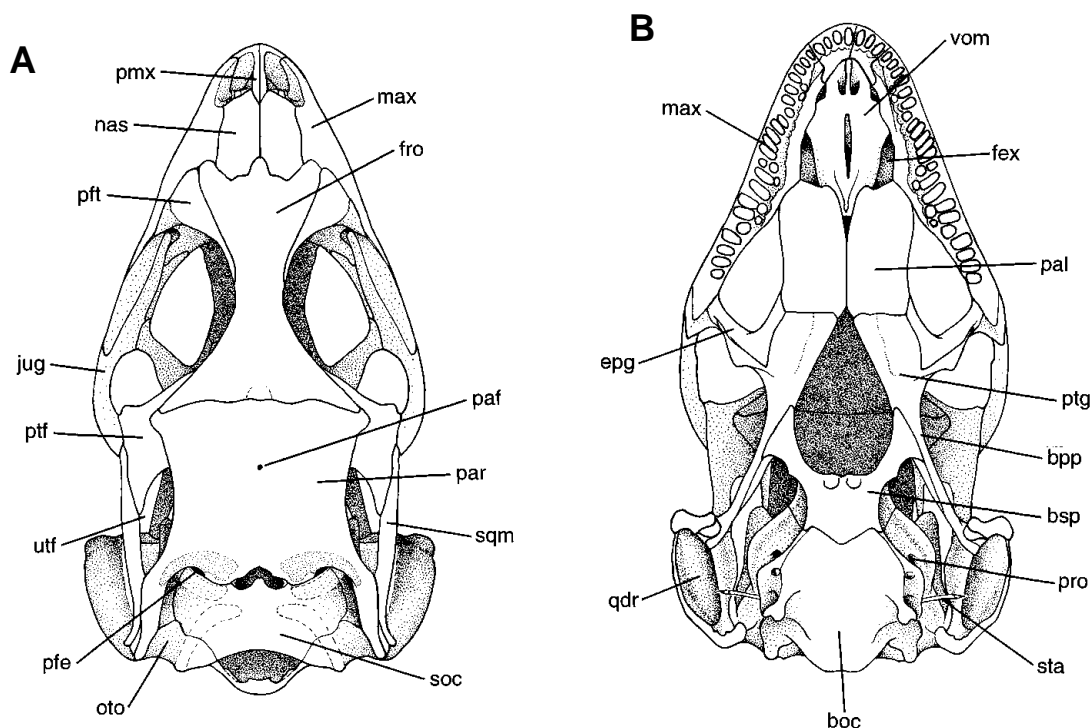
The skull of a relatively unmodified skink, *Ctenotus leae*, is shown in Figure 31.4 and can be taken as typical in many respects of the structure of a terrestrial, surface-dwelling skink. As in all Australian species, the premaxillae are paired and asymmetric, the right premaxilla bearing one more tooth than the left; symmetrical premaxillary counts are seen in a few taxa, for example most *Egernia* (Greer 1979b). Premaxillary tooth counts tend to be stable within related groups but vary between groups, thus providing a useful taxonomic character (Greer 1974, 1979b). In *Ctenotus* the paired nasals are not in contact with the prefrontals, the most common condition in skinks (Estes, De Queiroz & Gauthier 1988), although the complementary arrangement with a nasal-prefrontal suture is often seen (for example, most genera in the *Eugongylus* Group). The frontal forms the dorsal border of the orbit of most skinks, but in some species with reduced limbs, the pre- and postfrontals are closely apposed or in contact along the orbital margin, apparently correlated with reduction of the relative size of the orbit (Greer & Cogger 1985; Shea 1990). The lacrimal and postorbital are both absent in *Ctenotus leae*, and are at best only small in most lygosomines that retain them. Even when well developed, as in *Hemiergis*, the postorbital is excluded from the orbit by contact between the postfrontal and the jugal.

Members of the genus *Ctenotus* generally retain an upper temporal fenestra which is large for a lygosomine; most Australian taxa have a reduced or rudimentary fenestra as a result of closure by the posterior expansion of the postfrontal plus lateral expansion of the parietal. The post-temporal fenestrae are open in larger skinks. However, they are closed in small species, especially burrowers, and the posterior margin of the parietal is contiguous with the anterior margin of the supraoccipital (Rieppel 1984a).

The single parietal is pierced by a parietal foramen. In a minority of species, the foramen closes as the animal ages, such as in some *Egernia* (Hutchinson pers. obs.). The squamosal in skinks is said to contact the jugal, or nearly do so (Estes *et al.* 1988), but often terminates well short of the jugal in many Australian lygosomines. A small, slender supratemporal is wedged between the squamosal, laterally, and the extremities of the processus parietalis and crista prootica, medially (Rao & Ramaswami 1952).

In lateral view, most of the snout is formed by the maxilla, which extends posteriorly to form most of the lower orbital border. The dorsal ramus of the maxilla may contact the frontal (as in *C. leae*) or may be excluded because of contact between the prefrontal and nasal. The paired septomaxillae are mostly hidden within the nasal cavity but are visible as the posterior floor and internal lining of the external nostril.





**Figure 31.4** Skull of *Ctenotus leae* **A**, dorsal view; **B**, ventral view. **boc**, basioccipital; **bpp**, basipterygoid processes **bsp**, basisphenoid; **ect**, ectopterygoid; **fex**, fenestra exochoanalis; **fro**, frontal; **jug**, jugal; **max**, maxilla; **nas**, nasal; **oto**, otoccipital; **paf**, parietal foramen; **pal**, ventral lamina of palatine; **par**, parietal; **ptf**, post-temporal fenestra; **pft**, prefrontal; **pmx**, premaxilla; **pro**, prootic; **ptg**, pterygoid; **qdr**, quadrate; **soc**, supraoccipital; **sqm**, squamosal; **sta**, stapes; **utf**, upper temporal fenestra; **vom**, vomer. [J. Thurmer]

On the palate, the vomers are fused in *C. leae*, as in most lygosomines; the members of the *Egernia* Group retain paired vomers. The fissure (*fenestra exochoanalis*) which separates the vomer laterally from the maxilla is closed in life by a vomerine epithelial pad and the choanal opening has shifted posteriorly (see below). The postero-ventral ends of the vomers bear short tooth-like processes, which are fused into a triangular wedge in most lygosomines but posteriorly lengthened in *Egernia* (Hutchinson 1981; Greer 1989). In ventral view, only the ventral laminae of the palatines are visible in *Ctenotus* as in most Australian skinks, the exception being species of *Egernia* in which the ventral laminae do not meet medially in most species, leaving a cleft in the palate, through which the dorsal laminae can be seen. In the *Eugongylus* Group the postero-medial corner of the palatine is drawn into a prong which extends into the interpterygoid vacuity (Greer 1974; Hutchinson *et al.* 1990).

The palatal ramus of the pterygoid is only slightly expanded in *C. leae*, as in most *Ctenotus*, and makes virtually no contribution to the secondary palate. However, in many skinks of the *Sphenomorphus* Group the palatal rami of the pterygoids are expanded and in medial contact, and prolong the palate to the level of the basipterygoid articulation. In some members of both the *Eugongylus* and *Sphenomorphus* (for example, *Ophioscincus*, Greer & Cogger 1985; *Saiphos*, Greer 1983b) groups, the pterygoids are not in contact on the palate but send postero-medial prongs into the interpterygoid vacuity (forming the so-called beta palate configuration; Greer & Parker 1968; Greer 1974, 1979b). The function of this structure was suggested by Greer & Parker (1968) to be a 'catch' which prevents excessive antero-posterior movement of the pterygoids on the basipterygoid processes. However, in life the area over which the pterygoids

could apparently move is filled with cartilage so that little displacement is possible. It appears more likely that the pterygoid prongs serve to extend the secondary palate further to the rear; as the palate expands posteriorly it must grow around the basipterygoid cartilage, creating the hooked shape of the pterygoid extension which supports the palatal mucosa. Pterygoid teeth, which occur in several groups of skinks (Kingman 1932; Greer & Parker 1968), are not found in any Australian species.

The neurocranium consists of the sphenoid, basioccipital, supraoccipital and paired otoccipitals and prootics (Rao & Ramaswami 1952; Skinner 1973). In most Australian species all bones fuse during postembryonic ontogeny, so that the sutures between the bones become difficult to see or are obliterated.

Other modifications of the skull involve the proportions of the skull as an entire unit, as well as alterations to individual bones. A consistent trend in burrowing and other reduced-limbed taxa is for the skull to become smaller, relative to body size, and for the dermal elements to become more closely applied to the neurocranium. The lateral skull bones, especially the jugal and squamosal become narrowed. As a result, the skull is longer and narrower in burrowing taxa than in surface-dwellers. The anatomical changes involved have been reviewed by Rieppel (1984a) for lizards in general, and by Greer & Cogger (1985) for several reduced-limbed Australian genera.

The mandible (Fig. 31.5) primitively retains the full complement of bones found in lepidosaurs, except that the articular is indistinguishably fused with the prearticular during early embryology (Skinner 1973). The surangular and the prearticular fuse progressively during postembryonic ontogeny. The suture on the labial surface of the mandible becomes obliterated first, followed by the suture on the lingual surface, and the anteriormost part of the suture, below the coronoid, usually persists. The angular is greatly reduced in most of the *Eugongylus* group, and is absent in some taxa (*Cryptoblepharus*, some *Carlia*). The splenial is also reduced to a greater or lesser extent in the *Eugongylus* Group. The groove for Meckel's cartilage is exposed on the lingual face of the dentary in most members of the *Sphenomorphus* Group, but is completely lost by overgrowth of the dentary in the other two Australian lineages, as well as in some *Sphenomorphus* Group taxa (*Notoscincus*, Greer 1979b; some *Lerista* and *Ctenotus*, Hutchinson pers. obs.). The retroarticular process varies greatly in shape, from the primitive (scincine and cordylid) condition showing a prominent inflection (Estes *et al.* 1988), which is largely retained in the *Egernia* and *Eugongylus* Groups, to the parallel-sided, often slender process characteristic of the *Sphenomorphus* Group.

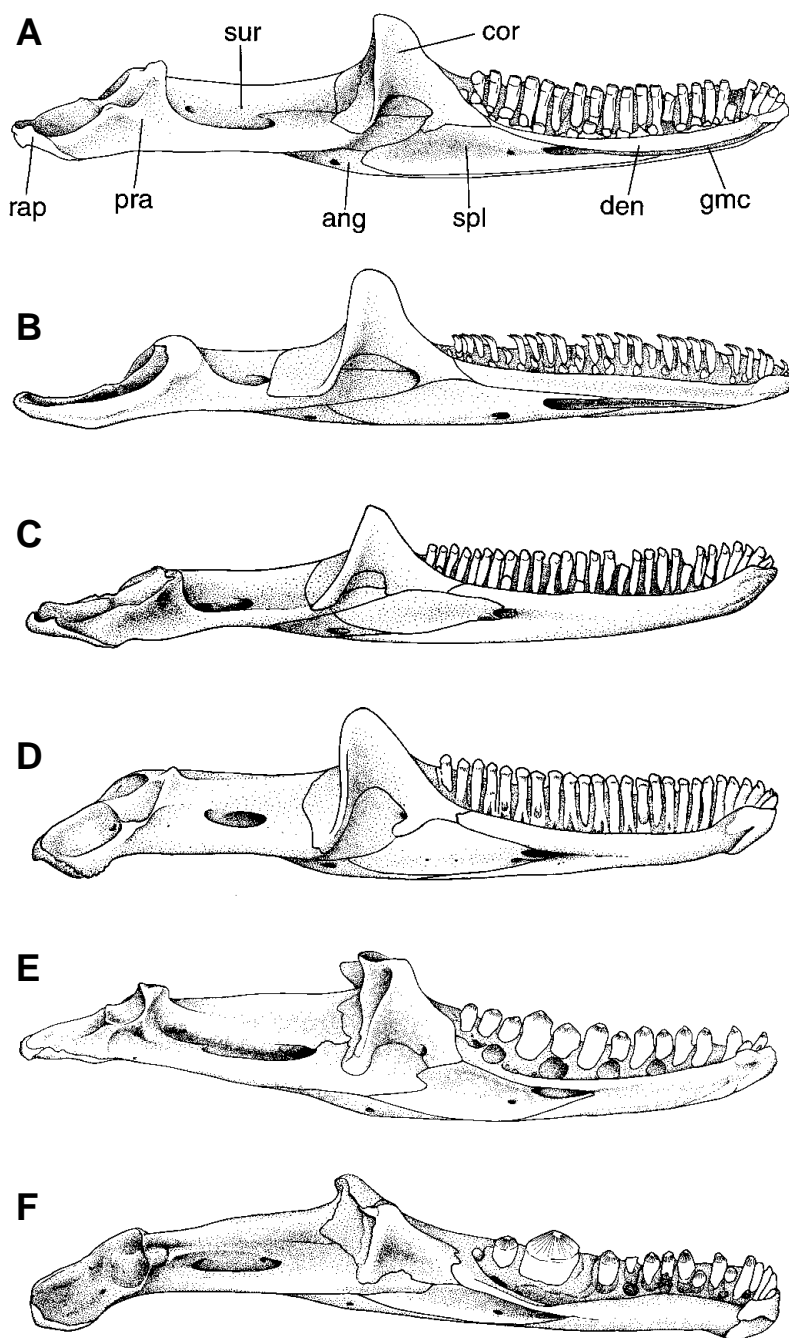
The hyobranchial apparatus is conservative in skinks, with practically no variation from the pattern reported by Rao & Ramaswami (1952) for *Mabuya* or King (1964) for *Eulamprus*. All of the elements present primitively in lizards are present in skinks (Camp 1923; Estes *et al.* 1988), although the epibranchials are reduced (EB I), or unossified and not in contact with the corresponding ceratobranchial (EB II). This terminology follows that of Camp (1923), although Skinner (1973) identifies the free-lying element as the first, rather than the second epibranchial, and does not identify the terminal segment of the first ceratobranchial (although she illustrates it).

The vertebrae are procoelous, with a centrum that tapers posteriorly (Siebenrock 1895; Hoffstetter & Gasc 1969). Primitively there are 26 presacral vertebrae in skinks (Hoffstetter & Gasc 1969), and this count is retained in the normally proportioned members of the *Egernia* and *Sphenomorphus* Groups.

The atlas-axis complex of *Eulamprus quoyii*, described by King (1964), is typical in that the atlantal neural arches are separated dorsally and not fused to the centrum ventrally (Greer 1989). In some members of the *Eugongylus* Group, the neural arches fuse to the centrum (Greer 1989) and sometimes dorsally as

well (Sadlier 1990). The axis bears two hypapophyses, as the intercentra from both the second and third vertebrae are fused to the second centrum (Hoffstetter & Gasc 1969).

In the more elongate members of the *Egernia* and *Sphenomorphus* Groups, and in all members of the *Eugongylus* Group, presacral counts exceed 26. Normally-proportioned members of the *Eugongylus* Group usually have 27 to 29 presacrals. In elongate, reduced limbed species of all groups, the number of presacrals exceeds 30, and the highest counts are recorded in the limbless *Coeranoscincus frontalis*, which has 72 to 76 presacral vertebrae (Greer & Cogger 1985; Greer 1989, Table 3, for a summary of presacral counts).



**Figure 31.5** Mandibular variation in skinks. **A**, *Eulamprus murrayi*; **B**, *Coeranoscincus reticulatus*; **C**, *Eugongylus rufescens*; **D**, *Egernia cunninghami*; **E**, *Tiliqua scincoides*; **F**, *Cyclodomorphus gerradii*. **ang**, angular; **cor**, coronoid; **den**, dentary; **gmc**, groove for Meckel's cartilage; **pra**, prearticular; **rap**, retroarticular process; **sur**, surangular; **spl**, splenial.

[J. Thurmer]



All but the first five (less often four) caudal vertebrae have fracture planes, the line of weakness separating the anterior third of the vertebra and passing through the anterior part of the base of the transverse process (Etheridge 1967; Hoffstetter & Gasc 1969). In *Egernia stokesii* and *E. depressa* and in *Tiliqua rugosa*, fracture planes are absent, and they disappear ontogenetically in some other species of *Tiliqua* (Arnold 1988). Caudal chevrons start on the third (less commonly the second or fourth) caudal. They are usually placed slightly forward of the primitive intervertebral position, attached to the posterior end of the preceding vertebral centrum. Caudal vertebrae usually number between 40 and 50 in Australian species, and range from 14 in *E. stokesii* to 70 in *Emoia atrocostata* (Greer 1989).

The ribs of Australian skinks are simple and lack any processes for muscle attachment (but such a process, the pseudotuberculum, is seen in African acontines; Hoffstetter & Gasc 1969). In skinks, ribs are present on all but the first three cervical vertebrae. The nature of the rib contact divides the vertebral column into a cervical region, defined as ending with the last vertebra (the eighth) with an associated rib not attached to the sternum (Greer 1989; Siebenrock 1895), and the dorso-lumbar vertebrae which can be further subdivided on the rib attachments, as only the first five (vertebrae 9 to 13) have ribs contacting the sternum.

The sternal skeletal elements are fairly constant in morphology and in their relationships with the ribs in most normally proportioned skinks (Lécuru 1968b; Hutchinson pers. obs.). The presternum is a squat, kite-shaped element, occasionally with a small to large fontanelle, and in contact with three ribs (on vertebrae 9 to 11). The mesosternum is a rhomboid structure with a large fontanelle, in contact with the ribs of vertebra 12 laterally and vertebra 13 at its posterior vertex. Generally a complete inscriptional rib (vertebra 14) lies posterior to the mesosternal ribs. In some species (for example *Eulamprus quoyii*, see Fig. 10 in King 1964) there are additional chevrons lying free posterior to the complete inscriptional rib, associated with the fifteenth and sixteenth vertebrae. This is especially true of species with reduced limbs. In *Lerista*, species with more reduced limbs have sternal elements that are diminished in size, concomitant with shoulder girdle reduction, but this is compensated for by an increased number of complete inscriptional ribs which partly form a visceral basket under the anterior body organs (stomach, lungs and liver).

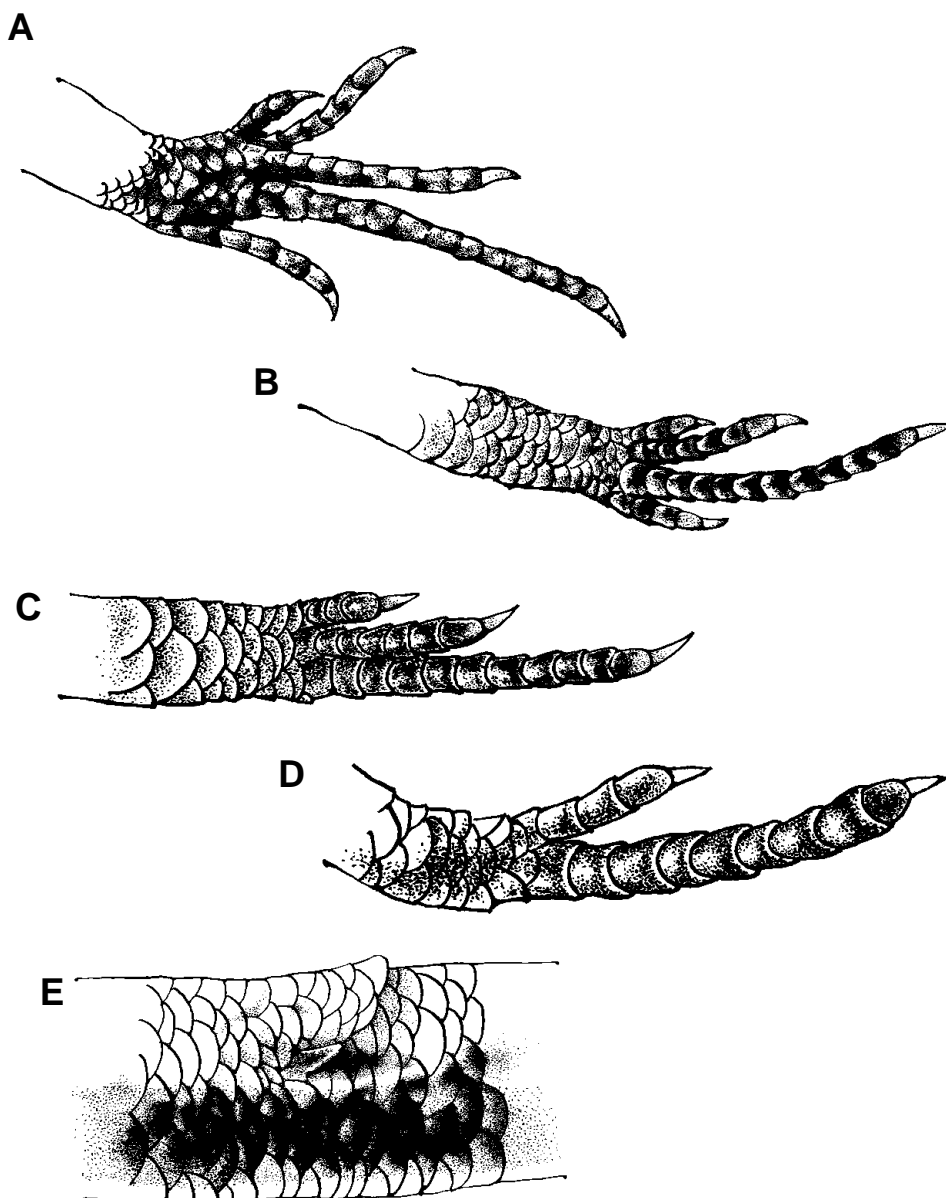
The shoulder girdle of *Eulamprus quoyii* was described by King (1964), and Lécuru (1968a; 1968b) reviewed this region generally in lizards, including species from the Australian genera *Cryptoblepharus*, *Egernia* and *Tiliqua*. The clavicles are generally perforated in Australian lygosomines, except in species of *Tiliqua*. In most small skinks, only the leading edge of the clavicle is well ossified, and the trailing edge that overlies the coracoid is a thin, often ragged-edged sheet. The interclavicle is well ossified and cruciform. The scapulocoracoid appears to be constant in shape, with no reported variation from the condition with three fontanelles described by Lécuru (1968a). Though the whole shoulder girdle becomes reduced in size in species with reduced limbs, all elements retain normal appearance and proportions until the limbs have completely disappeared (Howie 1963).

The pelvic girdle, as described by King (1964) for *Eulamprus quoyii*, varies little in skinks. Arnold (1984a) noted that unlike many lizards, skinks lack a well-developed hypischium, a cartilaginous rod which projects posteriorly from the ischial symphysis. Again, the pelvic girdle remains unmodified except in relative size in reduced-limbed species. In limbless species (*Coeranoscincus frontalis* and *Ophioscincus ophioscincus*), the pelvic bones are present, but the two halves no longer make contact medially (Howie 1963).

The manus and pes are primitively pentadactyl, with phalangeal formulae of 2.3.4.5.3 and 2.3.4.5.4 respectively. In reduced-limbed species, phalangeal loss commonly occurs (Chocquenot & Greer 1989; Greer 1990a), sometimes accompanied by brachyphalangy (for example, in *Anomalopus*, Howie 1963) (Fig. 31.6).

### Locomotion

Most skinks have well-developed limbs and are adept at running. Russell (1988) reviewed the limb muscles of lizards, including the skink genera *Ctenotus*, *Egernia* and *Tiliqua*. Speed depends to a large extent on limb length in normally proportioned species, but the tail and sinuosity of the body become significant in reduced limbed species (Gans 1975; John-Alder, Garland & Bennett 1986). Loss of the tail can enable normally limbed species to run even faster, but is likely to impede locomotion in reduced-limbed species and is known to greatly decrease swimming speed (Daniels 1985a).



**Figure 31.6** Variation in the structure of the foot in skinks. **A**, *Lerista microtis*; **B**, *L. dorsalis*; **C**, *L. terdigitata*; **D**, *L. edwardsae*; **E**, *L. stylis*.

[K. Bowshall-Hill]

There is some variation in detailed foot structure, which suggests mechanical adaptations that improve traction on certain surfaces. Several small skinks, such as members of the *Ctenotus schomburgkii* and *C. colletti* species groups, *Morethia adelaidensis* and *Cryptoblepharus carnabyi*, characteristically have spinose (mucronate) subdigital lamellae (Greer 1980b; Storr, Smith & Johnstone 1981). This list, however, demonstrates the difficulty of finding a functional explanation for such structures. The *Ctenotus* species are mostly sand-runners, *M. adelaidensis* lives in clayey and salt-pan areas, and *C. carnabyi* is a climber.

When running, the alternating gait used by skinks leads to some sinusoidal movement of the vertebral column, and this suggests that transition to a more snake-like locomotion is a relatively straight-forward process. Skinks show the morphological stages in this transformation better than any other lizard group. Reduction in the size of the limbs is usually accompanied by reduction of the size gradient between the toes, often with phalangeal loss, and is generally followed by digital loss, beginning with the smallest and outermost toes and progressing medially (Gans 1975; Lande 1978). Limb loss pattern in *Lerista* is unusual in that the toes tend to retain the proportions of a normal pentadactyl skink, even when greatly reduced in absolute size, and phalangeal reduction seems to be 'held off' until the digit is on the point of being lost (Greer 1990a).

Reduced-limbed species, even those with extremely small and seemingly almost useless limbs, use their legs to help obtain purchase, especially on smooth surfaces. In litter or soil these species progress primarily by undulation of the body and tail, the multiplication of presacral vertebrae seen in these forms increasing spinal flexibility and increasing the number of waves that can be developed along the body. A body muscle element, the *m. rectus abdominis lateralis*, is characteristic of skinks (and other taxa not included in the Iguania) (Moody 1983) and is thought to assist in undulatory movements of the lizard's trunk (Camp 1923). During undulatory locomotion the limbs stay folded against the sides of the body, often lying in shallow grooves behind the limb bases. In these species, the tail tends not to taper, staying the same length as the body until close to the tip. Presumably this prolongs the propulsive surface available, since the caudal musculature is effective for further along the tail than would be the case in a slender, tapering tail (Gans 1975). In spite of its apparent usefulness in locomotion, the tail of all of the reduced-limbed skinks is readily autotomised.

### Feeding and Digestive System

Skinks are usually regarded as relying heavily on the olfactory rather than visual senses for detecting prey, but most surface-dwelling species also depend heavily on sight, being quick to detect moving prey (Nicoletto 1985). Studies of actively foraging species of *Ctenotus* (James 1991; Pianka 1969c; Taylor 1986) and the American *Eumeces* (Vitt & Cooper 1986) reveal that they frequently appear to investigate potential hiding places of prey, presumably using olfaction to confirm presence or absence. Analysis of diet reveals the presence of cryptic prey items more likely to have been found by scent than sight. In litter and sand-swimming species, vision may well be much less important than olfaction in locating food, but the appropriate studies have not been done.

The skull of skinks is typically amphikinetic (Iordansky 1990), with flexible fronto-parietal, basiptyergoid, pterygo-quadrates and squamosal-quadrates joints and a pivoting epiptyergoid. Most species also appear to have some movement between the pterygoid and ectopterygoid (flexipalatality). The heavily armoured skull of *Tiliqua rugosa* has secondarily lost most of its kinetic capability, although the cartilaginous joints and appropriate muscles remain (De Vree & Gans 1987).



The tongue is used in conjunction with Jacobson's organ to locate and recognise food. Unlike agamids, skinks do not use the tongue to catch prey, although it is used in drinking. *Tiliqua* species use the tongue to remove broken pieces of shell when eating snails.

Dentition varies among skinks (Fig. 31.5A–F), although diets of too few species are known well enough to permit a functional interpretation of much of the variation. Most skinks have cylindrical teeth with obtusely pointed or chisel-shaped crowns, generally with an apical crest which may be emphasised by an apical groove. The small insectivores may have teeth which are more slender and more sharply pointed, while larger species tend to have blunter, more robust teeth.

The durophagous dentition of *Tiliqua* and *Cyclodomorphus* has been noted and described by several authors, starting as early as Wagler (1830), and more recently Edmund (1969) and Estes & Williams (1984). *Cyclodomorphus gerrardii* is the most specialised of this group, having an enormously enlarged molariform tooth towards the back of each tooth row (Fig. 31.5F). The enlarged teeth do not occlude, but instead the upper tooth closes in front of the lower, and produces a shearing action rather than a direct crushing effect on any object being chewed.

The species of *Coeranoscincus*, *C. reticulatus* and *C. frontalis*, have characteristic recurved teeth which are believed to be specialisations used in preying on earthworms (Ehmann 1987; Greer & Cogger 1985; McDonald 1977). No dietary information is available for the burrowing skinks of the genus *Ophioscincus*, which also have recurved teeth with flattened, slightly flared and bicuspid crowns. The primarily vegetarian species of the *Egernia cunninghami* species group (for example, *E. cunninghami* and *E. stokesii*) have many, small, close-packed teeth, with linguo-labially compressed crowns which collectively form a crude cutting edge along the tooth row (Fig. 31.5D).

The arrangement and innervation of the jaw musculature of lizards was described by Haas (1973) and Gomes (1974), although the only Australian skink species for which detailed descriptions exist are *Tiliqua rugosa* (see also De Vree & Gans 1987) and *T. scincoides*. Available data suggest that the layout of scincid jaw muscles is typical of lizards generally.

The gastrointestinal tract is simple in most species. The stomach is muscular, and the relatively simple, tubular small and large intestine terminate at a cloaca. Significant modifications occur in some of the larger omnivorous and herbivorous species, which have broadened, but not lengthened, hindguts (Mackenzie & Owen 1923; Pollock 1989; Yeatman 1988), apparently associated with an enhanced ability to digest vegetation (unpub. studies cited by Pollock 1989).

### Circulatory System

The structure of the heart in lizards was reviewed by Webb *et al.* (1974), and the innervation and layout of the major arteries in *Tiliqua* have been illustrated by Berger, Evans & Smith (1980), Burnstock & Wood (1967) and Rogers (1967). White (1976) reviewed the functional aspects of the circulatory system in lizards and other reptiles.

Skinks, like other lizards, probably use the circulatory system to assist in thermoregulatory control (White 1976). Head-body thermal differentials (Webb, Johnson & Firth 1972) and asymmetric heating and cooling curves have both been recorded in skinks, although the mechanisms behind these phenomena are not yet well documented. Studies of the large skinks, *Egernia cunninghami* and *Tiliqua scincoides*, show that they heat more rapidly than they cool (Bartholomew, Tucker & Lee 1965; Fraser 1985). In *T. scincoides*, differential

heating is partly the result of variations in heart rate, and heating animals have an accelerated rate compared with cooling animals at the same body temperature. However, several studies (Daniels, Heatwole & Oakes 1987a; Fraser & Grigg 1984; Spellerberg 1972c) have shown that such physiological control of temperature is not significant in small to medium-sized skinks, such as species of *Ctenotus*, *Eulamprus* and *Lampropholis*. Some inconsistency is evident in the results obtained by the three studies just cited. Spellerberg found that species of the *Eulamprus quoyii* complex, like the larger skinks, heated twenty to thirty percent faster than they cooled, while the other two studies (involving some of the same species) found that these skinks actually cool faster than they heat. Fraser & Grigg (1984) speculated that the disadvantage suffered by small lizards, in their lack of physiological control, is compensated for by the potential for rapid heat exchange, and allows opportunistic responses to brief periods of heat.

The nature of the heat shunting mechanisms suggested by these studies is not known in skinks. Hammel, Caldwell & Abrams (1967) showed that the head temperature in *Tiliqua scincoides* was more finely controlled than the body (colonic) temperature, and inferred the presence of hypothalamic sensory control systems. Analogy with other lizards suggests that such control systems would act to reroute blood circulation between peripheral and deep vascular circuits (White 1976) or to set up arterio-venous countercurrent heat exchanges. The peripheral vascular system can be elaborate to the tips of scales, and has been explained as facilitating heat uptake (though not retarding heat loss) in *Tiliqua scincoides* (Drane & Webb 1980). One technique denied skinks is cooling of blood in the suborbital sinus by panting. Apart from *Tiliqua*, in which the behaviour is probably secondarily derived, skinks do not pant (Heatwole, Firth & Webb 1973; Greer 1980a; Webb *et al.* 1972).

Red blood cells in skinks are elongate-oval in shape and nucleated, and range in size from 14 to 17 mm in length and 9 to 10 mm in diameter in *Ctenotus*, *Egernia* and *Tiliqua* (M.-C. Saint Girons 1970a). Packed cell volume (haematocrit) in Australian skinks is typically about 30% (Hutchinson unpub. data), which appears to be typical of the concentration found in other lizards (Dessauer 1970).

Research based largely on *Tiliqua* and the non-Australian scincine *Chalcides* shows that skinks have a well-developed immune system (Cooper, Klempau & Zapata 1985; Wetherall & Turner 1972). Humoral (immunoglobulin-based) antibody responses can be obtained to a variety of foreign antigens, including a vigorous secondary response following an initial immunisation. Two classes of antibodies have been recorded: a heavy 19S antibody and a light 7S antibody (single unit). These would be analogous, if not homologous, with eutherian IgM and IgG respectively, but unlike the situation in mammals, the heavy antibody persists in high concentration after the light antibody is being produced (Wetherall & Turner 1972).

Wetherall & Turner (1972) and Cooper *et al.* (1985) reported lymphoid tissue in a number of organs, including the marrow, spleen, thymus and kidney. Presumably the thymus (Sidky 1967, Fig. 2) is a vital part of the immune system, but reptilian thymic function has yet to be studied (Bockman 1970). The white blood cells of *Tiliqua scincoides* resemble those of mammals in producing a variety of chemicals, such as the prostaglandin PGI<sub>2</sub>, involved in inflammatory responses such as vasodilation and the inhibition of platelet aggregation (McColl & Daniels 1988).

The topology of the lymphatic system in lizards was extensively reviewed by Ottaviani & Tazzi (1977), but few data applied specifically to skinks; the European scincine *Chalcides ocellatus* was the only species discussed.

## Respiration

Tenney & Tenney (1970) described the lungs in a number of reptiles and amphibians, but included no skinks. In general they found that reptilian lung surface area is proportional to metabolic rate, and that reptile lungs are not simple sacs but show pronounced compartmentalisation.

Ventilation of the lungs is mainly achieved by contractions of the intercostal muscles (Wood & Lenfant 1976). Typical skink ventilation occurs in three phases—rapid expiration followed by rapid inspiration, then a pause with the lungs inflated. Greer (1989) reviewed variation in ventilation patterns in skinks, in which displacement of the rib cage laterally in the area behind the forelimbs represents the primitive condition. In sand-swimmers, a respiratory mode is used in which the ventral part of the ribcage moves, and causes a vertical rather than a lateral displacement. This mode was first described in skinks by Pough (1969b) for the African sand-swimmer *Lygosoma sundevalli*, and he suggested it is also used by the Saharan *Scincus* and *Sphenops*. To these, Greer added *Eremiascincus* and *Lerista*. Limbless skinks (except *Lerista* as noted above) expand and contract the chest cavity symmetrically, termed circumferential breathing by Greer (1989). Besides chest movements, the smooth muscle of the lung itself is involved in assisting inspiration and expiration, under the control of vago-sympathetic nerve trunks (Burnstock & Wood 1967).

Aerobic respiration is dependent on both the rate of breathing (ventilation frequency) and the amount of air exchanged with each breath (tidal volume). Bennett (1973b) reviewed these phenomena in lizards, including data on the skink *Egernia cunninghami*. In *E. cunninghami*, ventilation frequency is temperature sensitive, and rises from 22/min at 30°C to 38/min at 37°C, but is little affected by activity level. Increased oxygen demands made by high activity levels are met not by adjusting ventilation frequency, which increases by only about half again, but by three to six-fold increases in tidal volume during activity.

Exercise capability of skinks depends on both aerobic and anaerobic respiration, and like other lizards, they are less able to sustain high levels of activity than are mammals and birds. Standard metabolic rate, measured as oxygen consumption, is generally rather low in skinks, relative to other lizards (Andrews & Pough 1985). Skinks with normally developed limbs are capable of short bursts of speed of up to 2 m/sec or more (Huey & Bennett 1987; John-Alder *et al.* 1986), but short-limbed species are capable of much less (0.5 to 0.7 m/sec in *Hemiergis*). Stamina is also limited. *Egernia cunninghami* can reach nearly 3 m/sec in short bursts, but on average can maintain 0.27 m/sec (1 km/hr) for only seven minutes (John-Alder *et al.* 1986). Anaerobic respiration has been studied little in skinks, but Bennett (1982) reported that during strenuous activity about half (49%) of the energy produced by the scincine *Eumeces obsoletus* is contributed by anaerobic metabolism.

## Excretion

The kidneys lie posteriorly against the dorsal wall of the body cavity, and usually extend into the pelvic region. A bladder is known to be present in at least some skinks (Bentley 1976). Nitrogenous waste is excreted mainly in the form of uric acid, but some urea production also occurs (Dantzler 1976; Hunt 1972). The kidneys and bladder are both involved in ion exchange and water reabsorption (Bentley 1976; Schmidt-Nielsen & Davis 1968).

Osmoregulation has been studied intensively in *Tiliqua rugosa* (Bentley 1976 and included references). Like most lizards, and in contrast to mammals, *T. rugosa* is able to tolerate wide fluctuations in plasma sodium concentration,



from 152 to 240 mEq/l, which facilitates retention of body fluids during periods of desiccation. During such times these lizards seem able to shut down kidney function altogether.

A nasal salt gland was first identified in *T. rugosa* by Braysher (1971), and subsequent studies on its structure and function have been summarised by Bradshaw (1986). The salt gland only becomes active when the lizard's body temperature climbs above 30°C. It is capable of responding to both sodium and potassium loading by selectively secreting the ion in excess (Braysher 1971) and is a 'true' salt gland in that it produces a hyperosmotic secretion (Bradshaw 1986). It is not yet known whether the nasal glands of any other Australian skinks have a salt-excreting capacity.

### Sense Organs

The brain of skinks is similar in topology to that of other lizards (see Fig. 1 in Senn 1979); Snyder, Gannon & Baudinette (1990) show the outline of the major regions of the brain of *Tiliqua rugosa* and its vascular system.

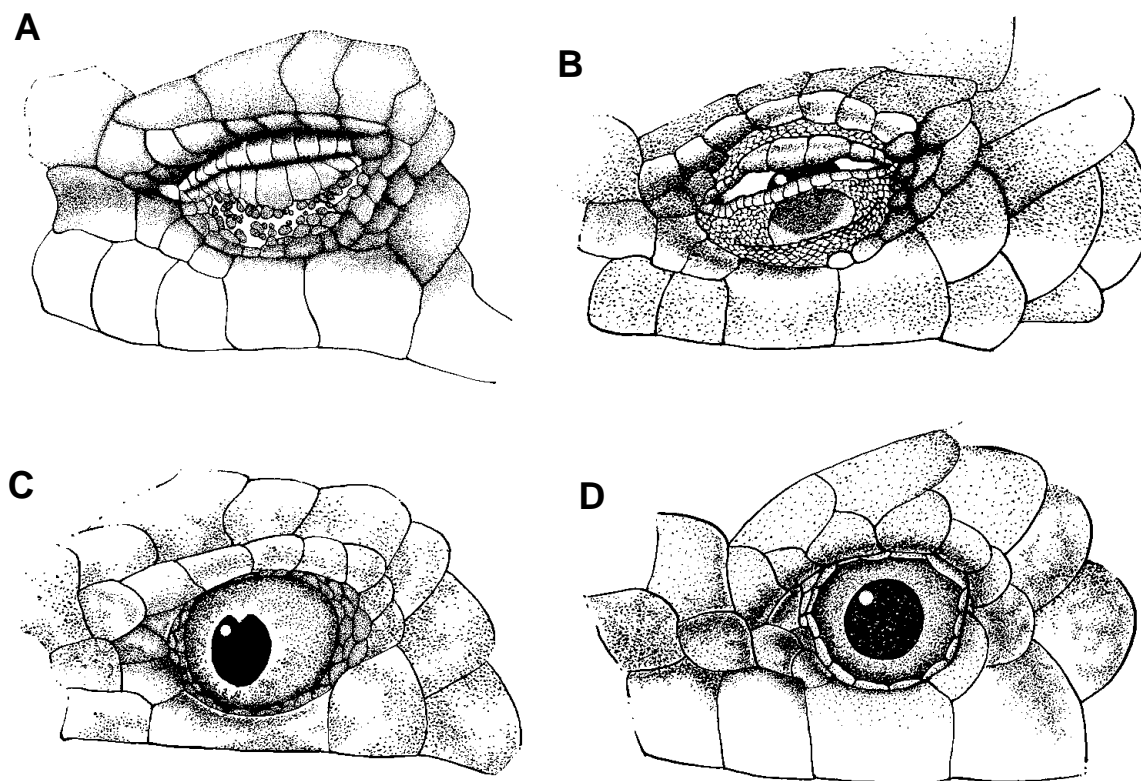
Relative brain size in skinks and other squamates was reviewed by Platel (1979), whose data indicated that skinks are unusually small-brained (low indices of encephalisation) compared to lizards in general. It is worth noting that most skinks examined by Platel were reduced-limbed, fossorial species in which the head is miniaturised (Rieppel 1984a), so that small indices of encephalisation could be expected. The one surface-dwelling, normally proportioned species examined (*Eumeces schneiderii*) had the largest relative brain size, and was close to the lizard average (index of encephalisation 90). The autonomic nervous system of lizards was reviewed by Berger & Burnstock (1979).

The eye is large and fully developed in most skinks, and usually has a round pupil, a distinct iris, a movable lower lid and a nictitating membrane (Fig. 31.7). The eyeball is lubricated by the posterior lacrimal and Harderian glands, sometimes supplemented by an anterior lacrimal gland (Saint Girons 1982). The eyeball is supported by a circumferential series of bony plates, the scleral ossicles (Underwood 1984), which usually number 14 (13 in some *Tiliqua*, Underwood 1970).

Little is known of the retinal structure of skinks (Peterson 1992) and no direct demonstration of colour vision has been made. Lizards have an all cone retina (Goldsmith 1990), with multiple visual pigments, and 'all species tested in discrimination studies have colour vision' (Cooper & Greenberg 1992), so that colour vision is probably normal for this group.

In the nocturnal species, *Egernia striata*, the pupil is vertically elliptical (Bustard 1970b), but this is not true of other nocturnal *Egernia*, or of nocturnal members of other genera, such as *Eremiascincus*. One lineage of skinks, the *Sphenomorphus* Group, is characterised by a very dark iris, from which the pupil can only be distinguished in good light. Some other species, for example *Tiliqua rugosa* and the alpine Tasmanian species of *Niveoscincus*, also have such a solidly black iris colour. Many skinks have a transparent disc (spectacle, window or brille), in the lower eyelid, and some have an immovable, transparent lower eyelid (the ablepharine condition, Greer 1974; Fig. 31.7C). The most likely adaptive explanation for the ablepharine spectacle is avoidance of corneal water loss in small species inhabiting habitats which are relatively drier than those of their relatives with movable eyelids (Greer 1983a).

All Australian skinks have a third light receptor, the parietal eye, which lies below a foramen in the parietal bone and is visible externally in most species as a circular spot in the rear half of the interparietal shield. The parietal eye in



**Figure 31.7** Variation in the lower eyelid in skinks. **A**, scaly and movable, *Egernia whitii*; **B**, movable, with a transparent 'window', *Carlia longipes*; **C**, transparent and immovable but distinct from the upper eyelid, *Lygisaurus foliorum*; **D**, transparent and completely fused to the upper eyelid, *Lerista xanthura*. [K. Bowshall-Hill]

skinks is probably both a light and heat detector, probably acting as in other lizards as a radiation dosimeter (Firth & Kennaway 1989; Ralph, Firth & Turner 1979a).

Most skinks have a well-developed tympanic membrane sunk in a moderately deep auditory meatus. The stapes in such species is golf-tee shaped, with a long, imperforate shaft and a moderate circular footplate. The quadrate has a well-developed conch which supports the leading edge of the tympanum on its outer rim. Some skinks, all litter dwellers or burrowers, have lost the eardrum, including all species of *Anomalopus*, *Hemiergis*, *Ophioscincus* and *Saiphos*. In these taxa, the quadrate has lost the conch and the stapedia shaft is short and stout with a ligamentous attachment to the skin. The attachment puckers the skin inwards at this point producing an externally visible depression.

The principle structure which acts as a sound transducer in the inner ear of reptiles is the basilar or auditory papilla, a structure which is elaborated into the organ of Corti in mammals (Romer 1970). The auditory papilla lies in the cochlear duct (Baird 1970), an antero-ventral extension of the membranous labyrinth of the inner ear which otherwise functions in the maintenance of balance. In skinks some hair cells of the papilla are free but those in a demarcated ventral lobe of the papilla are capped by a large cupula-like structure termed a culmen (Wever 1978). The tectorial membrane, which is the usual structure providing inertial control of the sensory hair cells of the auditory papilla in most lizards, is rudimentary in skinks.

Wever (1978), surveying auditory sensitivities in lizards, found that his small but representative sample of skink genera (including the Australian genus *Tiliqua*) have hearing which could be described as 'of better than ordinary

quality' by comparison with other lizards. The scincid ear is well adapted for the reception of faint sounds but poorly able to discriminate between frequencies. The single species studied which lacks a tympanum, the African *Acontias plumbeus*, retains an ability to detect airborne sounds, although with greatly reduced sensitivity.

Chemoreception in skinks, as in other lizards, is mediated by two structures, the sensory epithelium of the nose and Jacobson's organ (=vomeronasal organ) (Parsons 1970; Halpern 1992). The anatomy of the nose was reviewed by Parsons (1970). In skinks, the nasolaryngeal duct, which conducts air from the nasal cavity to the mouth cavity, is elongated, in accord with the more or less complete bony secondary palate, but in other respects appears to be similar to other scincomorphans lizards. In this group, non-sensory respiratory epithelium lines the choanal tube and the ventral surface of the nasal cavity, while sensory epithelium lies dorsally, especially over the surface of an internal fold, the concha, which projects into the medial wall of the nasal cavity of lizards.

In skinks, Jacobson's organ lies at the front of the roof of the mouth, supported below by the antero-lateral extremity of each vomer and protected above by the septomaxillae (Skinner 1973). A duct connects the sensory epithelium of this pouch-like structure with the mouth cavity. The precise manner in which scent particles are transferred to the sensory epithelium of Jacobson's organ is not certain. Pratt (1948), who included the Australian species *Tiliqua rugosa* in his study, suggested that ciliary action along the duct of Jacobson's organ would be sufficient to transfer chemical particles wiped off the tongue tip to the sensory region of the organ.

Jacobson's organ may provide fine discrimination at close range, while the nose is used to detect more distant chemical stimuli with less resolution (Cowles & Phelan 1958; Bellairs 1984). This accords with data which indicates that Jacobson's organ preferentially responds to non-volatile chemicals (Graves & Halpern 1989). Several studies have investigated use of chemical senses by skinks, based on North American species of the genera *Eumeces* and *Scincella* (Cooper & Vitt 1987; Nicoletto 1985; Simon 1983). However, comparable studies of Australian species are few (Graves & Halpern 1991).

### Endocrine and Exocrine Systems

The pituitary gland of reptiles was reviewed by Saint Girons (1970a), who described the scincid pituitary (including those of the Australian genera *Egernia* and *Tiliqua*) as having a unique morphology compared with several morphological trends seen in other families. Different aspects of cellular structure are similar to either anguoid or lacertoid lizards. The pituitary hormones of lizards have been reviewed by Licht & Rosenberg (1969).

The pineal complex (pineal organ plus parietal eye) is well-developed in skinks. Ralph *et al.* (1979a) and Ralph, Firth, Gern & Owens (1979b) have reviewed the function of this complex, and suggested that it has a major role in the control of thermoregulatory behaviour, including voluntary maximum and preferred body temperatures. Firth and coworkers (Firth, Kennaway & Belan 1991 and included references) have shown that in *Tiliqua rugosa* the pineal complex monitors both thermal and day-night cycles, reflected by cycles of melatonin production. The 24 hour melatonin cycles in turn are likely to be important in the timing of annual physiological cycles.

Lynn (1970) reviewed the general structure, function and variation of the thyroid in lizards and other reptiles. Lynn & Zmich (1967) reported on thyroid morphology in 56 species of skinks, including Australian species now placed in the genera *Anomalopus*, *Calyptotis*, *Cyclodomorphus*, *Egernia*, *Hemiergis*, *Lerista* and *Tiliqua*. In all of these the thyroid was single, usually strap-like in shape and located just anterior to the heart and ventral to the trachea. The



thyroid is similar in function to that of other vertebrates, and it secretes iodotyrosine hormones which are controlled by the pituitary and have stimulatory effects on several aspects of a lizard's metabolism (Hulbert & Williams 1988). Wilhoft (1964), studying *Carlia rubrigularis* (fide Ingram & Covacevich 1989), found that thyroid activity increased, especially in females, during peak reproductive metabolic activity (mating in males, yolk deposition in females). In at least some lizards (Maderson 1984), thyroid activity is correlated positively with rates of skin sloughing, although no data are yet available for skinks.

The parathyroid is located in the neck at the bases of the carotid arteries (Clark 1970), and is paired in the four species of skinks (including the Australian species *Tiliqua occipitalis* and *T. rugosa*) which have been investigated (Rogers 1963; Clark 1970). As in mammals, parathyroid hormones control phosphate and calcium levels. The effect of altered calcium levels was noted by Sidky (1966) in the Mediterranean skink *Chalcides ocellatus* when parathyroidectomised skinks became hyperexcitable and developed muscle spasms.

The pancreas in lizards (Miller & Lagios 1970) is a three-limbed structure, with projections towards the gall bladder, small intestine and spleen. It has not been studied in Australian skinks. The American *Eumeces fasciatus* had both alpha and beta islet cells, indicating the production of both glucagon and insulin and a glucose control system comparable to that of mammals. Studies of glucose control in skinks have not been done (Burton & Vensel 1966).

The adrenals are relatively slender and are attached to the mesentery of the gonad, lying medial to the latter. Two Australian species, *Tiliqua scincoides* (Gabe & Martoja 1961) and *Carlia rubrigularis* (Wilhoft 1964) have been the subjects of adrenal gland structural and functional studies. The general anatomy, embryology and function of the adrenal in reptiles was reviewed by Gabe (1970). The adrenal has been implicated as a major secretor of progesterone in *Tiliqua rugosa* (Bourne 1981; Bourne, Stewart & Watson 1986a).

Cephalic exocrine glands in skinks include a single lower labial, up to two palatines, two anterior sublinguals, sometimes a lingual, two to three nasals, and in the orbital region a Harderian and one or two (rarely none) lacrimals (Saint Girons 1988). The anterior sublingual glands are the main salivary glands, and, at least in *Tiliqua rugosa*, one of the nasal glands is a salt gland (Braysher 1971), while most of the others serve to lubricate exposed or sensory epithelial surfaces (Saint Girons 1989). The three orbital glands are usually present in species with a movable eyelid and nictitating membrane, but in ablepharine species the nictitating membrane is lost, and with it the anterior lacrimal gland (Saint Girons 1982, 1989). The Harderian gland may have functions other than that of orbital lubrication (reviewed by Saint Girons 1989) in some other reptile groups. Suggested functions include the enhancement of olfaction by improving the collection of dissolved particles by Harderian secretions or to improve lubrication during swallowing in snakes, but no such suggestion has been made for skinks.

Exocrine glands have been identified in the cloacal region of *Eumeces* (Trauth, Cooper, Vitt & Perrill 1987). These have been suggested as sources of both species-identifying chemical cues and female sex pheromones. Unlike many other lizards, skinks lack both femoral and preanal pores.

## Reproduction

The structure and position of gonads and reproductive tract were described and figured by Egan (1984) for *Tiliqua rugosa* and described briefly by Taylor (1985) for *Ctenotus taeniolatus*. The anatomy appears to be as conservative in

skinks as it is for lizards in general (Fox 1977). An unusual feature seen in one Australian skink, the limbless *Anomalopus pluto*, is loss of the right oviduct (Greer & Cogger 1985).

The male reproductive system includes the sex segment of the kidney. This androgen-sensitive region of uncertain function may possibly act in a fashion analogous to the mammalian prostate, and provide nutrient support for the sperm (Cuellar, Roth, Fawcett & Jones 1972). In the two Australian genera for which data are available, *Carlia* and *Tiliqua*, the sex segment involves the collecting ducts and the proximal portion of the ureter, in which the epithelium hypertrophies at the same time as testicular activity reaches its maximum (Egan 1984; Wilhoft & Reiter 1965).

Chromosomes of skinks are relatively conservative in number and morphology, and heteromorphic sex chromosomes are the exception rather than the rule (Donnellan 1985). Each lineage has a unique karyotype, which shows little major within-group variation, most of which involves pericentric rearrangements in a few chromosomes (Donnellan 1985; King 1973). The major group trends are: *Egernia* Group,  $2n=32$ , (nine pairs of macrochromosomes, pair 6 smaller than pair 5); *Eugongylus* Group  $2n=30$  (nine pairs of macrochromosomes, pair 6 smaller than pair 5); *Sphenomorphus* Group  $2n=30$  (eight pairs of macrochromosomes, pair six same length as pair 5). When present, sex chromosome heteromorphism in Australian species almost always involves pair seven, and for males and females is XY and XX respectively. Pair seven XY chromosomes characterise one lineage in the *Eugongylus* Group, namely *Bassiana*, *Morethia* and *Pseudemoia* (Hutchinson *et al.* 1990), and are present also in *Menetia greyii*, *Carlia* (*C. longipes* and *C. rhomboidalis*) and *Saproscincus czechurai*. Donnellan's (1991b) report of possible sex chromosomes involving a microchromosome pair (14 or 15) in *Lampropholis coggeri* (L. sp. D of Mather 1990) provides a unique exception to the general trend. Pair seven XY heteromorphism also occurs in the *Sphenomorphus* Group in some *Ctenotus* and two species of *Glaphyromorphus* (*G. fuscicaudis* and *G. nigricaudis*).

The timing of mating and gonadal cycles have been best studied in temperate southeastern Australian species (for example, Smyth & Smith 1968, 1974; Pengilley 1972; Taylor 1985), but several studies have also been carried out on tropical Australian and New Guinean species in the genus *Carlia* (Wilhoft 1963; Wilhoft & Reiter 1965; Zug, Barber & Dudley 1982). James & Shine (1985) summarised data on a variety of tropical taxa, and hormonal control of gonad activity was reviewed by Licht (1979).

Reproductive cycles of skinks vary in the timing of events and in the degree of synchrony of the cycles of the male and female reproductive organs. Taylor (1985) and Heatwole & Taylor (1988) have described eleven cycle types, but these tabulations contain several errors, and divide the variation rather artificially. In the most common cycle in temperate skinks, male and female gonads reach their maximum size in spring, and mating and fertilisation occur during late spring. Testicular and sometimes ovarian activity may begin before spring, as in *Eulamprus quoyii* (Veron 1969), *Nannoscincus maccayi* (Robertson 1981) and *Tiliqua rugosa* (Bourne, Taylor & Watson 1986b), or may be entirely confined to spring, as in *Ctenotus taeniolatus* (Taylor 1985).

Some temperate viviparous species are characterised by desynchronised gonadal cycles, in which the males undergo spermatogenesis in autumn, when mating occurs, while females overwinter with stored sperm and ovulate in spring, when fertilisation occurs. Such a pattern is known in *Hemiergis* (Smyth & Smith 1968) and *Pseudemoia* (Hutchinson & Donnellan 1992; Pengilley 1972; Rawlinson 1974b), and has been stated to occur in *Niveoscincus* (Rawlinson 1974a; 1975), although some field observations suggest spring mating in

*N. microlepidotus* (Hudson & Shine pers. comm.). Greer (1982), Hutchinson, Schwaner & Medlock (1988) and Hutchibson *et al.* (1989) reported that only about half of the females of *N. greeni*, *N. microlepidotus* and *N. orocryptus* are gravid in any one year. The extended cycle is not yet fully explained, but based on personal observations at Mt Wellington, females of *N. microlepidotus* give birth in November, while non-breeding females are ovulating. This implies that gestation is not complete before the onset of the alpine winter, and is only finished after the embryos have overwintered, leaving the female with insufficient time to provide ova with yolk during that spring. In contrast to the biennial female cycles, the testes of all males of *Niveoscincus* reach maximum size during autumn but the time of mating is not known.

Joss & Minard (1985) reported a double peak in the testicular cycles of *Lampropholis guichenoti* and *L. delicata* in early spring (September-October) and late summer (January-March). Peaks in testis mass are accompanied by maximum sperm production. In *L. guichenoti* these peaks coincide with, or follow shortly after, two episodes of ovulation in the female population. However, ovulation in *L. delicata* occurs in October-November, between the testicular peaks.

Cycles in tropical species have been less well studied, but were investigated in detail in *Carlia* by Wilhoft (1963; Wilhoft & Reiter 1965) and reviewed by James & Shine (1985). Tropical species may show almost continuous gonadal activity (*Carlia rubrigularis* and *Cryptoblepharus plagiocephalus*), or may show strong seasonality, with breeding during the wet season (*Carlia* spp., *Glaphyromorphus* spp.) or the dry season (*Morethia taeniopleura* species group). Both wet season and dry season breeders are known in tropical *Ctenotus* (James & Shine 1985). Arid zone species have not been much studied, but available data indicate late spring-early summer breeding in *Ctenotus*, *Egernia*, *Eremiascincus*, *Lerista* and *Morethia* (Henle 1989a, 1989b; Pianka & Giles 1982).

Ovulation is preceded by yolking (vitellogenesis) of the ovarian follicles. This occurs with great rapidity and seemingly relies largely on fat stores (Robertson 1981). The importance of caudal fat bodies is thus critical, especially in the *Sphenomorphus* Group, most members of which lack abdominal fat bodies (Greer 1986b). For this reason, use of caudal autotomy as an escape strategy can entail a considerable reproductive cost (Robertson 1981; Smyth 1974).

Androgens are known to reach a peak at the time of mating in at least some skinks, such as in a well-studied example, *Tiliqua rugosa* (Bourne & Seamark 1975, 1978; Bourne *et al.* 1986b). In other species, there is indirect evidence of a link between observed mating activity and testicular maximum, for example, in *Pseudemoia* (Hutchinson & Donnellan 1992), and by inference high androgen levels, but it is possible that mating activity in some species may be independent of androgen levels (*Hemiergus decresiensis*, Leigh pers. comm.), with copulation occurring at a time of testicular regression.

Steep increases (approximately eight-fold) in plasma oestradiol and progesterone levels occur during vitellogenesis in female *Lampropholis* (Joss 1985). Ovulation is preceded by a sharp drop in oestradiol levels and a peak in progesterone levels. In females of the viviparous Mediterranean genus *Chalcides*, oestradiol level peaks at ovulation, and progesterone levels are elevated through gestation until just before parturition, which is preceded by a minor peak in oestradiol (Ghiara, Angelini, Zerani, Gobbetti, Cafiero & Caputo 1987). Bourne *et al.* (1986a) reported that progesterone levels were elevated in gravid *Tiliqua rugosa*, and reached a maximum during the middle third of the 140 to 170 day gestation period. In this species, a significant proportion of the progesterone is adrenal rather than ovarian in origin (Bourne 1981).

Sperm storage by females over winter was reported by Smyth & Smith (1968) for *Hemiergis peronii*. Mating occurs in autumn, and females retain sperm until ovulation and fertilisation in spring. The oviduct is the site of sperm storage in those species of *Pseudemoia* with similar, desynchronised gonadal cycling (Pengilley 1972). The question of which sex stores the sperm relates to the issue of when mating occurs. In *Hemiergis decresiensis* from the Adelaide area (Leigh pers. comm.). The male stores the sperm, in the vasa deferentia, until mating in spring. This is in contrast to Pengilley's (1972) report of autumn mating in the south-eastern highlands population of *H. decresiensis*, and suggests an unexpected degree of lability in a physiologically and behaviourally complex characteristic.

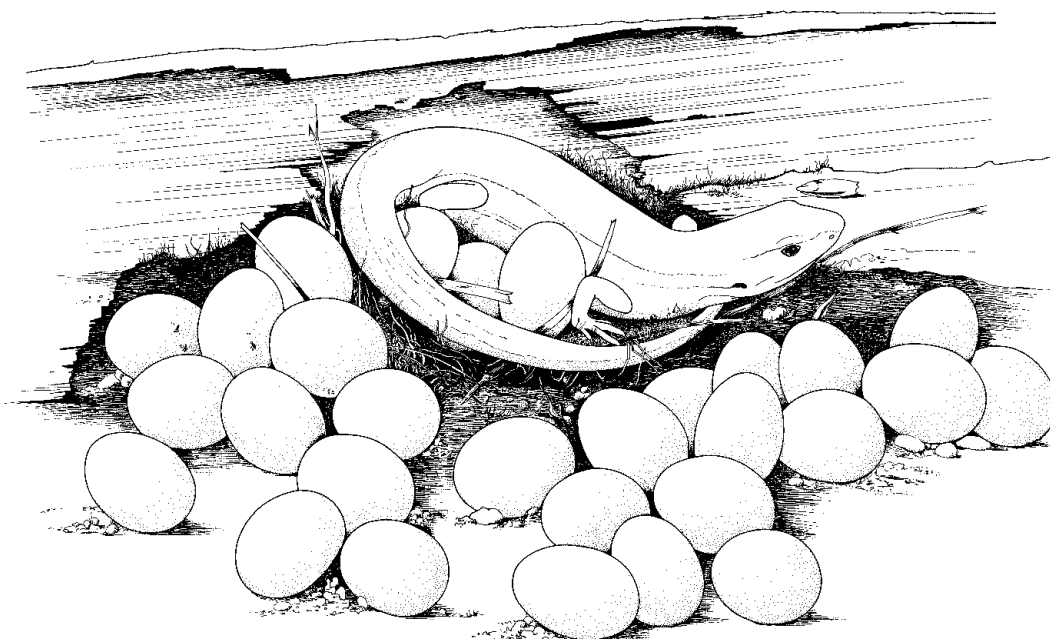
Skinks may be either oviparous or viviparous and there is almost a continuum of modes linking the two extremes, in which oviposition occurs soon after fertilisation, through varying degrees of egg retention to placental viviparity (Shine 1983b). In two Australian species, *Lerista bougainvillii* and *Saiphos equalis*, the degree of egg retention varies geographically (Greer 1989; Robertson pers. comm.), whereby populations from cooler parts of the species ranges are essentially viviparous (Bustard 1964; Rawlinson 1974a), while those from warmer areas produce nearly full-term young in poorly calcified eggs (*S. equalis* and some *L. bougainvillii*), or early embryos in well-calcified, normal eggs (most populations of *L. bougainvillii*).

Several oviparous *Eugongylus* Group skinks oviposit communally (Greer 1989), and large egg aggregations (over 50) have been reported for *Bassiana* (Rounsevell 1978), *Lampropholis* (Fig. 31.8) (Clarke 1965; Mitchell 1959; Wells 1981) and *Nannoscincus* (Robertson pers. comm.). Maternal care, in the form of nest attendance, in species of the non-Australian genus *Eumeces*, has been well documented (Shine 1988c), but until recently there was no indication that any Australian species showed such behaviour. Ehmann (1988) reported briefly on observations of captive female *Calypotis*, *Cautula* and *Saproscincus* and their newly laid eggs; females moved eggs by mouth from one site to another, reburied exposed eggs and seemingly attempted to prevent eggs from becoming too wet or too dry. The degree to which these behaviours persist beyond the post-laying period is not known, nor is the possible contribution to the observations from continued enforced proximity to the eggs as a result of the small size of the containers in which the lizards were kept.

Placentation in Australian skinks was first reviewed in detail by Weekes (1935), but has not been followed up by many subsequent workers. Most viviparous skinks studied have a simple, chorio-allantoic placenta with a large yolk sac, comparable to similar-sized oviparous species (Weekes 1934). Maternal and foetal circulations link simply through thinning and close contact with the epithelium of the maternal oviduct and embryonic chorio-allantoic membranes over the surface of the egg; this placental type is known in *Egernia*, *Eulamprus*, *Hemiergis* and *Tiliqua* (Weekes 1927, 1930). A more specialised placenta is known in *Pseudemoia* where yolk supply is much smaller than for comparable oviparous species (Weekes 1930; Stewart & Thompson 1993) and a specialised, elliptical, allanto-placental region develops in which maternal and foetal tissue interdigitate and fold together deeply (Harrison & Weekes 1925; Weekes 1930). Yaron (1985) reviewed reptile placentation generally, and Ghiara *et al.* (1987) and Blackburn, Vitt & Beuchat (1984) have reviewed the ultrastructural anatomy of the placenta in *Chalcides* and *Mabuya* respectively and its possible role in nutrient supply to the embryo.

Böhme (1988) reviewed hemipenial structure in lizards, although few skinks were considered. Two basic hemipenial types occur in the Australian fauna. One is relatively short and single (Greer 1979b). The second type is bifurcate, with elongate apical extensions, and is regarded as a synapomorphy of the





**Figure 31.8** Communal nesting, as shown by *Lampropholis guichenoti*, is a feature of several skink genera. [J. Thurmer]

*Sphenomorphus* Group. Arnold (1984a) reviewed cloacal and hemipenial musculature of lizards, suggesting that lygosomines may have a derived muscle complex.

Reproductive effort, as relative clutch mass, was summarised by Greer (1989), and Henle (1989a, 1989b, 1989c) has provided further data on this topic. Skinks generally produce clutches which weigh 30 to 40% of the female's body mass.

### Embryology and Development

The early embryological development of *Mabuya* was described by Pasteels (1970), and Dufaure & Hubert (1961) provided a standard set of embryological stages for lizards. Bellairs & Kamal (1981) reviewed lizard embryology in general and Weekes (1927, 1930) illustrated several early embryonic stages of Australian skinks and discussed aspects of development concerned with placental formation. Skinner (1973), also using *Mabuya*, described development of the cranium, hyoid and mandible. Incubation times for eggs are generally between 30 and 60 days (Greer 1989) and gestation in viviparous species is longer, between 50 and 100 days.

Growth of juveniles may be rapid, whereby sexual maturity is reached in less than a year (Henle 1989c; Joss & Minard 1985), or may be more prolonged (Bull 1987). Tilley (1984) found that juvenile *Eulamprus tympanum* grew at similar rates until reaching sexual maturity, after which continued growth occurred at quite uneven rates. Hudson (1989), however, found that uneven growth rates were evident from hatching and birth in *Bassiana duperreyi* and *Pseudemoiapagenstecheri*, so much so that some individuals took a year longer than others to breed for the first time. Like other lizards, skinks should have determinant growth (Estes *et al.* 1988), although the few available studies (for example, Hudson 1989; Tilley 1984) show that the oldest individuals in a population tend to be the largest. Possibly most skinks do not survive long enough to reach an age where growth has ceased completely.

Postembryonic ontogenetic changes include allometry and fusion of some bones of the skull, such as those of the braincase, anterior portion of the frontals in *Tiliqua* (Rawlinson 1974a; Hutchinson 1981) and fusion of surangular to prearticular (Hutchinson pers. obs.). Colour pattern changes during growth are most marked in *Coeranoscincus* (Greer & Cogger 1985; McDonald 1977), in which complex lined or banded juvenile patterns are reduced or lost in adults. In *Cyclodomorphus*, juveniles are usually more brightly patterned with stripes (*C. gerrardii*; Field 1980), spots (*C. melanops* and *C. maximus*, Hutchinson pers. obs.; Shea pers. comm.) or head patches (*C. casuarinae*; Hutchinson pers. obs.) which fade ontogenetically. A red tail forms part of a juvenile colour pattern in many *Morethia* and *Lerista*.

## NATURAL HISTORY

### Life History

Few Australian skinks have been subjected to detailed life history studies. Most skinks are small, weighing less than 10 g, so that by analogy with the better known birds and mammals they might be expected to have high rates of maturation and population turnover. One of the most complete demographic studies of a small Australian species shows precisely this type of life history. Henle (1989c) reported on the life history and ecology of *Morethia boulengeri* in western New South Wales. This small species (adult mass about 1.5 g) shows a high population turnover, in which mortality plus emigration total 84 to 89% of the population per year. Associated with this is a high reproductive effort. Females produce three clutches per year, with a mean clutch size of 2.8 eggs, and both sexes reproduce in their first year. At some of the sites in this study, rates of mortality depended upon both size and body condition.

The breeding biology of the small, abundant, eastern Australian skinks *Lampropholis delicata* and *L. guichenoti* has been studied by several workers (Pengilley 1972; Simbotwe 1985; Joss & Minard 1985). These studies report a similar rapid-maturing, high turnover demographic pattern, confirmed to some extent by direct aging of individuals by skeletochronology (Hudson 1989), which detected no animals as old as two years. In cooler areas (Pengilley 1972), *L. guichenoti* grows more slowly and lives longer, probably reflecting the shorter activity period. In the Sydney area, *L. guichenoti* can produce two broods per year (Joss & Minard 1985).

Not all small skinks follow this rapid-growth, high-turnover strategy. Hudson's (1989) study of *Bassiana duperreyi* and *Pseudemoia pagenstecheri* shows that they mature relatively slowly and are long-lived species. Some individuals of *P. pagenstecheri* breed in their first year, but others take two years to mature, while *B. duperreyi* takes two or three years. Rarity of juveniles between six months and two years of age implies a heavy juvenile mortality, but adults have a relatively long life expectancy of up to seven years.

Some larger species may mature rapidly. Henle (1989a) found that *Ctenotus regius* reached sexual maturity in less than a year, and estimated a mortality rate during spring (September–November) of 67%. Age-specific mortality was not assessed, so that the degree to which this mortality occurs among the juveniles is not known. Taylor (1985) found that *C. taeniolatus*, a temperate relative of *C. regius* and similar in size, took two years to reach sexual maturity. Other species in this medium size range (about 8 to 20 g body mass) are definitely longer-lived. Tilley (1984), using skeletochronology, found that *Eulamprus tympanum* may survive for up to fifteen years, and took two years to mature.

Juvenile mortality is apparently severe, but once these skinks mature, their life expectancy is high. Females had a better survival rate than males, living on average two years longer once sexually mature.

Larger skinks studied so far have proven to be relatively slow-growing species with low fecundity and long life expectancy. Barwick (1965) reported that individuals in his high altitude population of *Egernia cunninghami* took five years to mature, and Bull (1987) estimated that *Tiliqua rugosa* reaches maturity in three years and may survive for twenty or more.

### Ecology

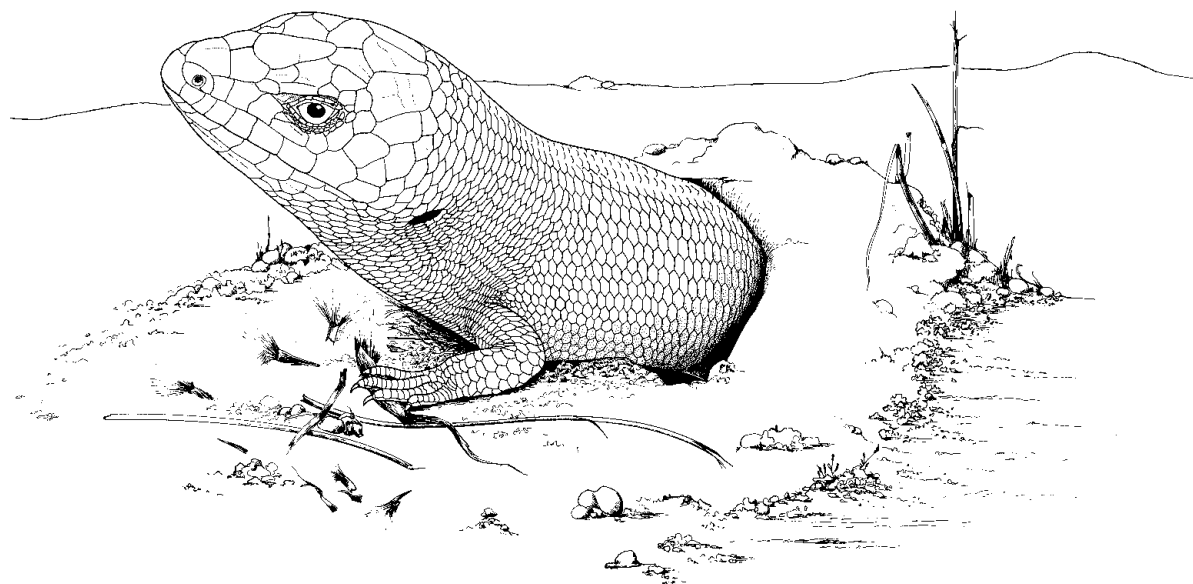
Australian skinks make use of the full range of habitats occupied by terrestrial vertebrates, with the possible exception of the outer tree canopy, though *Emoia longicauda* may come close in this respect (Ingram 1979). Most species are diurnally active on the ground surface, but there are rock specialists, for example the *Egernia cunninghami* species group, various species of *Carlia* (Ingram & Covacevich 1989) and *Niveoscincus* (Hutchinson *et al.* 1989). Members of some genera are primarily arboreal, usually on the trunks and lower branches, notably *Cryptoblepharus* species, *Pseudemoia spenceri* (Rawlinson 1974b; Webb 1985) and *Niveoscincus pretiosus* (Hutchinson *et al.* 1989). These species, as well as others such as *Egernia striolata*, are flexibly arboreal or saxicoline, depending upon the local availability of suitable hiding places, but truly saxicoline species include the alpine species of *Niveoscincus* (Hutchinson *et al.* 1989), several *Carlia* (Ingram & Covacevich 1980, 1989) and the robust, spiny-scaled species of the *Egernia cunninghami* species group.

The water skinks of the *Eulamprus quoyii* species-group are semi-aquatic (Daniels 1987; Daniels, Oakes & Heatwole 1987b) and exploit freshwater stream and lake margins. Other species may include the shoreline as one of several habitats exploited, of which examples are *Niveoscincus pretiosus* (Hutchinson *et al.* 1989), *N. metallicus* (Hutchinson pers. obs.), *Egernia coventryi* (Schulz 1985) and *Lerista arenicola* (Storr *et al.* 1981). *Cryptoblepharus litoralis* (Covacevich & Ingram 1978) and *Emoia atrocostata* (Ingram 1979; McCoy 1980) are confined to this habitat, the former species on rocky shores and the latter in mangroves.

Microhabitats chosen also vary widely. Many species with normal or long limbs are active on the surface of the ground, venturing into open areas to forage. Other species are more cryptic and stay within the shelter of loose leaf litter or inside grass tussocks. Species often show considerable fidelity to particular soil types or landforms. Thus *Ctenotus brooksi*, *C. schomburgkii*, *C. leonhardii* and *C. pantherinus* are restricted to sandridges, to sandplains, to *Acacia*-dominated sites, or to where *Triodia* is present, respectively (Pianka 1969c). The spiny desert grasses of the genus *Triodia* are particularly important. Many skinks spend much or all of their lives in and around *Triodia* tussocks (Pianka 1981; Coventry 1976), and much of the high diversity of Australian desert lizards has been attributed by Pianka to the presence of this grass (see also Morton & James 1988; Pianka 1989).

Saxicoline species may be confined to massive rock outcrops, where deep cracks provide shelter (the rock-dwelling *Egernia* species fit this description), or inhabit boulder screes, where shelter is obtained in the interstices between the loose rocks (Ingram & Covacevich 1980). *Tiliqua adelaidensis* maintains its cryptic lifestyle in the burrows of ground dwelling spiders (Fig. 31.9). Arboreal species tend to live on dead trees or the dead portions of living trees, and use splits in the wood or the space beneath the bark as refuges (Bustard 1970b).

Reduced-limbed species vary greatly in microhabitat exploited. Although often loosely characterised as fossorial, many such skinks do not truly burrow. Instead members of genera such as *Calypotis*, *Hemiergis* and *Nannoscincus* (Robertson



**Figure 31.9** The recently rediscovered pigmy bluetongue, *Tiliqua adelaidensis*, at the mouth of its burrow, a spider's tunnel. (After photo by P. Robertson) [J. Thurmer]

1981) move through dense grass or debris, or infiltrate soil cracks or the galleries of rotting logs. True sand or soil swimming fossorial types are generally recognisable by their wedge-shaped snouts, and often a countersunk lower jaw; the best examples are members of the genera *Lerista* and *Anomalopus*.

Skinks can be very numerous in some localities. Henle (1989c) estimated that *Morethia boulengeri* reached densities of 421 to 1823 individuals/ha in, and adjacent to, arid riverine woodland in western New South Wales, which represents a biomass of 0.6 to 2.4 kg/ha for this small skink. Henle's (1990a) estimate for density of another skink sympatric with *Morethia*, the comparatively gigantic *Tiliqua rugosa*, was one individual per hectare, or a biomass of about 0.8 kg/ha, based on an average adult mass for the area. Bull's (1987) more detailed study of a South Australian population of the same species yielded an estimate of 2.7 individuals/ha, and as the mean adult mass of *T. rugosa* was smaller in the South Australian population (about 575 g), the biomass estimate is again similar, at 1.6 kg/ha. These species are apparently uniformly distributed in their habitat. Other species may be highly clumped because of dependence on a particular microhabitat. Examples of this are found in species of *Egernia*, which may achieve high densities in optimal habitat but be virtually absent from intervening areas, for example *E. cunninghami* (Barwick 1965) and *E. striolata* (Bustard 1970b).

Skinks are usually solitary, but some are colonial, the best examples being species of *Egernia*, such as *E. multiscutata* (Coventry & Robertson 1980), *E. whitii* (Hickman 1960), *E. cunninghami* and *E. saxatilis* (Hutchinson pers. obs.), and some of the arboreal species in the *Eugongylus* Group, for example, *Pseudemoia spenceri* (Rawlinson 1974b), *Niveoscincus pretiosus* and *Cryptoblepharus virgatus* (Hutchinson pers. obs.). In these species, individuals may be very tolerant of one another and show little aggression, for example, *E. cunninghami* (Greer 1989), or, paradoxically, aggression may be quite intense, as shown by members of the *E. whitii* complex (Hutchinson pers. obs.). In all of the species mentioned above, juveniles and subadults may share home sites with adults, presumably their parents (Hickman 1960).



Territoriality and home range have not been studied extensively in Australian skinks. The few available studies suggest a variety of strategies. Some species show very strong attachments to particular sites and move very little. Examples are the species of *Egernia* which construct their own burrows (Hickman 1960; Pianka & Giles 1982) or those species for which natural refugia are essential for survival, such as the crevices in logs or rocks used by *Egernia striolata* (Bustard 1970b) and *Eulamprus tympanum* (Tilley 1984). These species tend to defend their home sites strongly and to move only short distance from them. An intermediate strategy is for a species to move regularly through a home range, in which there may be one or more refuges which provide shelter. Such home ranges may overlap considerably and levels of overt aggression are relatively low, as in species of *Tiliqua* (Satrawaha & Bull 1981; Yeatman 1988). Some species, especially smaller skinks for which an abundance of refuges are available, show little evidence of even a home range (Milton 1980).

Skinks are generally regarded as 'widely foraging' predators (Huey & Pianka 1981), although Henle (1989a) and Pianka & Giles (1982) suggest that some species of *Egernia* (*E. inornata*, *E. striata* and *E. striolata*) are best described as sit-and-wait predators. *Ctenotus taeniolatus* uses both foraging modes (Taylor 1986), and adults actually spend much more time sitting-and-waiting than foraging widely. As predicted by Huey & Pianka (1981), periods of wide foraging are much more productive in terms of prey capture frequency (three-fold).

Scincid diets consist mostly of arthropods (Brown 1986, 1988; Bustard 1970b; Henle 1989a, 1989b; Pianka 1986; Taylor 1986; Wilhoft 1963), and skinks are predominantly opportunistic feeders (Brown 1991). Few reports indicate either dietary specialisation or predation on vertebrate prey. Large species of *Tiliqua* and *Egernia* are omnivores (Brown 1991), although the enlarged cheek teeth of both *Cyclodomorphus* and *Tiliqua* suggest that their diets would include hard-shelled prey, such as beetles and snails, as has been observed in field studies (Dubas & Bull 1991; Shea 1988; Yeatman 1988). *Cyclodomorphus gerrardii* is probably a specialised mollusc-eater (Field 1980).

The fossorial *Coeranoscincus reticulatus* is a specialist earthworm feeder (Ehmann 1987; McDonald 1977), and the same may be true of *C. frontalis*, which has similar (although not identical) dentition (Greer & Cogger 1985). Termites form the predominant prey of several of the species of *Ctenotus* studied by Pianka (1969c) in the Great Victoria Desert, but it is not yet clear whether this represents opportunism, in taking advantage of an abundant resource, or a genetically programmed adaptation. Monitoring of populations over more than one season has shown that one species, *Ctenotus pantherinus*, acts as a termite specialist year-round, but other sympatric *Ctenotus* may prey heavily on termites at some times, while taking very few at others (James 1991). *Eulamprus quoyii* takes up to a quarter of its prey from the aquatic environment (Daniels 1987), including anuran tadpoles, which it catches as they rise to the water surface. Small skinks are a minor dietary component for larger skinks; specimens of the genera *Lerista*, *Morethia*, *Menetia* and *Pseudemoia* have been found in the guts of species of *Ctenotus* (Brown 1991; Henle 1989a).

Alpine skinks of the genus *Niveoscincus* include nectar and berries (possibly *Podocarpus*) in their diet (Kirkpatrick, Hutchinson, McQuillan & Nielsson 1991), and larger skinks take variable amounts of leafy or floral vegetation (Brown 1991). Only a few skinks are predominantly vegetarian, for example, large species such as *Tiliqua rugosa* (Dubas & Bull 1991; Henle 1990a) and the members of the *Egernia cunninghami* species group (Barwick 1965). Pollock's (1989) demonstration that *E. cunninghami* is able to survive and grow on a vegetarian diet right from birth, indicates considerable digestive efficiency, and is contrary to the generalised prediction of Pough (1973) that herbivory is only likely to be efficient in large lizards (greater than 100 g). However, no

Australian species is known to be an obligate vegetarian, and even species such as *E. cunninghami*, in which plant material forms over 92% of the diet (Brown 1991), will gorge on insect prey, such as swarming field crickets, *Teleogryllus*, when they are abundant (Hutchinson pers. obs.), and will grow faster if reared on an animal rather than a plant diet (Pollock 1989).

Taxa recorded as predators of skinks include mammals, birds, other reptiles and some invertebrates (Daniels & Heatwole 1984). Among the most important predators are several genera of elapid snakes, notably *Cacophis*, *Demansia*, *Drysdalia*, *Rhinoplocephalus* (= *Cryptophis*), and *Suta* (including *Unechis*), which feed predominantly or entirely on lizards, most of which are skinks (Shine 1980a, 1980b, 1981b, 1984a, 1988a). Most skinks are diurnal and surface-dwelling and it could be expected that their snake predators would have similar habits, as is true for *Demansia* and *Drysdalia*. However, an interesting strategy has been adopted by the other genera, which are nocturnal and locate and prey upon diurnal skinks in their night-time refuges.

The pygopodid lizard *Lialis* is an ambush predator of lizards and captures skinks almost exclusively (Murray, Bradshaw & Edward 1991; Patchell & Shine 1986b). *Lialis* has numerous, peculiar, recurved teeth which are attached ligamentously ('hinged'), and are similar to those seen in snake genera, such as the Asian *Sibynophis* and South American *Scaphiodontophis*, which also prey mainly on skinks (Patchell & Shine 1986c; Savitzky 1981). These predators are thought to have developed the dentition in response to the presence of the skin-toughening osteoderms of skinks (Savitzky 1981), whereby the numerous teeth catch on, rather than pierce, the scale edges. On this basis, *Lialis* appears to have adapted more completely to eating skinks than any other Australian predator.

Other reptile predators recorded as preying on skinks include varanids (King & Green 1979; Pianka 1968, 1970b; Shine 1986d) and the colubrid snake *Dendrelaphis punctulatus* (Webb & Rose 1985; Shine 1991c). Avian predators include accipitrids, falconids and alcedinids (Barker & Vestjens 1989), artamids (Lea & Gray 1936) and corvids (Rowley & Vestjens 1973). Foxes (Coman 1973; Croft & Hone 1978) and domestic cats (Jones & Coman 1981), regularly include reptiles as a minor dietary component.

Several invertebrate taxa are known to prey on small vertebrates and have been recorded eating skinks. Examples are the spider *Latrodectus*, noted feeding on *Anomalopus* and *Cryptoblepharus* (Raven 1990) and *Lampropholis* (McKeown 1952), the scorpion *Urodacus* observed feeding on *Morethia* (Hutchinson pers. obs.) and *Lerista* (Henle 1989b), and the centipede *Scolopendra* feeding on *Bassiana* (Robertson pers. comm.).

Parasites of skinks include ectoparasitic mites and ticks (Bull, Burzacott & Sharrad 1989; Domrow 1987; Domrow & Lester 1985; Roberts 1970) and a variety of internal helminths (Adamson 1984; Ali, Riley & Self 1984; Angel & Mawson 1968; Daniels 1990; Daniels & Simbotwe 1984; Johnston & Mawson 1947; Jones 1985b) and protozoans (Ayala 1978; Johnston 1932; Mackerras 1961; Paperna & Landau 1990).

## Behaviour

Much of skink behaviour is associated with thermoregulation. Most skinks are diurnal and heliothermic, and most studies of thermoregulation have been carried out on temperate species (Bennett & John-Alder 1986; Brattstrom 1971a; Spellerberg 1972a, 1972b). Preferred body temperatures range from a low of 20.1°C in *Nannoscincus maccoyi* (Robertson 1981) to 38.1°C in *Ctenotus leonhardii* (Pianka 1986). Mean values for critical thermal maxima range from 45°C down to 32.9°C (Greer 1980a) and some rainforest species, such as *Calyptotis thorntonensis* (Greer 1983b) and *Saproscincus graciloides* (Hutchinson pers. obs.) are so heat sensitive that they may die after being held in

the hand for a relatively brief period of time. At the other extreme, several cold temperate species can survive supercooling, for example, to  $-1.2^{\circ}\text{C}$  in *Eulamprus kosciuskoi* (Spellerberg 1976). Garland *et al.* (1991) concluded that preferred temperature and critical thermal maximum are significantly positively correlated in Australian skinks but the suggestion by Huey & Bennet (1987) that there is also a positive correlation between optimum exercise temperature and either preferred or critical temperatures could not be confirmed.

Spellerberg (1972a) and Rawlinson (1974a) have distinguished two strategies among temperate heliothermic species: the shuttling heliotherms (members of the *Eugongylus* and *Sphenomorphus* Groups) and the posturing heliotherms (members of the *Egernia* Group). Shuttling heliotherms control the body temperature almost entirely by relocation, constantly moving from sun to shade when active, whereas posturing heliotherms tend to stay in a preferred area, but reduce or increase heat uptake by altering the angle of the body to the sun or adopting heat-absorbing or retarding postures (Fig. 31.10). This option may be open to the *Egernia* group purely because of the large size of most species, which enables significant physiological control of temperature flux (Fraser & Grigg 1984). As a consequence, or perhaps it is a cause, shuttling heliotherms show wide normal activity ranges, low voluntary maxima and weakly evident preferred body temperature, while posturing heliotherms have a relatively narrow normal activity range, higher voluntary minima and body temperatures grouped tightly around the preferred temperature.

Thigmothermic skinks include all of the fossorial and degenerate-limbed forms and nocturnal species such as *Eremiascincus*. Some rainforest genera, such as *Gnypetoscincus*, are probably also thigmotherms (Greer 1989), although they have not studied in detail. Thigmotherms have generally lower thermal preferenda than do heliotherms, and narrower thermal tolerances (Rawlinson 1974a). Bennett & John-Alder (1986) found that *Eremiascincus* and *Hemiergis* species selected warmer body temperatures at dusk and early evening than they did during the day. This is explicable as a strategy which minimises energy loss during inactivity while the warmer temperatures selected during the time of peak activity permit greatest metabolic scope.

Many physiological processes only function well or even at all when the lizard's body temperature is at or close to the preferred body temperature. As an example, Hulbert & Williams (1988) demonstrated that the thyroid, a prime



**Figure 31.10** Thermoregulatory posture of the water skink, *Eulamprus tympanum*, in which the limbs are raised and held along the sides of the body. (After photo by M. Hutchinson)

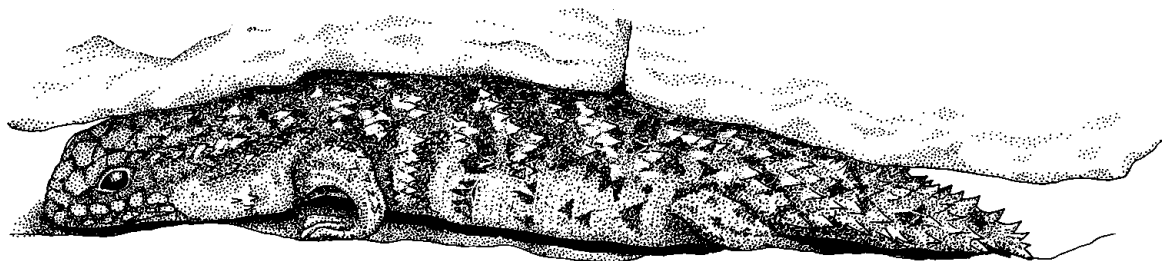
[J. Thurmer]

controller of metabolic rate, is inactive at 20° to 22°C in *Tiliqua rugosa*, and this species is also insensitive to injected thyroxin at this body temperature; at 30° to 32°C thyroid activity and thyroxin sensitivity are fully functional.

Defensive behaviour includes crypsis, twisting, biting, tail-waving and threat displays. Large species of *Tiliqua* have an elaborate threat display, which includes body inflation, spreading the ribs and tilting the body towards the stimulus, hissing, gaping and tongue protrusion. The elongate *Cyclodomorphus casuarinae* rears the forebody while keeping the front legs pressed tight against the flanks, flickers the tongue and snaps the jaws, and produces a very snake-like overall effect. Most other species flee to cover when detected and will twist and bite if held. Longitudinal twisting of the body is particularly apparent in species of *Lerista* which are amazingly strong for their size. Spiny *Egernia* species hold the limbs against the body and arch the back to more firmly lodge themselves into the crevices in which they shelter (Fig. 31.11).

Caudal autotomy (Arnold 1984b, 1988; Bellairs & Bryant 1985; Dial & Fitzpatrick 1984; Greene 1988; Vitt & Cooper 1986) is an important method of predator avoidance in all skinks except *Tiliqua* and the short-tailed *Egernia depressa* and *E. stokesii* (both *Egernia* species use the short, flat and extremely spiny tail to block the entrances to their crevice retreats (Fig. 31.11)). The riparian *Eulamprus quoyii* alters its behaviour after autotomy, and seeks shelter on land or relies on crypsis, rather than swimming, which is inefficient in tailless lizards (Daniels 1985a; Daniels & Heatwole 1990). Juveniles of most species of *Morethia* and many *Lerista* have red tails, or blue in *L. chalybura*, which may serve to draw the attention of a predator towards this disposable structure. In *Eumeces*, blue juvenile tail colouring may be more important in acting as a social signal to inhibit attacks by adult males (Clark & Hall 1970). The bright red tail in the *Morethia taeniopleura* species group, and the blue tail of *Ctenotus calurus* are retained into adulthood. The costs and benefits of having a tail which draws attention have not been determined. Clearly, it is of advantage to lizards for predators to be encouraged to seize them by the tail rather than by the body, but the bright colour seems likely to compromise crypsis. A possible explanation is that the species concerned are particularly 'busy', widely foraging, surface active species (Greer 1989; Pianka 1969c). When inactive they are under litter, so that crypsis would count for little, and when active, they are likely to betray themselves by their movement. In such a case, detection being inevitable, it is easier to see the value of an eye-catching target to misdirect the attack of a visual predator.

In view of their strong development of chemical sense organs, skinks could be expected to use chemical cues to mediate social interactions. Studies of American species in the genera *Eumeces* and *Scincella* show that this is indeed the case, with skinks able to identify conspecifics and sex of individuals by scent



**Figure 31.11** Skinks of the *Egernia cunninghami* species group, such as *E. depressa* shown here, wedge themselves into crevices for defence. The spiny scales discourage attack by predators and catch on the surroundings, preventing dislodgement. (After photo by G. Shea) [M. Cilento]



(Cooper & Vitt 1987; Duvall, Herskovitz & Trupiano-Duvall 1980; Trauth *et al.* 1987). The capacity for individual recognition shown by *Tiliqua rugosa* (Bull 1988) and for recognition of 'self' versus 'stranger' scent by *Tiliqua scincoides* (Graves & Halpern 1991) suggests social behaviour that is more subtle than the simple extremes of aggressive combat or indifference previously invoked (Done & Heatwole 1977).

Agonistic behaviour involving neck arching, nose to tail side-on posturing and biting is known to vary considerably in intensity between related species (Done & Heatwole 1977, *Eulamprus*). Done & Heatwole (1977) reported that periods of fighting in captive groups of *Eulamprus kosciuskoi*, mainly among males, were followed by emergence of a single despot which dominated all other lizards and also defended an exclusive core area, although it was active throughout the enclosure. The degree to which these observations are artifacts of captivity has not been assessed by field studies. Little of the expected level of male-male aggression has been recorded in species showing strong dichromatism, for example, *Carlia*, *Pseudemoia* (Maryan 1989, reported combat in *Bassiana trilineata*), and there seems to be no record of male-female displays which emphasise male colouration. Work by Whittier (1992) on *Carlia rostralis* shows that males do use throat colour (black in males, white in females) to make an initial identification of a conspecific's sex, but chemosensory cues are also important.

Mating behaviour in skinks is not well recorded, and there are no records of any preamble apart from approach and pursuit by the male (Wilhoft 1963; Done & Heatwole 1977). Before copulation, the male grasps the female in his jaws, usually seizing the skin over the shoulders or with the upper jaw on the dorsal surface and the lower jaw on the ventral surface. This grasp can be forceful enough to draw blood (Hutchinson pers. obs.) and can leave characteristic V-shaped lines, termed 'mating marks' by Pengilley 1972. A receptive female becomes relaxed in this grasp and raises her tail; the male wraps the rear of his body under the base of the female's tail and a hemipenis is erected into the female's cloaca.

Bull (1988, 1990) discovered a unique behavioural phenomenon in the well-studied *Tiliqua rugosa*: monogamy with mate fidelity. During the spring mating season, the same male-female pair remains together for up to eight weeks, and in successive years 74% of the females and 67% of the males recaptured were with the same partner. Monogamy within a breeding season was predicted by Stamps (1983) for large, non-territorial lizards, but breeding season fidelity is unexpected in a species which is solitary for the rest of the year. Bull suggested that fidelity may ensure that males mate with known mature females, rather than risking mating with an immature, or that the familiarity of the partner might facilitate quicker recognition, mating and thus earlier breeding.

Members of the *Egernia whitii* species group are able to construct quite complex burrow systems. At their simplest (Hickman 1960; Pianka & Giles 1982), burrows have a main entrance and a blind tunnel ending just short of the surface, through which the skink can escape if threatened. More elaborate systems can occur (Coventry & Robertson 1980; Pianka & Giles 1982; Hutchinson pers. obs.) in which there are multiple entrances, branching underground tunnels and even an underground 'latrine' (Hutchinson pers. obs. for *Egernia inornata* in the Simpson Desert).

### Economic Significance

Skinks have virtually no direct economic impact. Waite (1929) reported that *Tiliqua rugosa* was a minor pest of soft fruit, such as strawberries and tomatoes, and that it had been 'charged with eating fowls' eggs'. The popularity of the large, omnivorous species of *Egernia* and *Tiliqua* as pets leads to a small-scale trade in these animals in those states where commercial sale is legal.

Skinks are otherwise only likely to impinge on the economy as victims of human activities, leading to the diversion of resources to ensure the preservation of species or populations. No species of skink is known to have become extinct in Australia since white settlement, but several, mainly those with localised geographic distributions, are threatened or vulnerable to varying degrees. Examples are *Tiliqua adelaidensis* (Armstrong *et al.* 1993), *Eulamprus leuraensis* (Shea & Petersen 1985), *Ctenotus lanceolini* and *Lerista lineata* (Ehmann & Cogger 1985) and *Niveoscincus palfreymani* (Rounsevell, Brothers & Holdsworth 1985). Resources are also directed to stemming the overseas smuggling trade (of unknown scope, Ehmann & Cogger 1985) in Australian reptiles. Many of the larger skinks are highly prized by European and North American reptile fanciers.

## BIOGEOGRAPHY AND PHYLOGENY

### Distribution

Lygosomine skinks are worldwide in distribution and are the only skinks to occur in the Australian zoogeographic region (Greer 1970a). Geographically, the nearest non-lygosomines are the scincine genera *Brachymeles*, in the Philippines and Borneo (Hikida 1982), and *Davewakeum* in Thailand (Heyer 1972).

Skinks occur in all habitats and throughout Australia, from its southernmost land point (*Niveoscincus palfreymani*, Rounsevell *et al.* 1985) to the islands of Torres Strait, and from sea level to the summit of Mt Kosciuszko. In fact, the altitudinal range is encompassed by a single species, *Pseudemoia entrecasteauxii* (Hutchinson & Donnellan 1992). South-eastward from Wallacea, skinks are diverse through Melanesia to New Caledonia and New Zealand, and the genus *Emoia* has radiated through Polynesia.

Other centres of diversity are in sub-Saharan Africa and Madagascar. Outside these areas, skinks are much less diverse, although still widespread, being found through western Asia, North Africa and Mediterranean Europe and throughout temperate North America south to northern South America. In these latter areas, most species belong to a few widespread genera, notably *Eumeces* and *Mabuya*.

Cogger & Heatwole (1981) provided overall summaries of skink species density throughout Australia. In some areas, for example, western and arid Australia, the proliferation of species in two genera, *Ctenotus* and *Lerista*, leads to high species abundance though there is actually only moderate diversity at the generic level. The richest area is south-eastern Queensland which supports over 40 skink species in 15 genera. The distribution of skink genera within the major biogeographic subregions of Australia is shown in Table 26.2.

*Lampropholis delicata* has become established in two other countries, New Zealand and Hawaii (McKeown 1978; Robb 1980), presumably following accidental introduction. In Hawaii, this species has been accused (McKeown 1978) of supplanting the resident species, *Lipinia noctua*, itself probably a colonist which reached the islands with the Polynesian people. In New Zealand this species may occupy a previously empty niche, as it is considerably smaller than any of the native New Zealand skink species.

### Affinities with other Squamates

The Scincidae are well-established as members of the lacertilian infraorder Scincomorpha (Camp 1923), which also includes the Cordylidae, Gerrhosauridae, Gymnophthalmidae, Lacertidae, Teiidae and Xantusiidae (Estes *et al.* 1988; Lang 1991; Presch 1988). None of these other families occurs in Australia, the nearest being the lacertid genus *Takydromus* which reaches Java (De Rooij 1915).

Relationships within the Scincomorpha are still uncertain. Greer (1979b) suggested that the gerrhosaurs are the closest relatives of skinks, although this may mean only that the two taxa share several features which are primitive for a scincid + gerrhosaurid + cordylid clade. Estes *et al.* (1988) indicated that a number of synapomorphies favour such a clade, which they identified as the superfamily Scincoidea. However, the study by Presch (1988), which employed a data set partly overlapping that used by Estes *et al.* (1988), placed the gerrhosaurs and cordylids closer to the Xantusiidae than to the skinks. Lang (1991) redefined the Cordylidae and reinstated the Gerrhosauridae as a separate family. He supported Estes *et al.*'s (1988) concept of a superfamily Scincoidea and found that the evidence favouring gerrhosaurs as the sister group of skinks was significant, although he preferred the arrangement: ((Cordylidae, Gerrhosauridae) Scincidae). Estes *et al.* (1988) and Lang (1991) noted convergence in almost all of the morphological characters used to establish relationships between the scincomorphan families, leading to uncertainties in phylogenetic interpretation.

The possibility that the Scincidae might be paraphyletic potentially confounds the situation. Studies by Rieppel (1984a) and Greer (1985), as well as the review of Estes *et al.* (1988), showed that the enigmatic limbless lizards of the family Dibamidae share many characteristics with acontine and feyline skinks. The latter two studies equivocated on the taxonomic position of the dibamids, because of the many autapomorphic and lost characters of these extremely specialised burrowers, but it seems possible that future definitions of the Scincidae might have to include dibamids.

### Affinities within the Scincidae

The phylogenetic relationships within the family are being unravelled slowly, and most progress has occurred since Greer began his studies of phylogeny. The current subfamilial scheme (Greer 1970a) defines three derived taxa (Lygosominae, Acontinae and Feylininae) and one grade group, the stem group Scincinae (see Fig. 26.7).

The possible paraphyly of the scincines is an obstruction to understanding the relationships of the Lygosominae. Most scincines are actually highly derived in being attenuate litter swimmers and fossorial types, but retain the primitive states of the three characters which define the Lygosominae (the Mascarene-Seychelles genera are partial exceptions, Greer 1970b). Relatively few scincine taxa retain well-developed pentadactyl limbs, 26 presacral vertebrae and relatively unmodified head shields, all characters retained in the 'ancestral lygosomine'. The genus *Eumeces* comes close to being a model for the sister taxon of the Lygosominae, but only because it retains the plesiomorphic character states noted above. Because of its primitiveness, *Eumeces* also qualifies as the sister group of all other skinks.

In Australia and its external territories, all skinks belong to the subfamily Lygosominae. Although some authors have singled out the distinctive genera *Egernia* and *Tiliqua* as having separate affinities, for example, Mittleman (1952), as Scincinae, and Fuhn (1972), as Tiliquinae, they possess the three lygosomine synapomorphies (Greer 1970a; 1986a): fused frontal bones, well-

developed palatal laminae (which make contact medially in almost all lygosomines) and the antero-ventral extremity of the frontal is separated from the antero-dorsal extremities of the palatines by the expanded prefrontals.

Greer (1979b) identified three monophyletic lineages within the Australian lygosominae, termed the *Sphenomorphus*, *Egernia* and *Eugongylus* Groups. Later, Greer (1989) expanded his *Egernia* Group to combine it with several other genera, previously informally assembled as the *Mabuya* Group (Hutchinson 1981). However, as there is no strong evidence for the monophyly of the *Mabuya* Group, this review continues to use the earlier (Greer 1979b) concept of the *Egernia* Group, which is monophyletic based on biochemical and chromosomal evidence (Hutchinson 1981; Baverstock & Donnellan 1990; Donnellan 1991a). The current composition of these groups is shown in Table 31.1. Phylogenetic relationships between these three were set out by Greer (1979b), who showed that the *Sphenomorphus* Group is the sister lineage of the other two. Relationships within each lineage and between them and other lygosomines are not yet well understood.

The *Sphenomorphus* Group is the most morphologically diverse and most speciose skink lineage in Australia. However, it is the least well understood in terms of intergeneric relationships. Greer & Parker (1967) tried to unravel relationships within the group by concentrating on the huge and obviously artificial stem genus for the group, *Sphenomorphus*. They suggested the existence of two major radiations, termed the *variegatus* and *fasciatus* groups. This has not yielded much phylogenetic information, especially in Australia where the unmodified members of the *Sphenomorphus* Group tend to show intermediacy in the characters used to diagnose the *variegatus* and *fasciatus* assemblages, and also because much of the Australian fauna consists of highly derived taxa. Relationships within the group must be summarised on a genus by genus basis, but for many genera, including the largest, *Ctenotus*, there are no hypotheses on such relationships.

The genus *Sphenomorphus* in Australia has consisted of those members of the *Sphenomorphus* Group too generalised to be placed in other genera; it is a grade taxon. The morphology of the type species of *Sphenomorphus* indicates that this name applies strictly to a primarily Melanesian group of species not present in Australia. Recently, Cogger (1986) and Greer (1989) have adopted the use of *Eulamprus* for the larger, viviparous species and *Glaphyromorphus* for the more elongate, short-limbed forms. Some data (Greer 1989, 1992) indicate that the former taxon may be monophyletic, but the remaining Australian '*Sphenomorphus*' form only an irreducible cluster of species allocated to a genus (*Glaphyromorphus*) by default.

Within the polyphyletic *Glaphyromorphus*, possible sister species have been identified for *Lerista* (*G. crassicaudus* species group, Greer 1979c), *Eremiascincus* (the *G. douglasi* species group, Greer 1979a) and *Hemiergis* (*G. gracilipes*, Choquenot & Greer 1989; Hutchinson 1983). A sister-group relationship has also been proposed between the genera *Calyptotis* and *Saiphos* (Greer 1983b).

Recent attempts to elucidate intergeneric relationships within the *Sphenomorphus* Group using microcomplement fixation comparisons of serum albumin have not been very informative. The principal finding of these studies (Donnellan pers. comm.) is that all Australian genera are closer to each other than to any exotic taxon, in spite of the wide variety of morphologies. However, relationships within Australia have not been clarified. Some lineages, for example *Ctenotus*, seem to have originated earlier than others, but the overall amount of albumin sequence divergence within the Australian *Sphenomorphus* Group is too small and too evenly spread to enable the generation of well-resolved phylogenies.



The *Egernia* Group has relatively low generic diversity, and only four genera are currently recognised: *Cyclodomorphus* (Shea 1990), confined to Australia, *Egernia* and *Tiliqua* which are primarily Australian, with one species in each occurring in New Guinea, and *Corucia*, a Solomon Islands endemic. *Cyclodomorphus* and *Tiliqua* are sister genera (Shea 1990). Their close relationships have long been recognised, generally by combining the two as *Tiliqua* (Hutchinson 1981; Mitchell 1950; Smith 1937). The problem genus is *Egernia*, which is a grade group of relatively unspecialised species. Several more or less distinct species groups are recognisable in *Egernia* (Horton 1972; Storr 1978b), but relationships among them are poorly understood, and the relationships between *Egernia* and the other Group members are also not yet clear. One derived character state present in *Egernia* is the closure of the secondary palate by extensions of the vomers (Hutchinson 1981; Greer 1989). However, *Corucia* has the same structure (Hutchinson 1989), so that the feature may be primitive for the Group as a whole, or may define only a *Corucia* + *Egernia* lineage within the Group.

The *Eugongylus* Group has been subjected to the greatest scrutiny of the three, and is better understood in terms of its internal relationships. The core of the group has been the genus *Leiopisma*, which in Boulenger's scheme was the largest of several sections within his unwieldy genus *Lygosoma*. Greer (1974) greatly reduced the size of this genus by describing several new genera and modifying or validating other generic groupings suggested by earlier workers, notably Mittleman (1952). Hardy (1977), Sadler (1987) and Hutchinson *et al.* (1990) have divided the genus further, and, to varying degrees, the four studies have also shed light on the relationships between the genera of this group.

Comparisons of the molecule serum albumin using micro-complement fixation suggest that within Australia several lineages arose early in the history of the *Eugongylus* Group (Hutchinson *et al.* 1990). One of these is represented by the genera *Bassiana*, *Morethia* and *Pseudemoia* and probably also *Proablepharus*; the latter genus was not included in the biochemical study of Hutchinson *et al.* (1990), but its affinities have been discussed by Greer (1980b). The grouping based on biochemistry is supported by chromosomal data (presence of an XX/XY chromosome heteromorphism in males; Donnellan 1985), morphology (combined elevated presacral vertebral counts of 28 to 30 or more) and red breeding colouration in males. Another lineage which is biochemically cohesive but less easy to define morphologically consists of *Lampropholis*, *Saproscincus*, *Niveoscincus*, *Cautula*, *Bartleia*, *Carlia*, *Lygisaurus* and *Nannoscincus*. Within this group, four genera (*Carlia*, *Lampropholis*, *Saproscincus* and *Lygisaurus*) cluster biochemically, share two derived morphological character states (the beta palate and a mitten-like hemipenis, Greer 1989) and probably form a sub-lineage. The pattern of relationships among the other genera in this second lineage is not yet clear. Genera which are not obviously part of either of the radiations identified by MC'F include *Menetia*, *Cryptoblepharus*, *Emoia* and *Eugongylus*. Greer (1989) tentatively suggested a relationship between *Cryptoblepharus* and *Menetia*. Cogger (1992) placed the Lord Howe/Norfolk Island endemic *lichenigerum* in the Australian genus *Pseudemoia*. However, it is immunologically remote from the Australian mainland species and probably close to the New Zealand genera *Cyclodina* and *Oligosoma* (Hutchinson *et al.* 1990).

Greer (1989) reported that the fusion of the atlantal neural arches to the centrum could be used to define a monophyletic lineage within the *Eugongylus* Group. Such a division does not completely accord with the biochemical and some other morphological data, but does support the association of the beta palate genera with *Nannoscincus*, *Cautula* and *Bartleia*, and also links *Cryptoblepharus* and *Menetia* with this group. Points of difference between the relationships indicated by neural arch condition and primarily biochemically-

derived phylogenetic schemes include the relationships of *Pseudemoia* and *Nannoscincus*. Based on MCF data, *Pseudemoia* is most closely related to *Bassiana* and *Morethia*, taxa with the atlantal neural arches not fused to the centrum. If this is the true state of relationships, then neural arch fusion has occurred in parallel in *Pseudemoia* and the other Australian species, or *Bassiana* and *Morethia* have undergone a reversal, and other features common to the three genera (heteromorphic XY chromosomes; elevated presacral count; males with red ventral colouration) are convergent or primitive. Parallel evolution of the fused condition has probably occurred within *Niveoscincus*. Serum albumin (Hutchinson *et al.* 1990) and electrophoretic comparisons (Hutchinson & Schwaner 1991) provide very strong evidence that *N. palfreymani* (neural arches fused to centrum) is more closely related to other *Niveoscincus* (neural arches not fused to centrum) than to other taxa with the fused condition.

*Nannoscincus* as presently recognised comprises one Australian species and five in New Caledonia (Sadler 1990). '*Nannoscincus*' *graciloides* (Czechura 1981) is morphologically very distinct from the other species in the genus, and was not included by Sadler (1987) when he revised the genus. In colour pattern and proportions, *graciloides* is much closer to *Saproscincus*, especially *S. tetradactylus* (Greer & Kluge 1980). For this review it is included in *Saproscincus*, although *graciloides* lacks (Greer 1974) the beta palate shared by all other *Saproscincus*. If *N. maccoyi* is congeneric with the New Caledonian species, then a member of this genus must have crossed the ocean gap between Australia and New Caledonia relatively recently, probably post-Miocene, given the low level of albumin divergence between *N. maccoyi* and genera such as *Lampropholis* and *Cautula* (Hutchinson *et al.* 1990). MCF data are not available for New Caledonian species of *Nannoscincus*, but data on other New Caledonian skinks, as well as skinks from other land masses outside Australia consistently suggest no recent interchange between the two faunas. Sadler (1990) has placed *N. maccoyi* in a separate subgenus, *Nannoseps*; perhaps this subgenus will prove to warrant full generic status.

A clearer understanding of relationships within genera is beginning to emerge. Early definitions of subgroups within genera were mainly attempts to assist taxonomic descriptions, and the species groups of Storr *et al.* (1981) in *Ctenotus* and *Lerista* are good examples. However, other workers were interested in evolutionary relationships, and tried to define lineages reflecting phylogeny (*Egernia*, Horton 1972; Australian *Leiopisma*, Rawlinson 1975). Recent studies are based on more explicit analyses of morphology (*Lerista*, Greer 1986c; 1990b; *Morethia*, Greer 1980b) or on biochemistry (*Niveoscincus*, Hutchinson & Schwaner 1991).

### Fossil Record

The fossil record of skinks worldwide is poor, and until recently was practically non-existent in Australia. Estes (1984) described the only pre-Pleistocene skink from Australia, a species of *Egernia* which was left unnamed as to species. He also reported the presence of *Tiliqua* in this deposit but no description was provided. These finds are from the Etadunna formation of northeastern South Australia, dated at the time of Estes' writing as Middle Miocene (*ca.* 15 million years ago), but now thought to be Late Oligocene to Early Miocene (21 million years ago, or earlier, Flannery 1988; Archer, Godthelp, Hand & Megirian 1989). Pledge (1992) reported *Tiliqua* from cave deposits of probable Pliocene age from the Yorke Peninsula, South Australia.

The extensive Tertiary limestone deposits near Riversleigh, Queensland, have yielded abundant vertebrate remains, including evidence of a diverse skink fauna. Preliminary study of this material has already identified a new and dwarfish species of *Tiliqua* (Shea and Hutchinson 1992) and many other taxa

remain to be described (Hutchinson 1992). Most of the Riversleigh skinks are from the System B sites of Archer *et al.* (1989), and probably date from the Early Miocene. All three of the major lineages of lygosomines in Australia were present in Australia at this time; the *Sphenomorphus* Group is the most abundant and the *Eugongylus* Group the rarest. Among the remains (mostly dentaries, maxillae and partial lower mandibles) are forms virtually indistinguishable from living taxa, such as some species groups of *Eulamprus* and *Egernia*, while there are also some distinctive *Sphenomorphus* Group fossils which do not closely resemble any of the living species examined so far.

The Riversleigh finds indicate that the Australian skink radiation predates the Oligo-Miocene boundary, implying that the origins of the three Australian lineages date back to the early Tertiary at least. The fossil data are in broad accord with the MCF data (Baverstock & Donnellan 1990) which suggested that the Australian skink lineages have been separate from the earliest Tertiary. These fossils also indicate that considerably older finds, possibly Mesozoic, will be required to clarify the ultimate time of arrival of the skinks in Australia, and the extent to which the present diversity was generated within Australia or resulted from immigration.