FAUNA
of
AUSTRALIA

24. MORPHOLOGY AND PHYSIOLOGY OF THE SQUAMATA

Philip C. Withers & James E. O'Shea

The lizards (suborder Sauria) and snakes (suborder Serpentes) comprise the order Squamata of the class Reptilia. Like other reptiles, squamates have horny epidermal scales, internal fertilisation, ectothermy and a cleidoic egg. The Squamata are distinguished from the other reptilian orders by adaptive modifications to the temporal region of the skull, and the presence of two hemipenes in the males.

The Squamata represent over 95% of all reptilian species. Of the almost 6000 species in the order, Australia has approximately 480 species of lizards and 170 species of snakes. They represent five of the 18 recognised lizard families—Agamidae (dragons), Gekkonidae (geckos), the Scincidae (skinks), Pygopodidae (legless lizards) and Varanidae (goannas)—and seven of the 11 to 14 recognised families of snakes—Acrochordidae (file snakes), Boidae (pythons), Colubridae, Elapidae, Hydrophiidae and Laticaudidae (sea snakes) and Typhlopidae (blind snakes).

EXTERNAL CHARACTERISTICS

Detailed information on the external characteristics of Australian squamates is provided by Bustard (1970b), Wilson & Knowles (1988), Gow (1989), Greer (1989), Hoser (1989) , Shine (1991a) and Cogger (1992).

Australian squamates range in size from the gekkonid lizard *Diplodactylus savagei*, with a snout-vent length of up to 46 mm and weighing only a few grams, to the perentie, *Varanus giganteus*, which has a snout-vent length of over 750 mm (Storr 1980) and weighs 17 kg (Butler 1970), and the pythons, *Morelia amethistina* and *M. oenpelliensis* which may exceed 5 m in length (Shine 1991a).

The basic body plan of squamates, which is derived from the ancestral stem reptiles, is an elongate cylinder with a well-defined head separated from the trunk by a prominent neck, and four well-developed limbs supported by pectoral and pelvic girdles. The tail tends to be slender in skinks, dragons, legless lizards and goannas, but is often bulbous or expanded laterally and compressed dorso-ventrally in geckos. Geckos and some skinks and legless lizards can autotomise and regenerate their tail. The tail often is used for fat storage and may change in diameter seasonally. A few long-tailed lizards, particularly arboreal goannas and geckos, have a prehensile tail (Bustard 1970b; Czechura 1980). In some aquatic snakes, and in dragons and goannas that swim habitually, the tail is laterally compressed and/or extended dorso-ventrally.

A covering of rough loose skin in the region of the throat may form a pendulous sac or gular pouch, a feature seen in some geckos and, most prominently, in dragons (Pl. 5.3) and goannas. In dragons, the scales of this region often are extended into mats of spines, giving rise to the common name of bearded dragons (Pl. 5.8; Throckmorton *et al*. 1985). In the frill necked lizard, *Chlamydosaurus kingii*, the gular skin is particularly loose and is supported by hyoid bones that allow the 'frill' to be erected when the animal is threatened (Pl. 5.9; Saville-Kent 1895; Beddard 1905). Some dragons have a central crest of rough and spinose scales along the neck or back (Pl. 5.7).

Among the Sauria, dragons, geckos, goannas and most skinks show the tetrapod condition, whereas some skinks have a reduced size and number of both digits and limbs (Mitchell 1958; Greer 1987a, 1989). Almost complete limb reduction typifies legless lizards. The limb-reduced lizards have a long tail, that often exceeds the snout-vent length. Limb reduction is virtually complete in the Serpentes, although a vestigial flap may remain. Snakes differ fundamentally from the limb-reduced lizards in that their body attenuation and elongation is primarily of the trunk rather than the tail.

Usually the head is flattened dorso-ventrally and simple; notable exceptions are the spinose head of *Moloch horridus* and the nuchal crests of rainforest dragons such as *Hypsilurus boydii*. The snout is usually short, except in carnivores such as goannas, legless lizards, and pythons. Lizards usually have external ear openings. The head scales decrease in size at the edge of the ear opening, and the skin that is firmly attached to the underlying tympanic membrane usually lacks scales. In some terrestrial or burrowing skinks, the tympanic membrane is located on the external surface of the skull, and it is covered by scaly skin or occluded by the jaw musculature in some dragons. Snakes and a few legless lizards have no external ear opening. Diurnal lizards have small eyes with round or ovoid pupils, whereas nocturnal squamates tend to have large eyes with elliptical pupils. However, the nocturnal file snakes have very small eyes. The fossorial typhlopid snakes and some *Lerista* have vestigial eyes, covered by scales. The eyes and nostrils often are positioned on the dorsal surface of the head in squamates that swim.

The condition of the front and hind feet varies, from pentadactyl limbs (five digits) that terminate in keratinised claws, to the near or total absence of digits in legless lizards, snakes and some skinks. Modification of the pentadactyl condition usually is related to changes in the locomotory mode. Not even dragons or goannas that habitually swim have any webbing between their digits.

Reduction in the length of the digits in both the front and hind feet is comparatively minor in both dragons and geckos, but skinks, especially *Lerista*, display a comprehensive series of digit reductions (Mitchell 1958; Greer 1989). The length of the metatarsi is increased in dragons that stand on their rear limbs using the tail as a prop (Swanson 1976; Greer 1989). Some goannas have a similar extension of the hind foot digits, which contributes to their ability to stand and to run bipedally. The relative size of the claws is related to arboreality or digging. For example, the arboreal goanna *Varanus gilleni* has strongly curved claws (Pianka 1969a). Some arboreal dragons and skinks have similar digit and claw extension, and opposable digits.

Geckos have specialised foot pads that increase traction, in addition to claws and opposable digits. The underside of the digits of the arboreal skink, *Emoia cyanogaster*, have between two and three times as many transverse scales as do closely related terrestrial species (Williams & Peterson 1982; Greer 1989). The water dragon, *Physignathus lesueurii*, has a single row of subdigital keels rather than the typical double row of dragons (Greer 1989). Rock-climbing goannas such as *V. glebopalma* (Mitchell 1955; Swanson 1979) and arboreal species such as *V. prasinus* (Czechura 1980; Greene 1986) produce a secretion on the base of the feet that may increase traction.

The cloacal opening (vent) is a transverse ventral slit at the base of the tail, usually covered by a posteriorly projecting shield of scales. Internal fertilisation is by one of a pair of male intromittent organs, the hemipenes. When flaccid, the hemipenes lie under the skin of the ventro-lateral region of the tail in penial sacs that open into the posterior of the cloaca. Before copulation, both hemipenes are expanded and everted through the vent, but only one is used. A hemipenial groove, the *sulcus spermaticus*, transports sperm from the cloaca. The hemipenes of most lizards are simply pleated and folded, whereas those of snakes often are covered with hooks and circles of projections called calyces. Hemipenial structure can be a useful taxonomic tool.
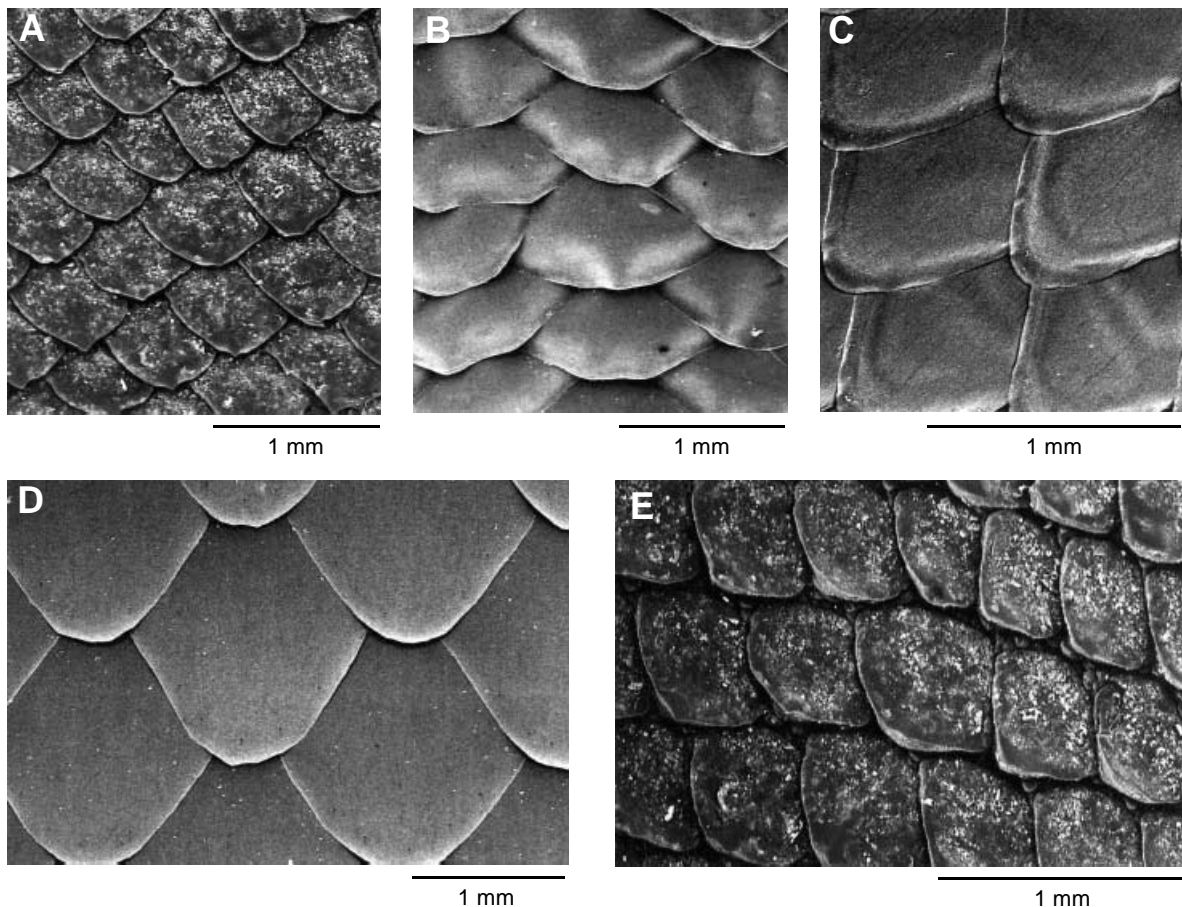
INTEGUMENT

Squamates have a water-conserving, scaly integument with few glands. The epidermis consists of a basal germinal layer (*stratum germinativum*) and three outer layers culminating in a thick, dead, keratinised layer (Lillywhite & Maderson 1982). The scales are covered by thick epidermis, and are joined at

their base to adjacent scales by a thin region of epidermis that acts as a hinge. This continuity of the scales is a seal against water loss, infection and parasitism, provides mechanical strength, and facilitates simultaneous shedding of the entire skin. The outer epidermis is periodically shed and replaced by underlying layers of cells, derived from the *stratum germinativum*. Shedding is necessary because the inelastic skin retards growth. While snakes, geckos and many legless lizards shed their skin in a single piece, dragons and goannas shed their skin in sections.

Scale morphology ranges from the minute granular scales of file snakes, geckos and legless lizards, to the smooth and overlapping scales of blind snakes, some skinks and snakes, and the elaborate, spiny scales of dragons (Fig. 24.1). Often scales are covered by a microscopic series of ridges, or pockets, that may reduce friction and prevent dirt adhesion in burrowing species, provide a water-repellant surface, or influence rates of radiative heat exchange. There is also regional specialisation of scales. Those covering the skull are often larger and more specialised than those in other regions of the body. The epidermal scales, particularly in skinks, overlay dermal scales that may be fused to the bony plates of the skull to form a robust, immobile skull. A modified scale, the spectacle, covers the eye of snakes, geckos and legless lizards. It reduces evaporative water loss in terrestrial species and provides mechanical protection in fossorial species. Most terrestrial snakes and some non-fossorial legless lizards have wide ventral body scales (gastrosteges) that span the width of the animal. Fossorial blind snakes and many totally aquatic snakes have uniformly small, ventral body scales.

Figure 24.1 Scanning electron micrographs of integumental scales representative of squamate groups. **A**, Agamidae; **B**, Scincidae; **C**, Gekkonidae; **D**, Pygopodidae; **E**, Elapidae.
[Photos by J. O'Shea, P. Withers & T. Stewart]

Arboreal geckos have toe pads of highly modified digital lamellae, called scansors, and the prehensile tail of *Pseudothecadactylus* has a terminal pad. Foot pads have evolved independently several times within the geckos (Russell 1976, 1979). Terrestrial geckos usually lack scansorial pads. The scales on the ventral surface of the scansorial pads have an extended surface area and microscopic projections called setae (Fig. 24.2; Ernst & Ruibal 1966; Ruibal & Ernst 1965) which increase their adhesive capacity dramatically. The number of toe lamellae and their surface area has been correlated with arboreality (Collette 1961; Hecht 1952).
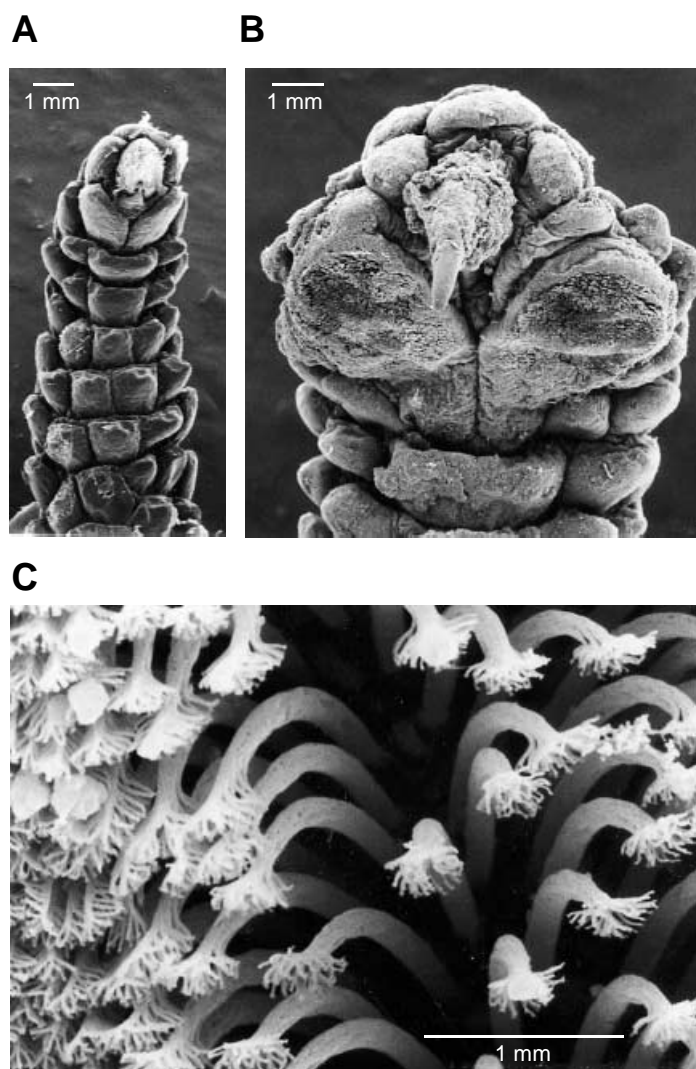
Figure 24.2 Scanning electron micrographs of the subdigital pads of geckos to show lamellar scale morphology. **A**, the terrestrial gecko *Rhynchoedura ornata*, shows the primitive condition in which subdigital pads are absent; **B**, the arboreal gecko *Diplodactylus assimilis*, showing the presence of subdigital pads; **C**, the numerous setae on the pads of *D. assimilis*, seen at higher magnification.   [Photos by P. Withers, J. O'Shea & T. Stewart]

The colour of terrestrial reptiles can be diverse and their pigmentation complex, but less so in fossorial groups. Colouration has been related to camouflage, warning, thermoregulation, protection from ultraviolet rays, behavioural interactions and sexual dimorphism. Colouration is under physiological control (neural or endocrinal). Some legless lizards mimic the colour and sometimes the behaviour of elapid snakes (Hall 1905; Kinghorn 1924; Waite 1929; Bustard 1968c, 1970b; Greer 1989).

Although squamates generally have few glands, femoral, pre-anal and cloacal glands are often prominent. When molested, some snakes expel a pungent cloacal secretion that may deter predators. Secretions from cloacal glands have also been related to mate attraction, particularly in female pythons which lay scent trails to attract males. The ability of blind snakes, which prey almost exclusively on termite and ant pupae, to forage within colonies without being attacked has been related to repellent cloacal secretions smeared over their body (Gehlbach, Watkins & Reno 1968). Some skinks have a postanal gland. Some terrestrial colubrids have a chain of small nucho-dorsalis glands which secrete a pheromone that irritates mucous membranes and may deter predators. A similar defensive function is performed by a sticky, noxious secretion from the tail of members of the gecko genus *Strophurus* (previously a part of *Diplodactylus*).

Femoral and pre-anal pores are found in many dragons, legless lizards and geckos. These pores are often arranged as V-shaped series or clusters anterior to the anus; for example, *Pygopus lepidopodus* has 10 preanal pores, each leading to an expanded gland (Underwood 1957). Males and females often have the same number of pores, but they are usually larger in males; females lack them in some species. These pores are the openings of papillary, follicular dermal glands (Cole 1966a). Glandular activity appears to be greatest during the breeding season, and may be under the control of androgens (Cole 1966a; Fergusson, Bradshaw & Cannon 1985). A thick, horny, yellow secretion, which often forms short plugs extending from the pore, may be a pheromone, a copulatory adhesive, or may provide a tactile cue during mating. The pores have some phylogenetic significance in amphiboluroid dragons (Greer 1989).

SKELETAL SYSTEM

The skeleton of a quadrupedal lizard (Fig. 24.3) has a moderately robust skull and a moderately long trunk. The appendicular skeleton consists of a pectoral girdle and forelimbs, and a pelvic girdle and hind limbs. The limbs are typically short and laterally orientated. The skeletal osteology of a squamate is directly related to its mode of locomotion (Romer 1956; Bellairs 1969; Porter 1972; Parker & Grandison 1977; Goin, Goin & Zug 1978; Greer 1989).
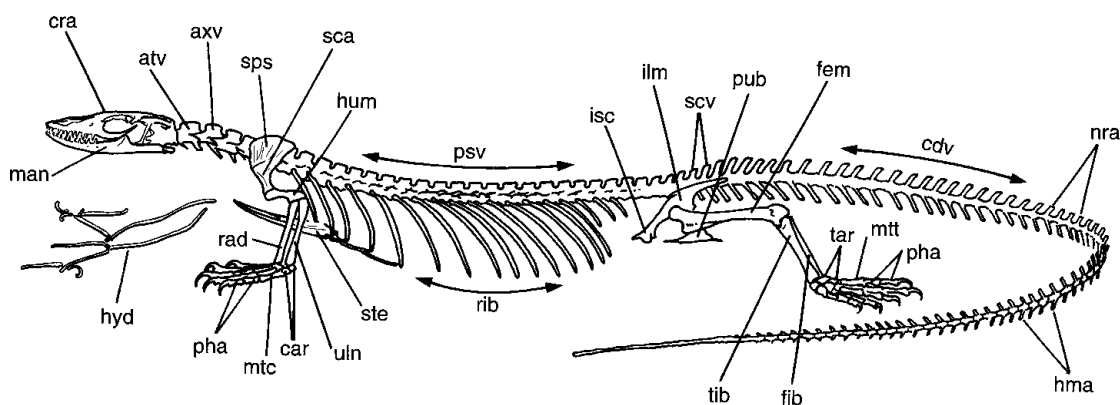
Figure 24.3 The skeletal osteology of *Varanus gouldii*, a typical quadrupedal lizard. Note that the limbs terminate in five digits (pentadactyl condition) and are directed at right angles to the axis of the body. **atv**, atlas; **axv**, axis; **car**, carpals; **cdv**, caudal vertebrae; **cra**, cranium; **fem**, femur; **fib**, fibula; **hma**, haemal arch; **hum**, humerus; **hyd**, hyoids; **ilm**, ilium; **isc**, ischium; **man**, mandible; **mtc**, metacarpals; **mtt**, metatarsals; **nra**, neural arch; **pha**, phalanges; **psv**, presacral vertebrae; **pub**, pubis; **rad**, radius; **rib**, ribs; **sca**, scapula; **scv**, sacral vertebrae; **sps**, suprascapula; **ste**, sternum; **tar**, tarsal bones; **tib**, tibia; **uln**, ulna.   [M. Thompson]

The Skull and Mandible

The squamate skull is derived from a primitive condition with two openings in the cheek or temporal region that allow for expansion of the jaw musculature and, in advanced forms, greatly increases the mobility of the lower jaw. This diapsid condition defines the subclass Lepidosauria, which consists of the orders Rhynchocephalia and Squamata. Two complete arches are found only in the Rhynchocephalia (tuatara, *Sphenodon punctatus*; Fig. 24.4A). Squamates have a modified or reduced diapsid condition. Lizards have lost the quadratojugal bone and the process of the jugal that formed the lower arch in the primitive condition (Fig. 24.4B). Snakes and some lizards have lost the upper as well as the lower arch (Fig. 24.4C), leaving the cheek region free of dermal bone and allowing great mobility of the quadrate bone which supports the lower jaw.
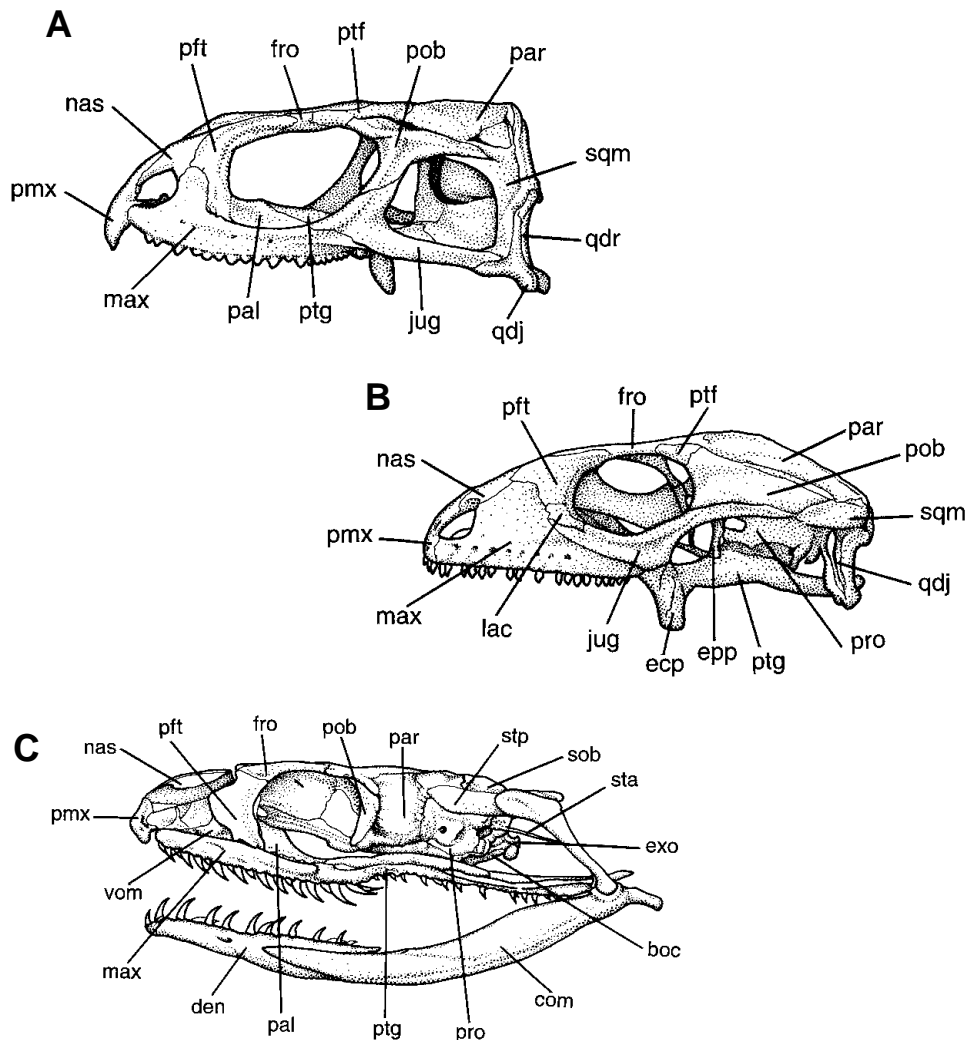
Figure 24.4 Skulls representative of the subclass Lepidosauria, showing modifications to the temporal region of the skull. **A**, *Sphenodon punctatus*, order Rhynchocephalia, in which the diapsid condition of two temporal openings is best seen; **B**, skull of a lizard, showing loss of the lower temporal bar; **C**, skull of a snake, in which upper and lower temporal bars have been lost. **boc**, basioccipital; **com**, compound; **den**, dentary; **ecp**, ectopterygoid; **epp**, epipterygoid; **exo**, exoccipital; **fro**, frontal; **jug**, jugal; **lac**, lachrymal; **max**, maxilla; **nas**, nasal; **pal**, palatine; **par**, parietal; **pft**, prefrontal; **pmx**, premaxilla; **pob**, postorbital; **pro**, prootic; **ptf**, postfrontal; **ptg**, pterygoid; **qdj**, quadratojugal; **qdr**, quadrate; **sob**, supraorbital; **sqm**, squamosal; **sta**, stapes; **stp**, supratemporal; **vom**, vomer. (Modified from Parker & Grandison 1977)   [M. Thompson]

The brain case is caudal to the eyes. The posterior margin is formed by the fusion of four occipital bones. The supraoccipital forms the postero-dorsal portion of the brain case. The two exoccipitals form the posterior lateral margin of the neurocranium and the basioccipital forms the posterior ventral margin. The foramen magnum perforates the centre of the fused occipital bones. Raised extensions of the exoccipital bones unite at the margins of the foramen magnum, and with a similar protuberance from the basioccipital bone, form the tripartite occipital condyle, the point of articulation of the skull with the vertebral column. The roof and floor of the brain case are formed by the parietal and basisphenoid bones, respectively. The fused parietal bones form a flat plate extending anteriorly over the brain to the frontal bones. Antero-laterally the parietal joins the postorbital bones posterior to the orbits. Postero-laterally, the parietal bone is connected to the squamosal bones. In primitive or non-specialised forms, the cheek region behind and below the orbits is formed by the jugal, quadratojugal, squamosal and quadrate bones. Surrounding the orbit are the prefrontals, frontals, postfrontals and postorbitals. The snout and upper jaw are formed by the nasals, maxillae and premaxillae. The ventral portion of the skull is formed from the vomers, palatines, ectopterygoids and pterygoids, together with ventral extensions of the maxillae and premaxillae anteriorly, and the fusion of the basisphenoids with the basioccipital posteriorly. The anterior portion of the brain is poorly protected by bone in the Sauria. In contrast, the ophidian brain is enclosed by the downward growth of both the frontal and parietal bones (Fig. 24.4C).

In some squamates, reduction or loss of the temporal arches increases mobility of the quadrate bones. This and the independent movement of the pterygoids increases lower jaw mobility (streptostyly). Streptostyly increases the gape and also allows the jaws to move backwards and forwards, thus permitting extreme feeding specialisation. Many legless lizards, goannas, geckos and snakes also have highly kinetic skulls (Albright & Nelson 1959a, 1959b; Bolt & Ewer 1964; Frazzetta 1966; Gans, de Vree & Carrier 1985; Gans & de Vree 1986). Such movable joints may occur between the occipital and parietal bones (metakinesis), and parietal and frontal bones (mesokinesis). The snout and palate may also have some mobility, related to an inertial feeding strategy (for example, *Lialis*), or digging by limb-reduced fossorial forms such as *Delma*.

The internal nares and the ducts of Jacobson's organ each open into the anterior roof of the mouth. In some reptiles, the internal nares are located towards the back of the oral cavity, and separate it from the respiratory pathway. The palate is formed by the fusion of the premaxillae and the maxillae, and occasionally includes the palatines and pterygoids.

The lower jaw bones (Fig. 24.5) consist of the dentary, distinguished by the presence of teeth, the coronoid (which is usually lost), and the articular, prearticular, surangular, angular and splenial. These last five bones usually fuse to form the compound bone. The dentaries are fused anteriorly and are immobile in most of the lizards or held together loosely by elastic ligaments in most snakes and some legless lizards.

Dentition

All squamates have well-developed teeth at the edges of the premaxillae, maxillae and dentary (Fig. 24.5). Some, particularly snakes, also have teeth on the palatine and pterygoid bones. These marginal teeth are of two types, pleurodont and acrodont. The pleurodont tooth found in all snakes and most lizards, develops on a shelf on the lingual side of the jaw and when mature fuses with the inner jaw bone margins. Acrodont teeth develop on the lingual side of

the jaw but migrate to and fuse with the crest of the jaw bones and with each other to form a chisel shaped wedge. Agamids are unusual in having both tooth types (Fig. 24.5A; Greer 1989).

Pleurodont teeth are replaced regularly in a posterior to anterior sequence. Simultaneous addition of new teeth posteriorly in sub-adult individuals ensures that a diffuse and diverse dental array is always available to maintain effective biting (Cooper 1965). Acrodont teeth are not replaced over time and wear produces a cutting ridge.

The majority of skinks, legless lizards and geckos have non-specialised peg-like teeth with a vertical orientation (Fig. 24.5B–D). The large size of the molariform teeth of *Tiliqua* (Greer 1989) may be related to omnivory (Estes & Williams 1984). The pygopodid *Lialis burtonis* has many sharp, recurved teeth, like some
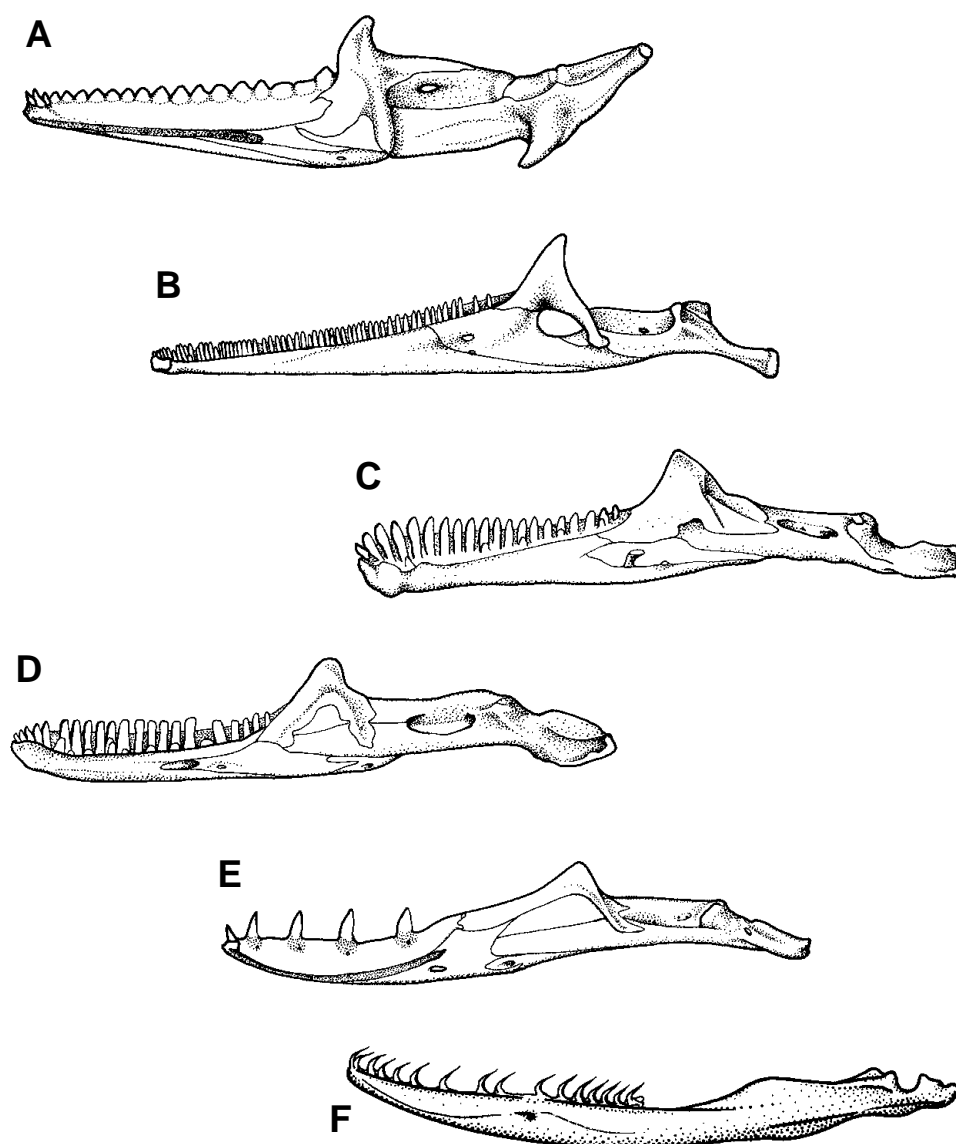
Figure 24.5 The mandible, in lingual view, from representatives of five families of lizards and one family of snakes. **A**, *Lophognathus gilberti* (Agamidae); **B**, *Carphodactylus laevis* (Gekkonidae); **C**, *Pygopus lepidopodus* (Pygopodidae); **D**, *Egernia saxatilis* (Scincidae); **E**, *Varanus timorensis* (Varanidae); **F**, *Pseudonaja affinis* (Elapidae). (Modified after Greer 1989) [M. Thompson]

snakes (Savitzky 1980, 1983; Patchell & Shine 1986a). The teeth of the goannas may be recurved, or laterally compressed and serrated; older non-curved rear teeth may wear to grinding, as opposed to cutting, surfaces.

Snake teeth have more positional differentiation than lizard teeth. Some are long, narrow, highly recurved and hinged to grasp and work the prey into the mouth. Aglyphous snakes have no fangs, but some teeth are modified as fangs for venom delivery in opisthoglyphous (rear-fanged) and proteroglyphous (front-fanged) snakes. The fangs often possess an open or partially closed groove running from the base to the surface for effective venom delivery (Fig. 24.6A). Fangs may be permanent or replaceable. Most of Australia's snakes, including the terrestrial elapids, hydrophiids and laticaudids, are front-fanged and venomous.

Venom enters the prey by capillary action in rear-fanged snakes, such as some colubrids, which rely on multiple fangs and chewing to provide primary skin abrasion. In contrast, the comparatively long fangs of front-fanged snakes are capable of hypodermically injecting large quantities of neurotoxic venom deep into prey.

Vertebral Column

The vertebral column protects the spinal cord, supports the trunk and limbs, and provides leverage for locomotory muscles. Vertebrae show regional specialisation in number and morphology. This is most pronounced in short-bodied lizards such as *Moloch horridus* and least in limb-reduced, attenuated forms, particularly snakes.

Typical vertebrae have a solid bony centrum. Lateral plates from the dorsal surface of the centrum fuse to enclose the spinal cord and form a neural arch. Similar ventral extensions may enclose the blood vessels of the tail and form haemal arches. In all snakes and lizards, except some geckos, vertebrae articulate by procoelous ball-and-socket joints formed by the interaction of the concave anterior surface of one vertebra with the convex posterior surface of the preceding vertebra. The amphicoelous vertebrae of some geckos are concave at both ends. Each vertebra is supported by two pairs of articulating zygapophyses that prevent rotation of the vertebral column. Each postzygapophysis extends posteriorly and laterally from the posterior of each neural arch, where its ventro-lateral surface articulates with the dorso-medial surface of the prezygapophysis of the adjacent vertebra (Fig. 24.6A). Snakes and some legless lizards have two additional pairs of zygosphenes which extend anteriorly from the base of each neural arch to articulate with specialised postero-lateral zygantra of the preceding vertebra (Fig. 24.6B).

The neck usually has no more than eight cervical vertebrae. The first and second (atlas and axis respectively) support the skull and allow its movement. The other cervical vertebrae usually bear ribs that increase progressively in length posteriorly, although none reach the sternum. Thoracic vertebrae have ribs which reach the sternum (except in snakes). Lumbar vertebrae have no ribs, or short ribs that do not reach the sternum. Frequently the two sacral vertebrae are fused, and have lateral plates for pelvic girdle support. The distinct tail may have as few as 14 vertebrae or less in the skink *Egernia stokesii* and most snakes, or as many as 139 in the goanna *Varanus varius* (Greer 1989). The anterior intermediate vertebrae lack a haemal arch, but it is present on the more posterior caudal vertebrae. Sacral and some caudal vertebrae have antero-lateral processes, especially in species that show tail loss. Where tail autotomy occurs, the vertebrae may have a connective tissue or cartilage fracture line or be uniformly fragile (Etheridge 1967). The replacement tail has an internal cartilaginous rod, which sometimes is calcified, but vertebrae are not reformed.
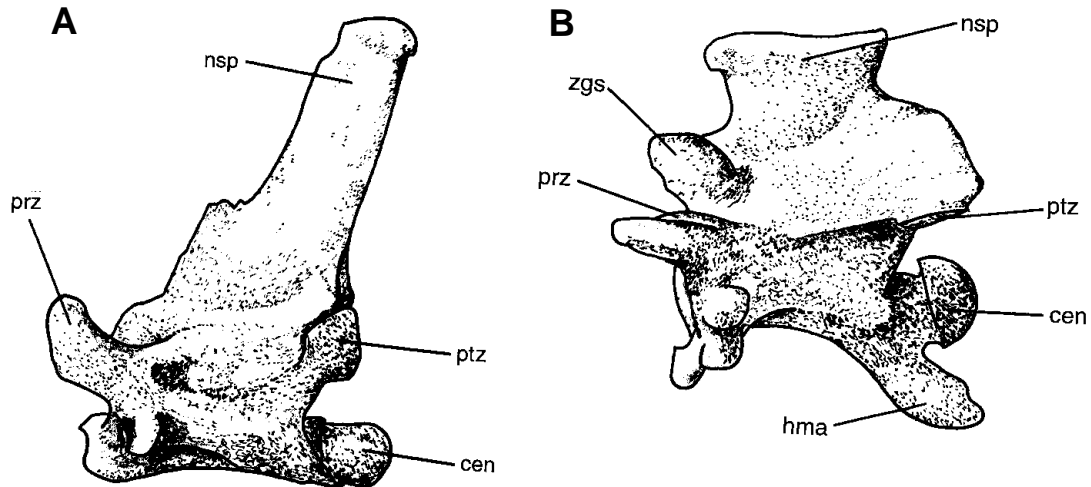
Figure 24.6 Lateral view of typical procoelous vertebrae. **A**, lizard; **B**, snake. **cen**, centrum; **hma**, haemal arch; **nsp**, neural spine; **prz**, prezygapophysis; **ptz**, postzygapophysis; **zgs**, zygosphene. (Modified after Parker & Grandison 1977)   [J. O'Shea]

Numbers of presacral vertebrae are usually used for comparisons between groups. Agamids typically have 22 to 24 presacral vertebrae (20 to 22 in *Moloch horridus*), and geckos have 25 to 27; skinks, goannas and legless lizards have 26 to 75, 28 to 32 and 44 to 95, respectively (Greer 1989). The highly attenuated and apparently limbless pygopodid genus *Aprasia* has up to 137 presacral vertebrae (Parker 1956; Greer 1989). Snakes, which lack a sacrum, have between 120 and 320 precloacal vertebrae (Hoffstetter & Gasc 1969).

Limbs and Girdles

The pectoral girdle of a typical tetrapod lizard consists of two halves joined ventrally by a cartilaginous sternum (Fig. 24.7A), each comprising precoracoid, coracoid, interclavicle, clavicle, scapula and suprascapula components. All lizards, including those with limb reduction or loss, have a pectoral girdle; snakes do not.
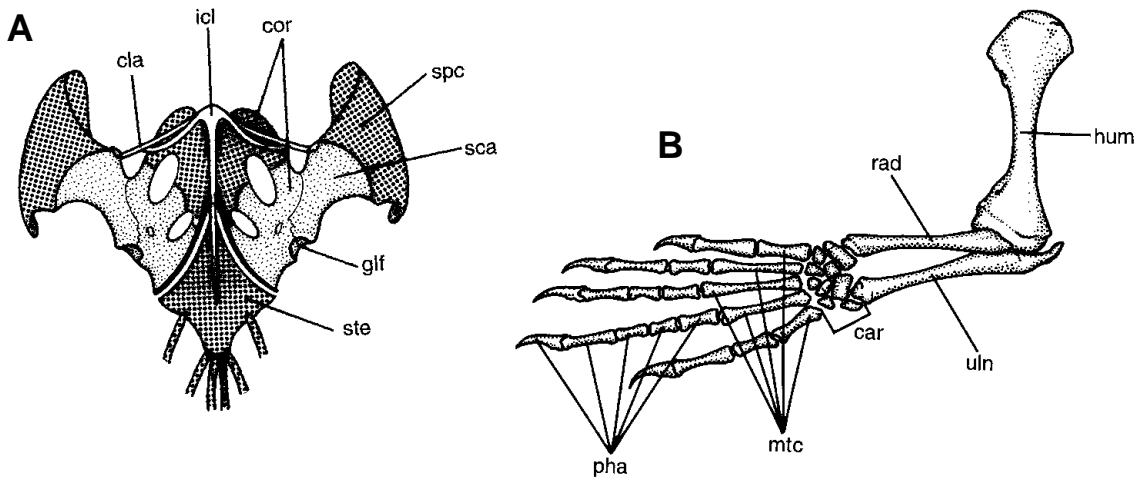

Figure 24.7 Pectoral girdle and forelimb of a varanid lizard. **A**, pectoral girdle, in ventral view; **B**, forelimb, in lateral view. In A, light and dark stippling represent bone and cartilage, respectively. **car**, carpals; **cla**, clavicle; **cor**, coracoid; **glf**, glenoid fossa; **hum**, humerus; **icl**, interclavicle; **mtc**, metacarpals; **pha**, phalanges; **rad**, radius; **sca**, scapula; **sps**, suprascapula; **ste**, sternum; **uln**, ulna.   [M. Thompson]
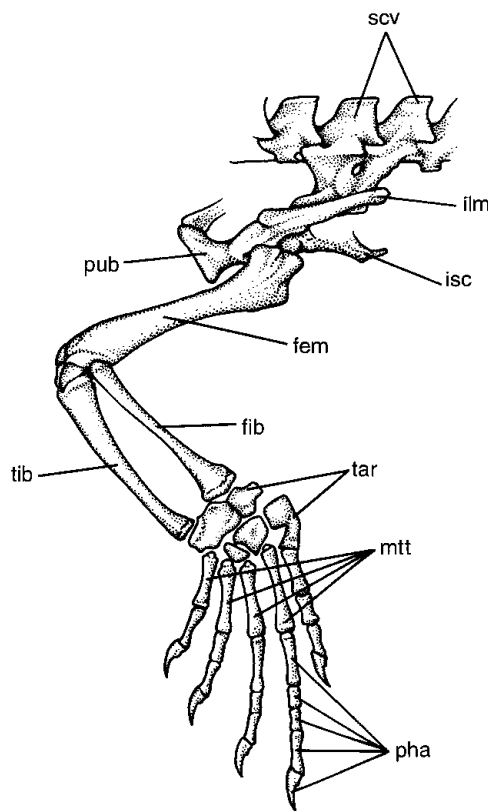
The forelimb typically consists of a humerus that articulates proximally with the glenoid fossa of the pectoral girdle and distally with the ulna and radius (Fig. 24.7B). The carpals, which articulate with the radius and ulna, consist of a radiale and ulnare, a small transitional bone between them, and four to six other small bones. The pentadactyl front foot is formed by five metacarpals, each of which articulates with one of five phalanges. The terminal digital phalanx usually has a claw. The phalangeal formula, or the number of phalanges in each digit from the thumb outward, is commonly 2, 3, 4, 5, 3 in dragons, goannas, geckos and some skinks.

There is considerable diversity in forelimb morphology. Short or absent forelimbs have been related to movement in closed vegetation or soil (Pianka 1986) and arboreality (Lundelius 1957; Collette 1961), and substantial forelimbs to digging (Ananjeva 1977). Pygopodids retain only the rudiments of the humerus. Some skinks, particularly *Lerista*, show intermediate stages from the 'normal' pentadactyl proportions (for example, fore and hind limbs with five digits; 5/5) through variable finger and toe reduction (for example, 4/4, 3/3, 2/2), and loss of forelimbs and reduction of hindlimbs (for example, 0/2, 0/1), to complete loss of external forelimbs and hindlimbs (0/0) (Fig. 24.8).
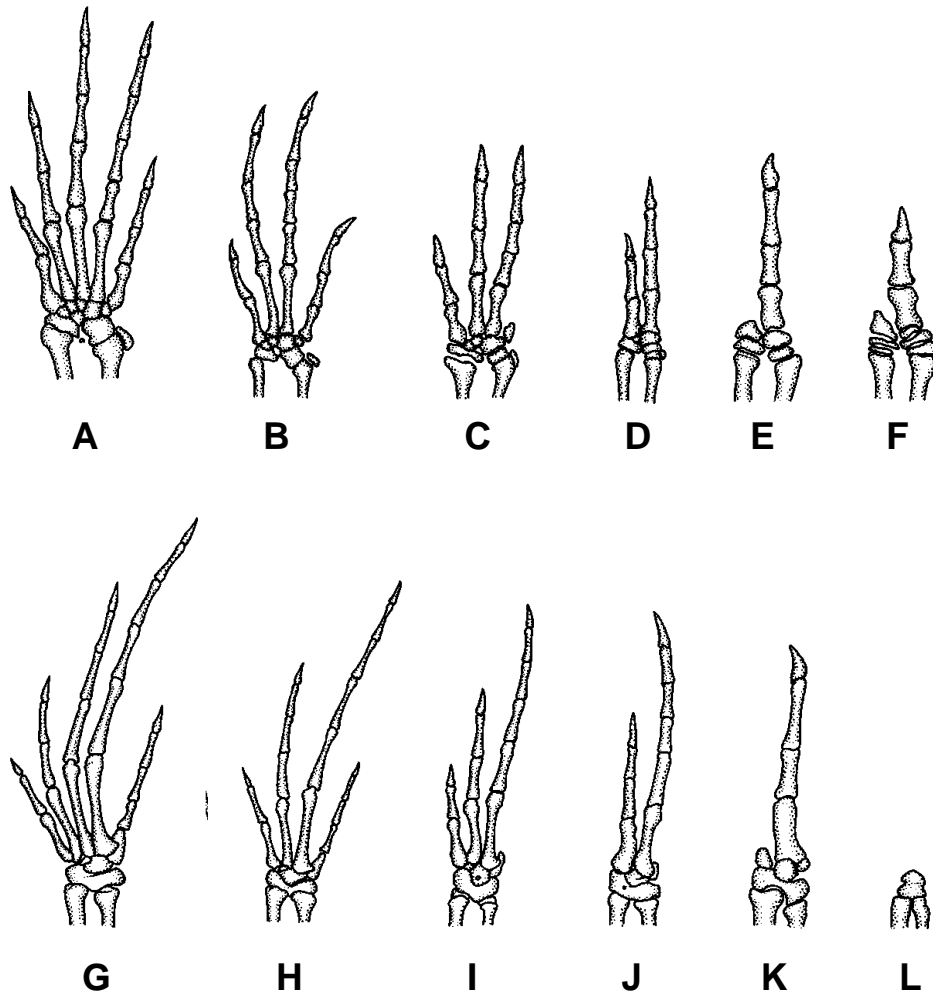
Figure 24.8 Limb reduction in species of *Lerista*. **A–F**; forelimb, showing reduction from the full phalangeal formula of 2, 3, 4, 5, 3 to 0, 0, 0, 2, 0; **G–L**, hindlimb, showing reduction from the full phalangeal formula of 2, 3, 4, 5, 4 to 0, 0, 0, 0, 0. **A**, **G**, *L. arenicola*; **B**, *L. distinguenda*; **C**, *L. fragilis*; **D**, *L. planiventralis*; **E**, *L. macropisthopus*; **F**, *L. punctatovittata*; **H**, *L. christinae*; **I**, *L. borealis*; **J**, *L. ips*; **K**, *L. cinerea*; **L**, *L. humphriesi*. (From Greer 1989)

[M. Thompson]

The squamate pelvic girdle, unlike the pectoral girdle, is bound dorsally to the vertebral column. Like the pectoral girdle, it consists of two halves that are joined ventrally by cartilage. Each half of the girdle is formed by the fusion of three bones, the pubis, ilium and ischium (Fig. 24.9). The ribs or lateral processes of the sacral vertebrae are fused to the posterior projections from each ilium. Ventrally, the anteriorly directed pubic bones are joined by cartilage at the pubic symphysis. The junction of the pubic bone with the ilium and posteriorly projecting ischium forms a specialised articulation socket, the acetabulum, which holds the head of the proximal limb bone, the femur.

Pelvic girdles show adaptive variation within the squamates. Reduction in the size of the components of the pelvis is invariably related to limb reduction in snakes, legless lizards and some skinks. All snakes except the pythons and a few of the more primitive groups lack a pelvis. Even when present in these snakes, the pelvis is vestigial. Pygopodids retain all of the components of the pelvis, most of the bones of the forelimbs and often have at least one phalange, even though they lack locomotory limbs (Greer 1989). The pelvis is usually well developed in groups capable of bipedal locomotion such as goannas and dragons. Modification of the pubic bones of the pelvis to produce anterior projections has been reported in dragons that climb and run quickly (Mitchell 1965; Greer 1989).

Figure 24.9 Pelvic girdle and hindlimb of a varanid lizard, in lateral view. The acetabulum, or socket for the head of the femur, is formed at the junction of the ilium, pubis and ischium. **fem**, femur; **fib**, fibula; **ilm**, ilium; **isc**, ischium; **mtt**, metatarsals; **pha**, phalanges; **pub**, pubis; **scv**, sacral vertebra; **tar**, tarsals; **tib**, tibia.
[M. Thompson]

The hindlimbs of squamates consist of a femur that articulates with the pelvis proximally and with the fibula and tibia at the knee (Fig. 24.9). The distal parts of the fibula and tibia articulate with the foot at the ankle. Proximally, the ankle is formed by a combination of the fibulare, astragalus and tibiale with several other tarsal bones forming articulations with the metatarsals. In the primitive condition, there are five metatarsal bones. Each of these bones is associated with a digit in the pentadactyl condition. Dragons and goannas, commonly show a full phalangeal formula of 2, 3, 4, 5, 4 in the hind foot. The occurrence and development of a claw on the terminal phalanx of each digit is variable and related to life strategy. As with the digits of the front foot, digit reduction in the hind foot is complete in the legless lizards and very common among some lizards, particularly skinks such as *Lerista* (Fig. 24.8G–L).

MUSCULAR SYSTEM

The axial musculature is derived from segmentally arranged myotomes (Romer & Parsons 1977) that are divided by septa of connective tissue during development into the dorsal epaxial muscles and the ventral hypaxial muscles. The epaxial muscles are lateral to the vertebrae and form the dorso-lateral trunk muscles extending from the skull to the tail. The hypaxial muscles form the ventro-lateral body musculature (Gasc 1981).

Squamates have well-developed appendicular muscles, reflecting their predominantly quadrupedal locomotion and semi-erect posture. There is a tendency for reduction in relative mass and importance of the epaxial and hypaxial musculature, with simultaneous development of the limb and girdle muscles. However, body elongation, attenuation and secondary reduction or loss of limbs has increased the development and level of differentiation of the trunk muscles in snakes, legless lizards and some skinks.

Dermal musculature is poorly developed in most squamates, but is well-developed in snakes to erect the ventral scales and reduce backward slipping. In wide-bodied snakes that use rectilinear locomotion, three pairs of dermal muscles are present between the ribs and the large ventral scales (Lissmann 1950).

The main masticatory muscles of the jaw are the *muscularis adductores mandibulae* that close the jaw, and a small *m. depressor mandibulae* that opens it (Hass 1973). In snakes, which can move the upper and lower jaws independently of the brain case and each other (streptostyly), the adductor muscles are divided into numerous subunits, and other muscle groups connect the lower jaws anteriorly.

The epaxial muscles of the trunk comprise longitudinal bundles attached dorso-laterally to the vertebrae from the skull to the tail. The hypaxial muscles, together with the ribs, support the viscera and provide respiratory ventilation. The major part of the tail is a continuation of the dorsal epaxial muscles and the ventral hypaxial muscles, but the ventral portion is typically less substantial because the muscle bundles are interrupted by the pelvic girdle. The epaxial muscles of the trunk continue forward to support and move the skull and neck. The neck may also be invested with a superficial sphincter colli muscle that is closely bound to the skin. Squamates lack facial muscles and cannot easily drink by sucking.

The muscular tongue is supported by the geniohyoideus complex of the hyoid arch. In snakes, the tongue is usually anteriorly divided into tapering, highly protrusible portions that have a sensory rather than a mechanical function (Condon 1989). The tongue of goannas is also anteriorly modified for olfaction, but retains posterior musculature for swallowing. Similarly, the tongue of *Lialis* is bifid anteriorly, but is still involved in prey manipulation and swallowing (Patchell & Shine 1986a).

The forelimbs and pectoral girdle of lizards are suspended from the anterior trunk by the muscles *m. trapezius*, *m. serratus* and *m. levator scapulae*. The humerus is attached to the scapula and to the body by muscles and tendons. On the dorsal side of the body, the *m. latissimus dorsi* and *m. subcoracoscapularis* adduct and rotate the humerus, and the *m. scapulohumeralis* and *m. deltoideus* abduct the humerus. Ventrally, the *m. pectoralis*, *m. supracoracoideus* and *m. coracobranchialis* muscles also adduct and rotate the humerus, and maintain semi-erect posture. The forelimb is extended by the *m. triceps* and flexed by the *m. branchialis* and the *m. biceps*. A group of ventral flexors and dorsal extensors move the front foot and its digits.

The musculature of the pelvic girdle and hindlimbs is less specialised than that of the pectoral girdle and fore limbs, because the pelvic girdle is fused to the vertebral column. Contraction of the ***m. puboischiofemoralis internus*** lifts the femur and the *m. iliotibialis*, *m. femorotibialis*, *m. ambiens* and *m. iliofibularis* extend the lower limb. A number of smaller more distal muscles extend the digits of the hind foot. Contraction of the *m. caudofemorales* returns the femur to a posterior position, pushes the body forward and provides much of the power for locomotion. The *m. puboischiofemoralis externus*, *m. ischiotrochantericus* and *m. adductor femoris* lower the femur. The *m. puboischiotibialis*, *m. flexor tibialis internus*, *m. flexor tibialis externus* and *m. pubotibialis* flex the hind limb. A few large muscles, including the *m. gastrocnemius* and *m. flexor digitorum longis*, extend the phalanges.

LOCOMOTION

Australian squamates move by burrowing, crawling, walking, climbing or swimming. In the typical slow, tetrapedal walk of a lizard, such as *Diplodactylus assimilis*, oscillatory movements of the limbs and undulatory movements of the body propel the lizard forward (Fig. 24.10). The centre of gravity is always within a triangle of three feet that are on the ground. Rapid running uses a similar pattern of limb and body movement, but the centre of gravity is not always supported by three feet. Bipedal running, which is a natural progression from rapid running, and bipedal standing and walking are observed in some dragons and goannas (Snyder 1962; Greer 1989). Many large goannas have a bipedal ritual combat 'dance'.

Terrestrial snakes typically move by lateral body undulations. Some snakes raise most of their body off the ground as they move forward at an angle to the body orientation ('side-winding'). In concertina locomotion, extension then contraction of body segments pulls the snake forward, as posteriorly-oriented scales prevent retrograde movement. Arboreal snakes tend to be very slender with elongate prehensile tails for climbing (Shine 1991a).

Undulatory locomotion over the ground, burrowing underground, and undulatory swimming are often associated with body elongation. The limbs are either tucked against the body during undulatory propulsion, reduced or lost.
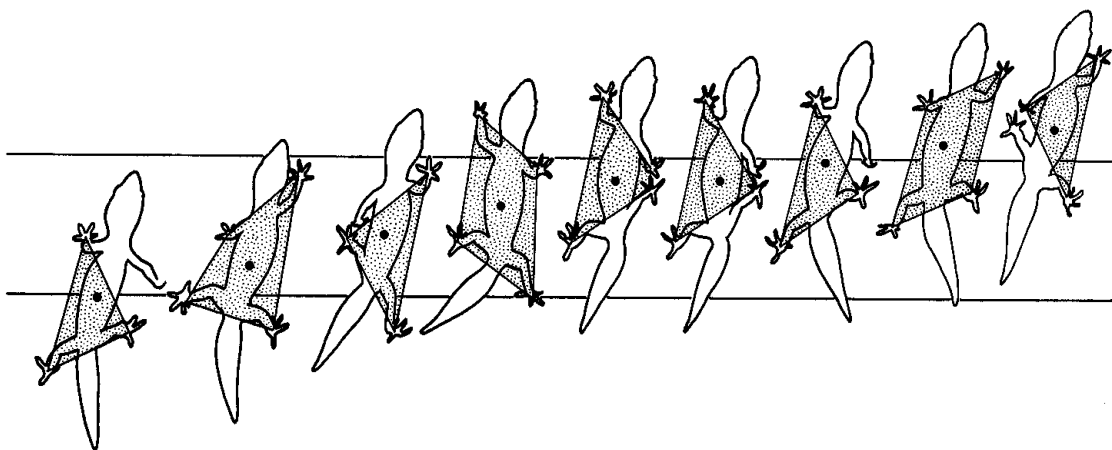
Figure 24.10 The locomotory strides of a gecko, *Diplodactylus assimilis*, involve repeated lateral undulations of the body and tail, and alternate movements of the feet. Stability is maintained by keeping the centre of gravity (l) within a triangle or quadrilateral formed by three or four feet that are on the ground. Horizontal lines are 5 cm apart, and consecutive positions of the gecko are at 40 msec intervals. [P. Withers & A. Roberts]

Burrowing is usually accompanied by limb and tail reduction (for example, *Lerista*). The skull of burrowers is often strengthened and the head scales reduced in number and increased in size to function as protective shields. Burrowing snakes tend to be short and stocky, in contrast to terrestrial and arboreal snakes, and have strong skulls with strengthening head scales (for example, *Ramphotyphlops*, *Vermicella*).

Undulatory swimming occurs in some limbed and limbless squamates. The laterally compressed tail of the semi-aquatic *Physignathus lesueurii* and water monitors, *Varanus indicus*, *V. mertensi*, *V. mitchelli*, acts as a rowing oar. The dorsally located nostrils of the latter two species allow breathing while the rest of the head is submerged. Seasnakes have flattened, paddle-like tails. The seasnake, *Pelamis platurus* has a ventral body keel, and subsurface swimming is achieved by torsional and rolling motions of the body rather than lateral undulation (Graham, Lowell, Rubinoff & Motta 1987). The flaccid skin folds of filesnakes act as a paddle.

In lizards, the metabolic rate during locomotion increases in linear proportion to velocity up to a maximum before reaching a plateau (Fig. 24.11A). Anaerobic metabolism contributes progressively more to energy production at higher velocities. The relationship between the rate of oxygen consumption and velocity extrapolates at zero velocity to slightly more than the resting and standard metabolic rates, and reflects an energetic cost of posture. The net metabolic cost of transport (COT_{net}) is the slope of the relationship between oxygen consumption rate and velocity. There is an inverse relationship for squamates between COT_{net} and body mass (Fig. 24.11B) that is surprisingly similar to that for mammals, birds, and arthropods (Taylor, Heglund & Maloiy 1982; Full 1989; Baudinette 1991).

Limbless squamates expend energy to push against objects by lateral undulation, but not for postural maintenance or limb acceleration/deceleration. The metabolic cost of lateral undulatory crawling by a snake increases approximately in linear proportion to velocity (Walton, Jayne & Bennett 1990) and COT_{net} is similar to that for a walking lizard of the same mass (Fig. 24.11B). The metabolic rate for a side-winding snake also increases approximately in proportion to velocity, but the COT_{net} is lower (Secor, Jayne & Bennett 1992). The metabolic cost of concertina crawling also increases approximately linearly with velocity, but COT_{net} is much higher than for lateral undulatory crawling (Walton *et al*. 1990). There are no estimates of the metabolic cost of burrowing.

The energy requirements are substantially different for swimming compared to land surface and burrowing movement. The major energy expenditure overcomes body drag but some is dissipated as surface waves and to overcome buoyancy. The long lung of seasnakes provides positive buoyancy, but this is reduced at depth by hydrostatic compression. Metabolic rate increases linearly with swimming velocity for marine iguanas and turtles (Prange 1976; Vleck, Gleeson & Bartholomew 1981), but both have a considerably higher metabolic rate than swimming fish. The net cost of transport for squamates is essentially independent of velocity for walking/running/crawling, and (despite theoretical considerations) for swimming. The COT_{net} is substantially higher for walking/running/crawling compared to swimming (Fig. 24.11B).

FEEDING AND DIGESTION

Feeding involves co-ordinated processes such as localisation, identification, capture, immobilisation, mechanical reduction and swallowing (de Vree & Gans 1987). Internally, the digestive system of squamates varies very little, apart from

A

B
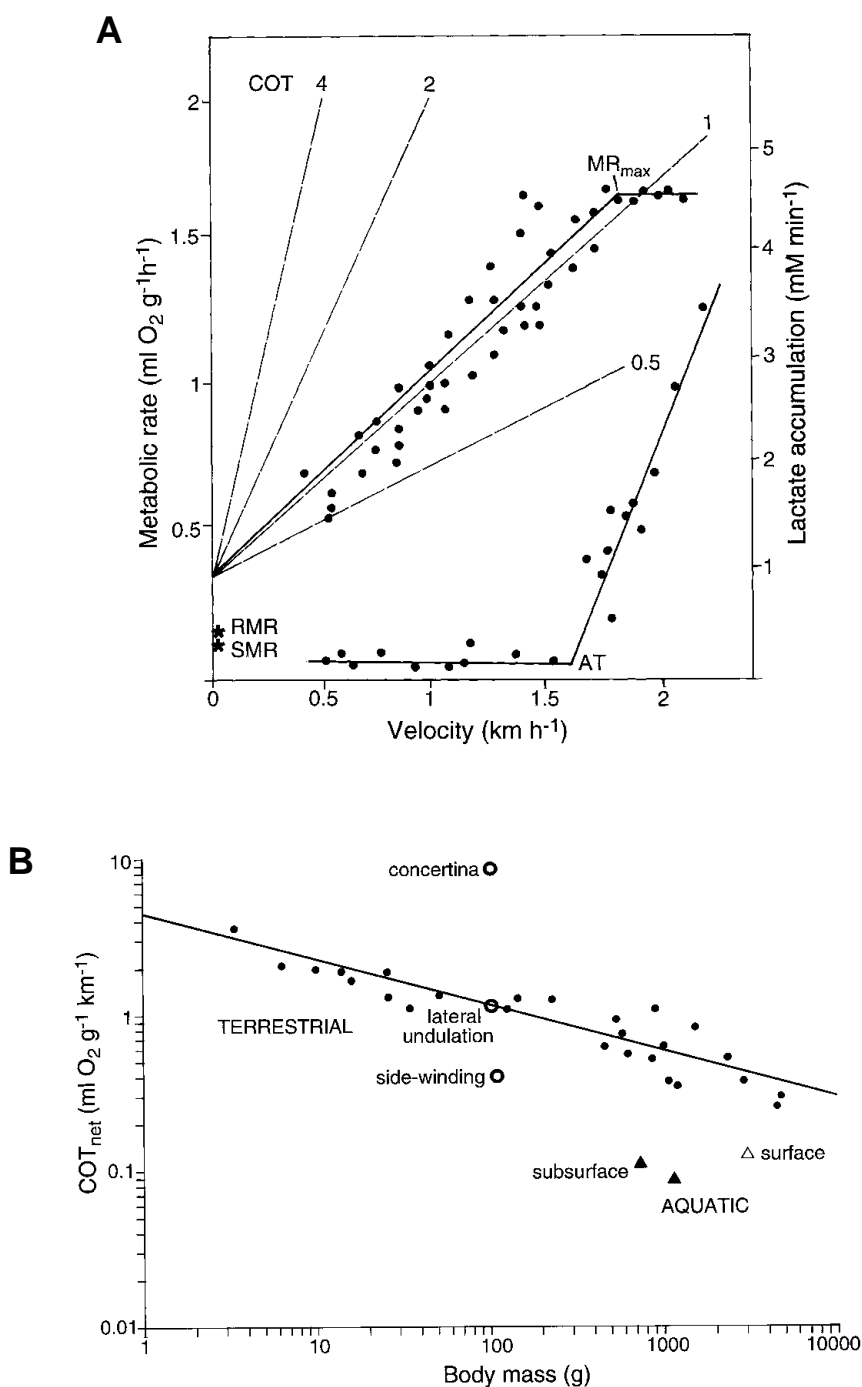
Figure 24.11 Metabolic costs of locomotion in squamates. **A**, metabolic rate and rate of accumulation of blood lactate of a goanna (*Varanus exanthematicus*) walking and running at a range of velocities. The standard metabolic rate (SMR), resting metabolic rate (RMR $\approx$ 1.3 x SMR), maximal metabolic rate (MR$_{max}$) and anaerobic threshold (AT) are indicated. The net cost of transport (COT) is the slope of the metabolic rate-velocity line; values for 0.5, 1, 2 and 4 ml O$_2$ g^{-1} km^{-1} are shown.; **B**, net cost of transport for terrestrial locomotion by lizards and snakes (concertina, lateral undulation and side-winding) and swimming (surface, Galapagos iguana; subsurface, green sea turtle). (A, data from Seeherman, Dmi'el & Gleeson 1983, predicted SMR and RMR calculated from Thompson & Withers 1992; B, data from John-Alder, Garland & Bennett 1986; Videlor & Nolet 1990; Walton *et al.* 1990; Secor *et al.* 1992)   [W. Mumford]

changes related to body shape, particularly body elongation. Few modifications or specialisations for chemical digestion or nutrient absorption have been reported.

Squamates are predominantly carnivorous or insectivorous. Snakes and goannas prey mainly on vertebrates and, with a few notable exceptions, geckos, dragons, legless lizards and skinks prey on invertebrates (Carroll 1977b; Greer 1989). Diet may be diverse in opportunistic omnivores (for example, *Egernia*; Barwick 1965; Shine 1971; Brown 1983) or very restricted and specialised, such as that of the myrmecophagous *Moloch* (Davey 1923; Paton 1965; Pianka & Pianka 1970). Some lizards, particularly skinks, change their feeding strategy from insectivorous as juveniles to omnivorous or herbivorous as adults (Ostrum 1963; Barwick 1965; Shine 1971; Brown 1983). This change has been related to both the difficulty for large lizards to catch enough small insects, and to an energetic constraint on large herbivores (Pough 1973; Wilson & Lee 1974).

Food Acquisition

Prey is detected, then localised and captured, using vision, olfaction and audition. Olfaction is used by active predators, such as snakes, goannas and geckos (Koch 1970; Cogger 1973; Schwenk 1993) in combination with vision. Typhlopids also use olfaction to locate ant larvae and eggs. Nocturnal opportunistic foragers, especially arboreal geckos and snakes, have comparatively large eyes (Werner 1969; Pianka & Pianka 1976; Shine 1991a). Most pythons have heat-sensitive pits in some labial scales (Bullock & Barrett 1968). Attraction of prey by tail luring is found in the elapid *Acanthophis* (Carpenter, Murphy & Carpenter 1978), the legless lizard *Lialis* (Bradshaw, Gans & Saint Girons 1980; Murray, Bradshaw & Edward 1991) and some skinks (Greer 1989).

Lizards tend to feed opportunistically. Tooth differentiation and specialisation of jaw musculature is primarily related to retention, immobilisation and swallowing, rather than dismembering or crushing. In the absence of mechanical reduction of prey by the teeth and jaws, the size of prey is, with the exception of *Lialis*, proportional to jaw length and head width. Jaw dimensions have been used as reliable indicators of prey size in geckos (Pianka & Pianka 1976) and skinks (Pianka 1986).

A grasping function for the jaws is not vital if the prey is relatively small. For example, *Moloch* captures small ants with its projectile tongue, without holding or crushing them with its jaws (Pianka 1986). The capture of large arthropod and vertebrate prey involves the jaws, teeth, neck and body musculature. Lizards cannot move their lips and have limited use of their limbs in feeding. Snakes, some goannas and *Lialis* feed on comparatively large vertebrates by lunging with the neck and/or body. Their teeth are often recurved to securely hold prey, and cranial kinesis facilitates grasping (Frazzetta 1962; Savitzky 1980, 1983; Patchell & Shine 1986a; Condon 1989). In snakes, the simultaneous and synchronised contraction of the jaw musculature in striking, holding and subduing prey is functionally very different from the alternating action of the jaws in swallowing (Van Ripper 1953; Albright & Nelson 1959a, 1959b; Frazzetta 1966; Kardong 1974; Cundall & Gans 1979). Small prey can be killed prior to swallowing, by crushing or piercing. Larger prey may be asphyxiated by the jaws and/or body coils prior to swallowing, or killed by digestive juices after swallowing.

Venom immobilises prey and begins chemical digestion (Zeller 1948; Skoczylas 1978). The venom is saliva secreted by the superior labial (Duvernoy's) gland in colubrids and a gland overlying the superior labial gland in elapids and seasnakes. The enlarged rear fangs of colubrids and front fangs of elapids are

grooved for venom delivery. Raised edges of the groove meet to form a discrete canal in some elapids (Fig. 35.8). This, together with the proximity of the venom gland to the large masseter muscles, effectively delivers venom into the prey.

The tongue of most squamates has an important role in manipulation and swallowing (Bels & Baltus 1989). Varanids, legless lizards and snakes typically swallow prey head first, using the musculature of the jaws and neck. Swallowing is assisted by large quantities of lubricating saliva and kinking of the throat and neck (Patchell & Shine 1986a). Varanids jerk prey backwards as the mouth is thrown forward, causing the prey to pass by its own inertia into the throat/oesophagus (Longley 1947; Gans 1961, 1969; Smith 1982). Snakes can work prey into the mouth by the alternate movement of the upper and lower jaws on each side (Frazzetta 1959, 1966; Gans 1961; Kardong 1977; Cundall 1983). In static inertial feeding, such jaw 'walking' allows a snake to pull itself over heavy prey (Bramble & Wake 1985).

Digestion

Chemical digestion in squamates is very similar to that described for other vertebrates (Stevens 1988). The digestive tract in both lizards and snakes consists of a muscular tube which commences as the oesophagus, passes into the stomach, small intestine and large intestine, and culminates in the cloaca (Fig. 24.12). The tube has muscular walls and an absorptive epithelium. It is lined throughout with mucous cells and, regionally, with specialised secretory cells that may be aggregated into glands.
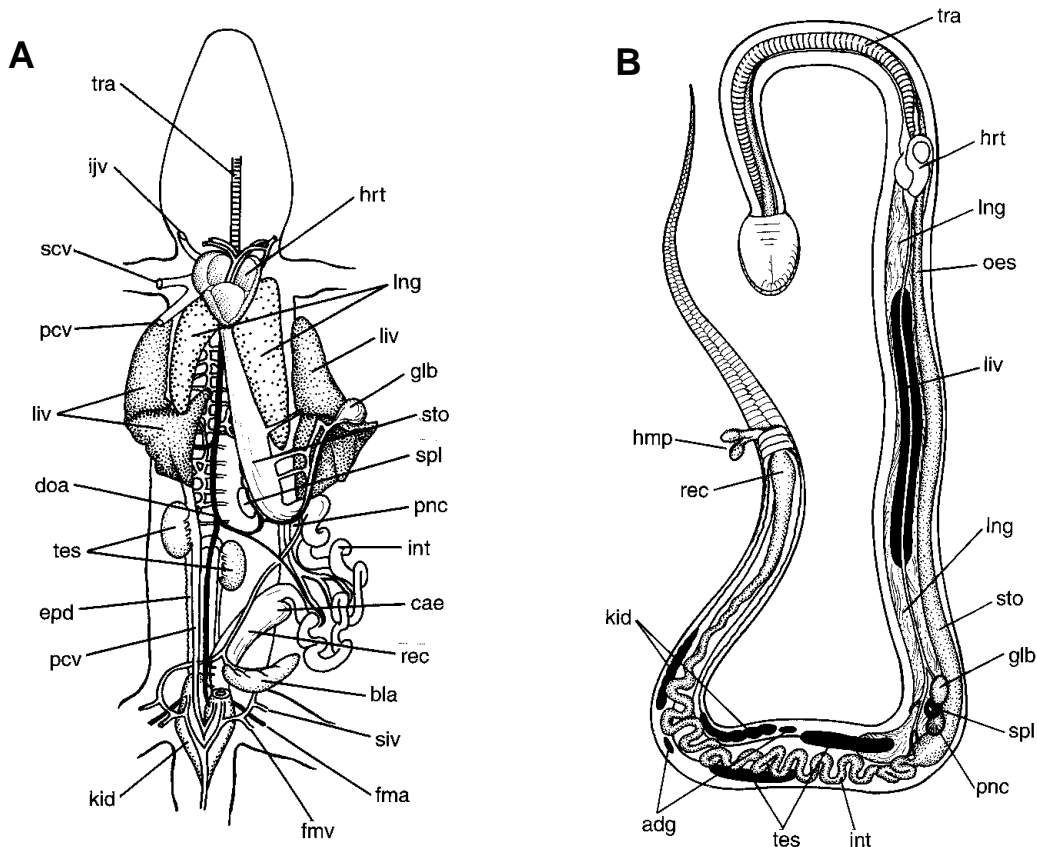
Figure 24.12 The arrangement of the viscera in squamates. **A**, a lizard; **B**, a snake. **adg**, adrenal glands; **bla**, bladder; **cae**, caecum; **doa**, dorsal aorta; **epd**, epididymis; **fma**, femoral artery; **fmv**, femoral vein; **glb**, gall bladder; **hmp**, hemipenes; **hrt**, heart; **ijv**, internal jugular vein; **int**, small intestine; **kid**, kidney; **liv**, liver; **lng**, lungs; **oes**, oesophagus; **pcv**, postcaval vein; **pnc**, pancreas; **rec**, rectum; **scv**, subclavian vein; **siv**, sciatic vein; **spl**, spleen; **sto**, stomach; **tes**, testes; **tra**, trachea. [M. Thompson]

The oral cavity is lined with ciliated or squamous epithelium containing mucin-secreting goblet cells. The oral glands include the palatine, lingual and sublingual, labial glands, mandibular and venom glands (Kochva 1978).

The palatine glands of the roof of the mouth, which are variously developed in lizards but absent in snakes, secrete mucin, as do other digestive glands. Sublingual glands are located on the floor of the oral cavity; those of some seasnakes are salt glands (Dunson 1976). Lingual glands are well-developed in geckos and dragons, but are lacking in goannas and snakes. Squamates have supra- and infralabial glands around the edges of both the upper and lower jaws. It has been suggested that the well-developed mandibular gland of goannas may secrete a venom (Gabe & Saint Girons 1969; Kochva 1978).

The longitudinally folded oesophagus is long and capable of substantial expansion in squamates that ingest large prey, and can be used for short term storage and chemical digestion. The ciliated lining of the oesophagus has many goblet cells (Parsons & Cameron 1977).

Food is stored and digested physically and chemically in the stomach. It is usually separated into fundic and pyloric regions, and a pyloric valve may be present. The lining is folded into prominent longitudinal rugae, in snakes, but these are less obvious in the thinner-walled stomachs of lizards (Parsons & Cameron 1977). The muscular walls mechanically mix and dismember prey. A variety of straight, tubular glands occur in the stomach of squamates (Luppa 1977).

The stomach capacity may be as high as 40% of the body weight in goannas and snakes that consume large prey (Weavers 1983; Greer 1989; Shine 1991a), while species consuming small prey may also have a substantial gastric capacity. For example, that of *Moloch* may hold up to 2,500 ants (Greer 1989).

Gastric juice has a low pH (about 2 to 3) and contains mainly proteolytic (pepsin) and also other enzymes (chitinase, amylase) (Skoczylas 1978). The low pH prevents putrefaction of prey, decalcifies the bone of vertebrate prey, and may help kill prey in colubrids. Chemical digestion employs hydrochloric acid (HCl) and pepsin, which is formed from pepsinogen at low pH. The dark cells of the main gastric glands in the fundus secrete pepsinogen and HCl. The pyloric glands are usually shorter and less branched than the main gastric glands, and secrete mucus and perhaps other materials.

The time required for food digestion in snakes, and presumably also lizards, is a function of both the size and type of prey being digested. It is directly correlated with the penetration rate of digestive juices and the neutralising capacity of prey tissue (Skoczylas 1970b). Fish are digested more quickly than frogs (Brown 1958; Abduschukuova 1965; Skoczylas 1970a, 1978), which are digested more quickly than mice (Root 1961). Gastric enzyme activity is reduced at low body temperatures (Henderson 1970; Avery 1973). Low temperature reduces both the activity of pepsin and the production and release of pepsinogen and HCl (Skoczylas 1970b).

The pancreas secretes a mixture of bicarbonate ions and digestive enzymes into the small intestine. The bicarbonate buffers the acidic fluid from the stomach to a near neutral pH. The enzymes digest carbohydrates (amylolytic), proteins (proteolytic) and lipids (lipolytic). Many insectivorous squamates produce chitinase (Jeuniaux 1961).

Bile, produced by the liver and stored in the gall bladder, emulsifies fat to assist the hydrolysis of triglycerides by lipases and facilitates absorption of the products of hydrolysis (Haslewood 1968; Tammar 1974).

The intestine is usually coiled and longer in herbivores and omnivores than carnivores. It completes chemical digestion and absorbs the products of digestion, water and some minerals. The surface area of the intestine, which

determines the rate of absorption, is increased by the presence of longitudinal folds, epithelial villi and cellular microvilli (Ferri, Junqueira, Medeiros & Medeiros 1976; Luppa 1977; Parsons & Cameron 1977).

The colon, which is usually separated from the small intestine by an ileocolic valve, typically has thin walls with little muscle. Its epithelium has goblet cells but no other secretory cells. It can be a site for fermentation of plant material. The hindgut is the primary site of the adaptive increase in gut length of herbivorous squamates (Skoczylas 1978; Stevens 1988).

The caecum, a thin walled extension of the colon at its junction with the small intestine, allows an increase in the volume of digested food and a variable passage rate for different foods. It is a common feature of herbivores and omnivores and may be a major site for symbiotic digestion of plant material (Mackenzie & Owen 1923; Greer 1989). However, dragons, which are primarily insectivorous (Pianka 1971c), possess a caecum, whereas it is poorly developed in some *Egernia* and *Tiliqua* that consume large quantities of plant material (Shine 1971; Brown 1983; Greer 1989).

The cloaca is the terminal part of the intestine where digestive and urinary waste is held prior to release. It is incompletely separated into the coprodeum, urodeum and proctodeum. The coprodeum is essentially the posterior portion of the large intestine. The urinary and reproductive tracts open into the central urodeum. The procotodeum is a short tube closed by the anal sphincter.

CIRCULATION

The circulatory system consists of a heart, a vascular circuit containing blood, and a lymphatic drainage system. It transports gases, nutrients, hormones and neurohormones. Hydrostatic pressure is generated for blood flow, glomerular filtration, and erection of hemipenes and other cavernous tissues such as the external narial sphincter. Cleaning of the eye by expansion of the orbital venous sinus, swelling of the head to initiate skin shedding, and predator defense by orbital blood squirting are also made possible by this pressure. The circulatory system also has a role in immune defense and thermoregulation. The cardiovascular adaptations of reptiles have been reviewed recently (see Lillywhite & Burggren 1987).

Heart

The heart of a typical lizard is located ventrally in the thoracic cavity between the left and right lungs, but is located more posteriorly in elongate lizards and snakes (Fig. 24.12B). It consists of a thin-walled sinus venosus, two atria, and a three-chambered ventricle.

Blood returns from the body via the anterior and posterior venae cavae to the thin-walled sinus venosus then to the right atrium, and from the lungs via the pulmonary veins to the left atrium (Fig. 24.13). The relatively thin-walled atria have a significant role in ventricular filling (Johansen 1959). The ventricle has three thick, muscular-walled chambers, the cavum venosum, cavum arteriosum, and cavum pulmonale. The right atrium communicates with the cavum venosum. The left atrium communicates with the cavum arteriosum, which would be blind-ending except that it connects to the cavum venosum via an interventricular canal. Atrioventricular valves control blood flow between the right atrium, cavum arteriosum and cavum venosum. The cavum venosum is partially separated by a thick muscular ridge from the third chamber, the cavum pulmonale.

There is considerable functional separation of oxygenated and deoxygenated blood in the squamate ventricle despite the anatomical continuity of its three chambers (Fig. 24.13; Webb, Heatwole & De Bavay 1971; White 1976). Deoxygenated blood enters the cavum venosum from the right atrium, and also passes across the muscular ridge into the cavum pulmonale. Oxygenated blood enters the cavum arteriosum from the left atrium, but remains there because the atrioventricular valves close the interventricular canal. During ventricular contraction, the atrioventricular valves close the atrio-ventricular openings and open the interventricular canal. Deoxygenated blood is first ejected into the pulmonary arteries from the cavum venosum and cavum pulmonale because of the low vascular resistance of the pulmonary circuit. As the ventricle further contracts, the muscular ridge separates the cavum venosum and cavum pulmonale. This allows oxygenated blood to flow from the cavum arteriosum into the cavum venosum then the left and right systemic arches, and prevents backflow of deoxygenated blood from the cavum pulmonale into the cavum venosum. The functional, but not anatomical, separation of oxygenated and deoxygenated blood can allow the systemic return to the heart to be shunted to the systemic output (right-to-left-shunt) to bypass the lungs during diving, or the pulmonary return to be shunted to the lungs (left-to-right shunt) during periods of intense lung ventilation. For example, blood flow completely bypasses the lung in the filesnake *Acrochordus granulatus* during prolonged quiescent diving but largely bypasses the systemic circulation during lung ventilation (Lillywhite & Donald 1989).
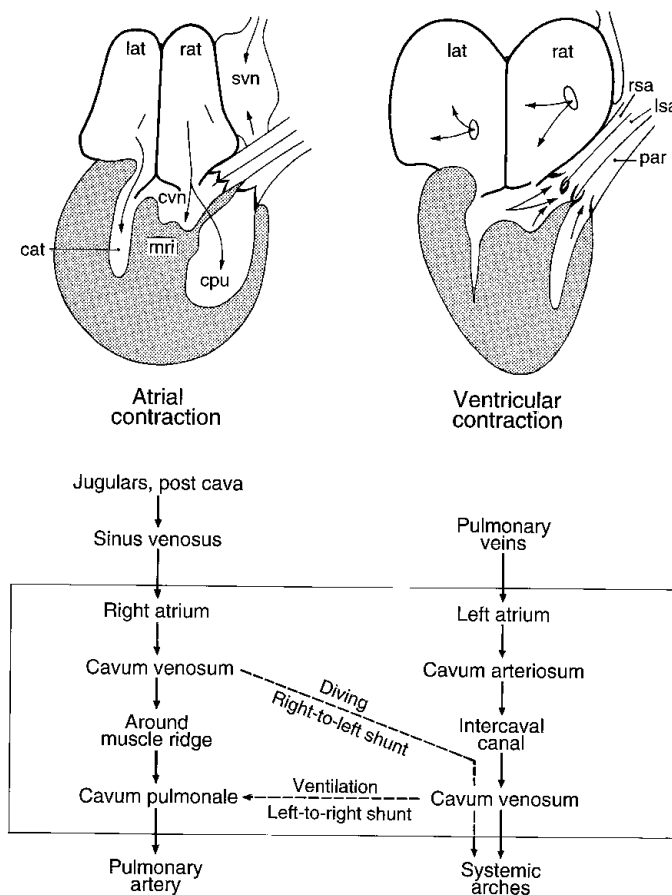
Figure 24.13 Diagrammatic representation of blood flow through the heart of a lizard, *Varanus* sp., during atrial contraction and ventricular contraction. **cat**, cavum arteriosum; **cpu**, cavum pulmonale; **cvn**, cavum venosum; **lat**, left atrium; **lsa**, left systemic arch; **mri**, muscular ridge; **par**, pulmonary artery; **rat**, right atrium; **rsa**, right systemic arch; **svn**, sinus venosus. (Modified from White 1968; Webb *et al.* 1971). [W. Mumford]

Heart rate is inversely related to body mass (Bartholomew & Tucker 1964; Licht 1965), and is generally higher during breathing than apneic periods. A diving bradycardia occurs during voluntary diving (Courtice 1981d, 1985). Temperature has a marked effect on heart rate, with a Q_{10} of about 2 to 2.5, but the maximal heart rate may decline above a critical body temperature (Bartholomew & Tucker 1963; Licht 1965; Bennett 1972; Wilson & Lee 1974). There is a considerable thermal hysteresis in heart rate (Bartholomew & Tucker 1963) during heating (higher rate) and cooling (lower rate). There is a substantial increase in heart rate during activity, but the scope for heart rate increment may decline at high body temperatures. The cardiac output of *Varanus exanthematicus* increases to match the 6.6-fold increase in O_2 demand during activity (Gleeson, Mitchell & Bennett 1980) by a 2.2-fold increase in heart rate, a 1.3-fold increase in stroke volume, and a 2.3-fold increase in the arterial-venous O_2 content difference.

Vascular System

The arterial circuit of the systemic system arises from the heart as right and left aortic arches. The carotid arteries supply the head (the right carotid is small, or absent, in many snakes). The posterior extensions of the left and right arches give rise to subclavian arteries, which supply the forelimbs, and then fuse to form the dorsal aorta. Branches from the dorsal aorta supply the gut, liver and kidneys (coeliaco-mesenteric, hepatic and renal arteries), hindlimbs (iliac arteries) and tail (caudal artery). The venous circuit enters the heart as left and right anterior and postcaval veins. Blood from the tail (caudal vein) and hindlimbs (iliac veins) can enter the renal portal system then return to the heart directly via the post cavae, or via the pelvic, ventral abdominal, and hepatic veins. Blood from the forelimbs returns via the subclavian veins then anterior caval veins to the heart. The anterior cardinal (jugular) veins drain the anterior body. An hepatic-portal system carries nutrient-rich blood from the digestive tract to the liver. The circulatory system of the limbless *Typhlops* has been described in detail by Robb (1960).

The pulmonary arch exits the cavum pulmonale then forms the right and left pulmonary arteries (the latter degenerates in snakes with a vestigial or absent left lung). Deoxygenated blood flows preferentially from the cavum venosum into the pulmonary arteries because the pulmonary vascular resistance is generally lower than the systemic resistance. However, a profound increase in pulmonary vascular resistance during diving can induce a right-to-left intracardiac shunt that bypasses the lungs (Lillywhite & Donald 1989).

During basking, a head-body temperature gradient can be maintained by countercurrent heat exchange between warm venous (internal jugular) blood and cool arterial (internal carotid) blood (Heath 1966). However, an internal jugular constrictor muscle can return cephalic blood preferentially to the body via the external jugulars, bypassing the countercurrent heat exchanger to cool the head and warm the body, and also cause the eyes to swell by expansion of the cephalic venous sinus. Such head-swelling can also loosen and break the skin for sloughing.

Terrestrial and, in particular, arboreal snakes experience gravitational hydrostatic pressure gradients, and must prevent peripheral blood pooling and maintain venous return. Their anteriorly placed heart minimises head-heart distance and their short, vascularised lungs reduce the risk of pulmonary oedema. Conversely, aquatic snakes rarely experience gravitational hydrostatic pressure gradients and may lack these circulatory specialisations (Lillywhite 1987a). For example, seasnakes have poor baroreceptor control of blood pressure (Lillywhite & Pough 1983).

There is a marked cardiovascular readjustment during voluntary diving (White 1976; Courtice 1981d, 1985; Seymour 1982). Heart rate declines dramatically, but arterial blood pressure is maintained by peripheral vasoconstriction. Cardiac output is redistributed by a right-to-left shunt that partially or completely bypasses the lungs. Cutaneous perfusion is elevated by local CO_2 in *Physignathus* and may facilitate cutaneous CO_2 excretion during diving (Courtice 1981c).

Blood

Blood has a variety of functions including transport of O_2, CO_2, nutrients, wastes, and hormones as well as pH buffering, defense, and maintenance of blood colloid osmotic pressure. Vasoconstriction and blood clotting (haemostasis) follow injury to the vascular system. Fibrinogen forms a fibrin clot, particularly in the presence of cellular factors released by tissue damage.

Blood contains many nucleated ellipsoid red blood cells (RBCs or erythrocytes) and fewer white blood cells (WBCs; Saint Girons 1970b; Courtice 1981a). RBCs vary greatly in size amongst squamate families (Wintrobe 1933/1934; Saint Girons 1970b). The RBC count of squamates is generally 5×10^5 to 2×10^6 mm^{-3} (Duguy 1970). It can vary between sexes, with age, over an annual cycle, and with pathological conditions, but generally does not increase with altitude. The WBCs include granulocytes (eosinophils, basophils, azurophils, neutrophils), lymphocytes, monocytes, plasma cells and thrombocytes (Saint Girons 1970b). The eosinophils are involved with allergic reactions and the basophils (mast cells) phagocytose foreign material. Lymphocytes have a cellular immune role. The small thrombocytes are involved with blood clotting. There is considerable variation in WBC count, from about 2 to 30×10^3 mm^{-3} (excluding thrombocytes). Lymphocytes are generally the most numerous (other than thrombocytes), and eosinophils are the second most abundant. Monocytes and basophils are the least abundant. There are generally about 50 to 300 thrombocytes per 100 other WBCs. WBC count and proportions of different WBCs vary between sexes, with age and moulting, with season, during pregnancy, and with pathological state.

The intracellular concentration of haemoglobin in squamate RBCs is about 32 g% and the oxygen carrying capacity of blood is about 8 to 10 volumes %, depending on the haemoglobin concentration. Reptilian haemoglobin tends to be more oxidised (met- haemoglobin) than mammalian haemoglobin (Wood & Lenfant 1976) and has a lower O_2 binding capacity. For example, the blood of *Physignathus* binds about 0.95 ml O_2 per gram of total haemoglobin (Courtice 1981a) compared to 1.2 to 1.3 ml O_2 g^{-1}. The sigmoidal O_2 dissociation curve reflects the cooperativity of haemoglobin subunits; cooperativity coefficients are typically 1 to 3 (Dessauer 1970; Wood & Lenfant 1976; Pough 1980a). The O_2 affinity of haemoglobin (P_{50}) is affected by body mass, temperature and pH (Bohr and Root effects). The P_{50} decreases with body mass in lizards from about 75 torr (mass <20 g) to about 50 torr (mass >1000 g); these P_{50} values are considerably higher than for mammals of comparable body mass (Bennett 1973; Pough 1977a, 1980a). In contrast, the P_{50} of snakes increases with mass (Pough 1977b, 1980a). Temperature affects the P_{50} of squamate blood (Pough 1969a, 1976; Courtice 1981a), but the low effect of temperature for some squamates minimises the effects of changes in body temperature on the O_2 transport capacity of blood.

Carbon dioxide transport depends on the reversible chemical combination of CO_2 with blood proteins (especially haemoglobin) and water, as well as dissolved CO_2. The CO_2 dissociation curve for blood of *Physignathus* is hyperbolic and the total CO_2 content is diminished at elevated temperature (Courtice 1981a).

Most diving reptiles do not have a higher haemoglobin content, blood O_2 capacity, blood volume and lower P_{50} than non-diving species, except for the file snakes (Johansen & Lenfant 1972; Feder 1980; Seymour, Dobson & Baldwin 1981; Seymour 1982; Pough & Lillywhite 1984; Heatwole & Dunson 1987). The blood of *Acrochordus* has a high Bohr effect to provide high utilisation of pulmonary O_2 stores during diving, and rapid reoxygenation of blood during respiratory periods (Johansen & Lenfant 1972; Seymour *et al*. 1981). The blood buffer capacity of aquatic squamates is similar to that of terrestrial species (Seymour 1982).

Lymphatic System

The lymphatic system returns interstitial fluid (lymph) from the tissues to the venous system. A major role is to return to the circulation plasma proteins that leak from the capillaries and to prevent vascular-interstitial fluid imbalance (oedema). The lymphatic system, which generally parallels the venous system, consists of superficial and deep lymphatic nets (microvascular vessels in most organs), which drain through lymphatic sinuses (or sacs, reservoirs) into lymphatic vessels and main lymphatic trunks to the venous system (Ottaviani & Tazzi 1977). However, there is considerable anatomical variation in reptiles. The reptilian lymphatic system lacks lymph nodes. In lizards, one pair of small, pulsating, vesicular lymph hearts are located near the first caudal vertebra, and their afferent and efferent lymph vessels have double valves. In snakes, the lymph hearts are postero-lateral to the cloaca, well protected against compression and trauma by the posterior ribs and vertebral zygapophyses. They communicate to the vertebral lymphatics via three valved openings, and to the renal portal veins via valved openings.

Immunology

Reptiles react to invasion by foreign material with an immunological response such as anaphylaxis and tissue rejection. Humoral (antibody-antigen) response and cellular (lymphocyte) responses occur. Specific plasma proteins, which are poorly characterised in squamates, agglutinate specific antigens to which the individual has been exposed. For example, blood of the boid *Morelia spilota* contains antibodies to antigens of infecting parasites. The immune response is temperature dependent, with a maximal response in antibody synthesis at a body temperature around 35°C. The thymus gland is presumably involved with aspects of adaptive immunity.

RESPIRATION

The primary role of the respiratory system is the supply of oxygen for cellular metabolism. Other roles include acid-base regulation (by CO_2 excretion), ionoregulation (nasal salt glands), chemoreception (olfaction and Jacobson's organ), thermoregulation (by panting or gular pumping), buoyancy (in aquatic species), vocalisation, and predator deterrence (by using lung expansion to wedge the body in crevices).

Pulmonary Gas Exchange

The respiratory system of a typical lizard consists of external nares, nasal cavity, pharynx, trachea, and two lungs. The lungs are the primary site of gas exchange. Air is usually inspired and expired via the external nares.

The external nares connect via a tubular vestibulum to a large nasal cavity, the *cavum nasi proprium* (Pratt 1948; Bellairs & Boyd 1950; Underwood 1957; Parsons 1970). A dorsal or tortuous pathway of the vestibulum prevents water or

particulate material from entering the nasal chamber. Cavernous erectile tissue surrounding the vestibulum may function as an external nareal valve in most squamates. The nasal cavity is usually partly divided by a single concha (projection of the lateral wall) into a ventral choanal tube lined by non-sensory epithelium, and a dorsal nasal chamber lined by olfactory epithelium. The nasal cavity can be connected to the pharynx by a discrete nasopharyngeal duct, but in most lizards the nasal cavity essentially opens directly to the internal choanae. Jacobson's organ, an important olfactory structure, is also connected to the pharynx. The external (or lateral) nasal gland is external to the nasal capsule, but is connected by a duct to the vestibulum near the nasal cavity. This branched, tubular mucous gland excretes salt in many lizards, but not in snakes (except *Pelamis*).

All snakes have a simple, short vestibulum, except for *Laticauda* which has folds, and the nasal cavity has a moderately well-developed concha. Aquatic snakes tend to have a simple tubular nasal cavity with no concha. All snakes have short nasopharyngeal ducts and the choanae open far forward on the palate, because the snout is very short. Jacobson's organ is large, even in aquatic snakes which generally have reduced olfaction.

Lung structure is highly variable in squamates (Perry 1992). Most lizards and snakes have simple, single-chambered or transitional lungs, with a relatively small surface area for gas exchange. The lungs of *Physignathus* have small internal septae that form air pockets. The anterior half of the lungs are more vascularised than the posterior portion (Courtice 1981a). In contrast, goannas have heterogeneous, multi-chambered lungs, with considerable compartmentalisation and a high surface area. The parenchymal lining of the lung can be simple and flat, with trabeculae of smooth muscle and elastic tissues lying against the wall. The trabeculae may extend from the wall to form ediculae (with trabecular chambers wider than they are high) or faveoli (with trabecular chambers higher than they are wide). Various parenchymal types can all be found homogeneously or heterogeneously within a single lung, but generally one parenchymal type predominates. Edicular parenchyma predominates in *Acrochordus* and *Varanus*, and faveolar parenchyma in colubrid snakes and lizards.

The maximal lung volume of reptiles is generally greater than that of a mammal of equivalent mass, but has only about one hundreth of the surface area for gas exchange (Wood & Lenfant 1976); this reflects their lower metabolic requirements. More active squamates, such as goannas, have a larger lung surface area than less active species, because a greater fraction of their lung volume is compartmentalised rather than a decreased diameter of 'alveoli' (Tenney & Tenney 1970).

The left lung is generally reduced in elongate squamates (Fig. 24.14). For example, the left lung is reduced to 8% and the right lung to 22% of snout-vent length in the limbless, highly-elongate *Lerista apoda* (Greer 1989). The left and right lungs of pentadactyl *Lerista* are both about 27 to 32% of the snout-vent length. The right lung is reduced in some skinks such as *Vermiseps*, but the left lung is reduced in *V. pluto*. In snakes, the left lung is typically reduced or vestigial, if not absent, but pythons have two well-developed lungs (Butler 1895). In some aquatic snakes (file snakes and hydrophiids) the large (right) lung has an avascular caudal portion that extends as far as the cloaca. In *Typhlops*, both lungs are well-developed and elongate, but the anterior (left) lung appears to exchange gases whereas the posterior (right) lung stores air (Robb 1960).

Lung ventilation is generally negative-pressure, aspiration breathing by movements of the rib-cage. Ventilation is typically a triphasic expiration-inspiration-expiration cycle, with a non-ventilatory (apneic) period of variable

duration. The breathing portion of the cycle begins with active expiration by contraction of intercostal muscles and collapse of the lung, followed by passive inspiration to resting lung volume by elastic recoil of the rib cage, then active inspiration by contraction of other intercostal muscles. The glottis is then closed, and passive recoil of the rib cage creates a positive pressure in the lung during the apneic period. In some lizards, the glottis remains open and there is a passive expiration before the apneic period.

Most lizards ventilate their lungs by axillary movements. A few skinks, such as *Eremiascincus* and some *Lerista*, ventilate by vertical chest movements. This forms a ventral air pocket which enables expansion of the lungs while submerged in loose sand (Pough 1969b). Burrowing snakes may switch from lateral to vertical breathing movements when buried. Limbless, humus-living squamates, such as *L. apoda*, legless lizards and snakes, have a circumferential breathing system whereby contraction of the entire anterior body compresses the lung for expiration.

Resting respiration is typically discontinuous, with breathing periods (of multiple breaths) interspersed with often long apneic periods (for example, *Physignathus*; Courtice 1981a). Breath-to-breath rate is optimised to reduce the mechanical cost (Frappell & Daniels 1991), but the average breathing rate over respiratory and apneic periods can be varied by modifying the relative length of the apneic periods. Much of the increase in lung ventilation during periods of elevated activity is the result of elevated tidal volume and decreased apneic period, rather than increased breath-to-breath ventilatory rate. In *Physignathus*, the breathing rate increases exponentially with temperature (Courtice 1981a).
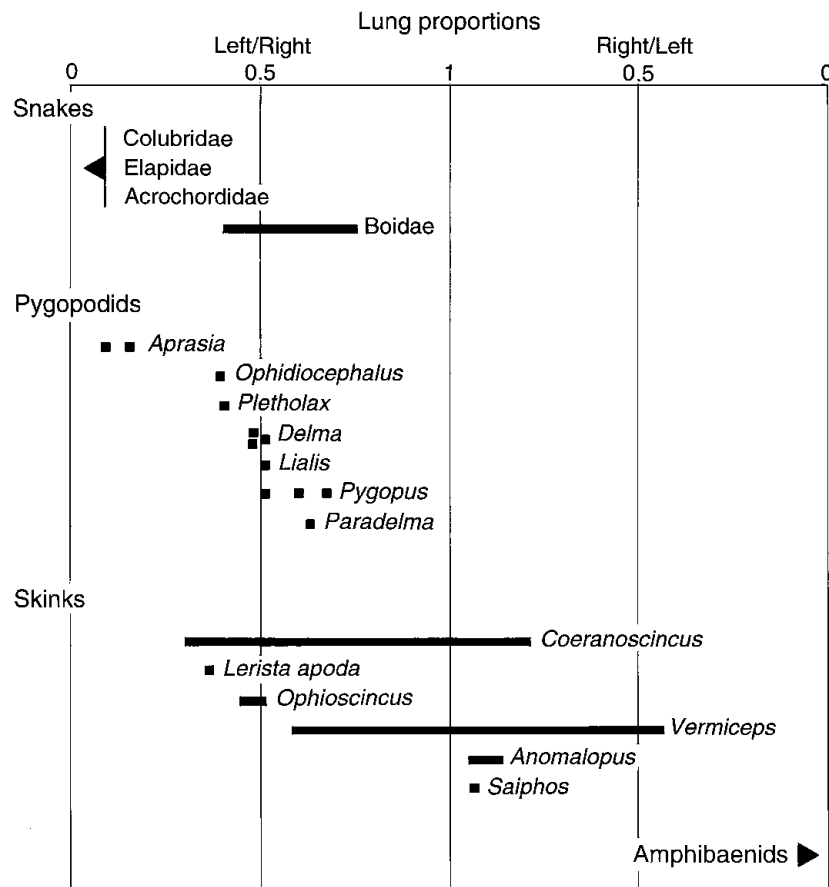
Figure 24.14 Relative proportions of the left and right lungs in various snakes and lizards.   [W. Mumford]

The concept of respiratory regulation is complicated for reptiles because of their arrythmic breathing pattern, particularly at rest (Wood & Lenfant 1976). Reptiles tolerate large fluctuations of blood gas tensions during the ventilation/ apneic cycle. Respiration is generally stimulated by CO_2, but tends to be less sensitive to CO_2 in diving and fossorial species. For example, respiration by the aquatic snake *Acrochordus* is more sensitive to O_2 than CO_2 (Wood & Lenfant 1976).

Cutaneous Gas Exchange

Squamate skin is highly keratinised to limit cutaneous evaporative water loss, and as a consequence there is limited cutaneous gas exchange. The cutaneous O_2 exchange is only about 2 to 3% of the total in terrestrial lizards and snakes, but is significant in aquatic lizards such as *Physignathus* (8% of total O_2 consumption rate, Courtice 1981b), filesnakes (8%, Standaert & Johansen 1974) and seasnakes (33%, Graham 1974a). Carbon dioxide is more readily exchanged across the skin than is O_2, because of its 20-fold higher diffusibility in water. Consequently, cutaneous CO_2 loss is substantial even in terrestrial reptiles (Graham 1974b; Standaert & Johansen 1974; Courtice 1981b). Over 20% of the CO_2 exchange is across the skin in the terrestrial *Boa constrictor*, 25% in the water dragon *Physignathus*, 33% in *Acrochordus* and 94% in *Pelamis*. However, no aquatic squamate has been shown to rely completely on cutaneous gas exchange. Furthermore, cutaneous gas exchange appears to be severely limited by diffusion and not amenable to physiological regulation (Seymour 1982).

Acid-base Balance

Acid-base balance is influenced by respiration, metabolism, excretion and body temperature. The pH is determined primarily by the CO_2/HCO_3^- buffer system, and hence the ratio of ventilatory CO_2 excretion to metabolic CO_2 production. Blood pH can be elevated in respiratory alkalosis by hyperventilatory excretion of CO_2, or by metabolic alkalosis due to renal excretion of H^+. Blood pH can be lowered in respiratory acidosis by hypoventilatory retention of CO_2 or metabolic acidosis as a result of renal retention of H^+. Body temperature also has a profound influence on acid-base balance because of the effects of temperature on metabolic rate, respiration and renal function, and a physico-chemical effect of temperature on the dissociation of water (Howell & Rahn 1976; Withers 1978).

Gas Exchange in Eggs

Most lizards and snakes lay eggs. Gas exchange during development occurs via pores in the eggshell. The water vapour conductance of flexible-shelled squamate eggs is up to 100 times greater than that of avian eggs (Deeming & Thompson 1991), but the rigid eggs of some geckos have a very low water vapour conductance, presumably because of the low numbers of pores. O_2 and CO_2 conductance is lower for squamate eggs than is predicted from the water vapour conductance, but it is not clear why. Gas exchange increases during incubation (Vleck & Hoyt 1991).

Metabolism

The metabolic rate of squamates varies with a number of environmental, physiological, behavioural, ecological and evolutionary variables. Metabolism is normally aerobic, but anaerobic metabolic pathways can be significant during intense activity or prolonged anoxia.

Most squamates have a considerable scope in metabolic rate, from a minimal standard metabolic rate (SMR) to a maximal metabolic rate (MMR). Some reptiles become dormant in the cold (brumation, hibernation) or heat (aestivation), and their metabolic rate is further depressed below SMR. Metabolic rate can also be depressed below SMR by anoxia.

The standard metabolic rate of squamates is very similar to that of other ectotherms (Bennett & Dawson 1976; Andrews & Pough 1985), but is about one fifth to one tenth of that of the basal metabolic rate of an equivalent sized bird or mammal, at an equivalent body temperature. The basal metabolic rate of an endothermic python (Van Mierop & Barnhardt 1978) is also about one fifth of that of a mammal at an equivalent body temperature.

The SMR is strongly influenced by body temperature, body mass and ecology (Andrews & Pough 1985). Day-active predators have a higher SMR than reclusive ones, which are higher than fossorial ones; herbivores have an SMR between that of day-active and reclusive predators. Body temperature has an exponential effect on SMR, with a Q_{10} typically between two and three (Bennett & Dawson 1976; Andrews & Pough 1985; Thompson & Withers 1992). Field metabolic rate (FMR) has been determined for many squamates (primarily lizards) to be about two to five times the SMR at 20° to 30°C.

The allometric relationship between metabolic rate and body mass is SMR = **a** Mass$^{\mathbf{b}}$, where **a** is the mass coefficient and **b** is the mass exponent. The interspecific value of **b** is about 0.8 for squamates (Andrews & Pough 1985), but there appear to be phylogenetic differences. For example, **b** is about 0.9 to 1.0 for goannas (Thompson & Withers 1992, 1994). The intraspecific allometric relationship is generally different from the interspecific relationship. The intraspecific mass exponents are generally less than 0.8, but vary dramatically from <0.6 to >1 for various species (Galvão, Tarasantchi & Guertzenstein 1965; Bennett & Dawson 1976; Andrews & Pough 1985; Dmiél 1986; Zari 1991; Thompson & Withers 1992).

Thyroid hormones (thyroxin, T_4; triiodothyronine, T_3) often affect the SMR of squamates, particularly if the body temperature is near the preferred range. Thyroxin administration generally elevates the SMR, whereas thyroidectomy decreases it.

Squamates commonly have seasonal patterns of inactivity (Gregory 1982). Hibernation is winter inactivity that occurs in temperate zones in response to cold and lack of food. Aestivation is summer inactivity that occurs in arid or tropical zones in response to heat and lack of water. The activity pattern may be bimodal, with periods of both hibernation and aestivation. The metabolic rate may decline during hibernation in some species, but with no metabolic depression other than a normal Q_{10} effect. However, the metabolic rate may be depressed even further in some species, by inverse acclimation. Some species remain active year-round and compensate for low temperatures by a partial thermal metabolic acclimation.

Squamates can rely on anaerobic metabolism of carbohydrate stores, especially glycogen, for considerable energy production during hypoxia, such as occurs during burst activity or extended submergence. Lactate is the primary metabolic endproduct of anaerobic metabolism for squamates, as for other vertebrates. The anaerobic capacity is about 1 mg lactate accumulated per gram body mass, and is essentially independent of body mass and body temperature (Bennett & Dawson 1976). The accumulation of lactate, and metabolic acidosis, make anaerobiosis a non-steadystate metabolic pathway and cause fatigue. Recovery from anaerobic metabolism is accomplished by either aerobically oxidising the accumulated lactate, or reconverting it to glucose and glycogen (Gleeson 1980). Some lizards and snakes can survive 20 to 90 minutes of anoxia (Belkin 1963).

TEMPERATURE

Almost all squamates are ectothermic because external heat sources determine their body temperature. Some thermoconform passively to their thermal environment, but others use behavioural and physiological mechanisms to regulate their body temperature (T_b). Only a few squamates are endothermic, using endogenous metabolic heat production for regulation of T_b.

Ectothermy

Thermoconformation. Some lizards and snakes, particularly nocturnal, fossorial, tropical or aquatic species, make little or no attempt to thermoregulate, and thermoconform to the ambient temperature. For example, the body temperature of many nocturnally-active geckos is essentially the same as the ambient air temperature (Fig. 24.16; Pianka & Pianka 1976). Aquatic species also thermoconform because the high specific heat and thermal conductivity of water preclude body temperature which is substantially above water temperature. For example, the T_b of the exclusively aquatic *Acrochordus arafurae* varies with water temperature from 22.6° to 35°C (Shine & Lambeck 1985). However, aquatic species such as *A. arafurae* can thermoregulate by selecting suitable microhabitats and there may be a slight body-water temperature gradient as a result of absorption of solar radiation (for example, *Pelamis platurus*; Graham 1974b).

Thermoregulation. The thermal biology of many terrestrial squamates is dominated by the behavioural exploitation of solar radiative energy for the regulation of body temperature (Spellerberg 1972a; Avery 1982; Bartholomew 1982; Huey 1982, 1991; Pough & Gans 1982; Bradshaw 1986; Heatwole & Taylor 1987; Greer 1989). Solar radiation can be used by basking in the sun (heliothermy) or by adpressing parts of the body to a substrate warmed by the sun (thigmothermy). Many snakes and lizards, including the dragon, *Ctenophorus isolepis*, precisely maintain T_b substantially above ambient air temperature by behavioural and physiological means. Some reptiles, such as the thorny devil, *Moloch horridus*, have an intermediate pattern of relatively imprecise thermoregulation. For *Moloch*, this may reflect its sit-and-wait foraging mode.

Numerous behaviours are associated with heliothermic or thigmothermic thermoregulation. A range of the options available and the behaviours used or exhibited by *Ctenophorus fordi* under a variety of conditions is shown in Figure 24.15. Radiative heat gain will be maximised by choosing an appropriately exposed perch, and by flattening and orientating the body perpendicular to the sun's rays. Once the preferred body temperature is attained, shuttling between sun and shade can maintain body temperature within precise limits. Appropriate postures (for example, head directed at the sun to minimise exposed surface area and so the pale chest maximally reflects radiation) can minimise radiative heat gain, or the animal can move to shade or a cool burrow. Raising parts of the body away from the ground ('stilting') or ascending into high vegetation ('breezing') to the cooler air away from the hot ground surface minimises conductive heat gain and promotes convective heat loss. Panting or positive-pressure gular pumping can augment evaporative heat loss.

Numerous physiological adjustments also facilitate behavioural thermoregulation (Bartholomew 1982). Regulation of heart rate, cardiac output, and central and peripheral circulatory patterns can promote or retard heat gain. For example, the Bearded Dragon, *Pogona barbata* has a marked hysteresis between heating rate (which is rapid) and cooling rate (which is slower; Bartholomew & Tucker 1963). Temperature gradients can be maintained between the head and the body by passive (relative surface-to-volume ratios) or

physiological means such as control of venous blood flow pattern, head orientation, or panting (Heath 1966; Webb & Heatwole 1971; Pough & McFarland 1976; Crawford, Palomeque & Barber 1977).

Many lizards can maximise radiative heat gain by adopting a dark colour, then reduce heat gain by 'blanching' to a paler colour. For example, the heliothermic dragon, *Ctenophorus nuchalis*, adjusts both dermal colour and peripheral blood flow; cool individuals have a low dermal reflectivity (about 23%) compared to warm individuals (about 32%; Rice & Bradshaw 1980). Many geckos, such as *Gehyra variegata*, exhibit profound colour change at different temperatures, generally being lightest at high temperatures (Rieppel 1971). Snakes, and some lizards, lack the capacity for colour change and may be restricted from occupying microhabitats with intense solar radiation.
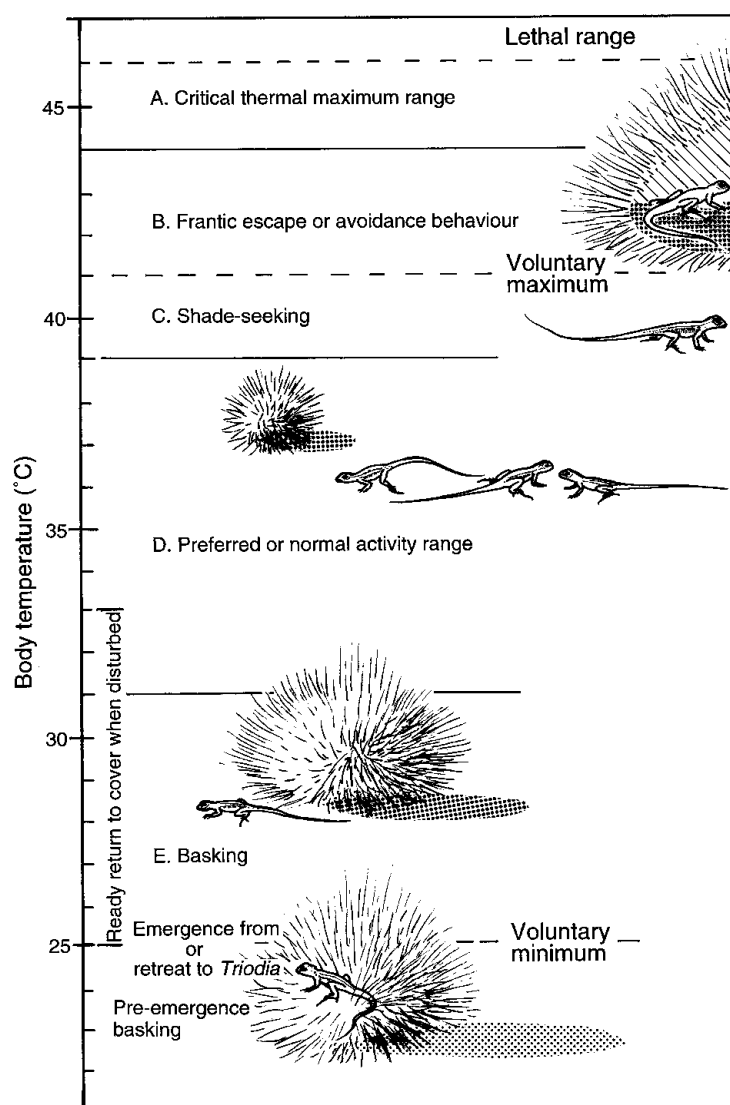
Figure 24.15 Range (**A**–**E**) of activity and thermoregulatory behaviours related to body temperature for the heliothermic dragon, *Ctenophorus fordi*. **A**, locomotor activity lost if avoidance behaviour unsuccessful; **B**, escape/ avoidance behaviour of open areas intense, shade-seeking and deep entry into *Triodia*, panting, eventual heat prostration if avoidance behaviour unsuccessful; **C**, shade sought, body/tail elevated in the sun, *Triodia* avoided, alert but inactive, **D**, head/foreparts raised, alert foraging, mating and other behaviours, pigmentation light dorsally, dark ventrally; **E**, under protective fringe of *Triodia*, head/body in contact with the substrate, pigmentation dark dorsally, light ventrally. (Modified after Cogger 1974)   [M. Thompson]

Terrestrial or arboreal dragons are heliothermic with conspicuous thermoregulatory behaviours that maintain preferred body temperature between 34° and 37°C (Bradshaw & Main 1968; Cogger 1974; Bradshaw 1977, 1986). Some geckos are thigmothermic while inactive during the day, and thermoregulate by moving about under the exfoliating bark of dead trees (Bustard 1967a) and some are even heliothermic (for example, the *Diplodactylus strophurus* group; Ehmann 1980). Little is known of the thermal biology of pygopodid lizards (Bradshaw *et al*. 1980). *Delma*, *Lialis*, *Aprasia* and some *Pygopus* are diurnal and bask, but some *Pygopus* are crepuscular or nocturnal (see Greer 1989). Terrestrial and fossorial skinks differ in thermal biology (see Greer 1989; Heatwole & Taylor 1987). Goannas are heliothermic and have high field body temperatures (34° to 38°C). Snakes, at least the diurnally active species, exhibit thermoregulatory behaviour and might be the most adept reptiles at controlling heating/cooling rates because of their elongate shape and extremely high surface-to-volume ratio. Extension of the body maximises surface area and facilitates heating, and coiling into a compact shape retards cooling. The elapid, *Pseudechis porphyriacus*, flattens its body markedly while basking, and often tilts perpendicular to the sun by using the tail as a prop (Heatwole & Taylor 1987). Its body temperature is maintained during activity between 28° and 31°C over a range of ambient temperatures and seasons (Shine 1987c).

At very high temperatures, dragons either seek cool burrows, or use arboreal perches for breezes; they will pant, but only as a last resort. When heat-stressed, geckos pant through the mouth and gular flutter. Skinks generally do not pant when heat-stressed (Greer 1989), except for members of *Tiliqua* (Heatwole *et al*. 1973). Goannas, like geckos, enhance evaporative cooling by gular pumping but do not pant like skinks.

Endothermy

Large reptiles have a low surface area to volume ratio and a high thermal inertia, and consequently warm and cool slowly. Endogenous heat production can elevate body temperature. However, the elevation of body temperature is only a degree or so, even for very large (17 kg) goannas.

A few squamates use endogenous metabolic heat production to elevate body temperature significantly above ambient temperature (Fig. 24.16). Some incubating female pythons use endogenous heat from muscle contractions to regulate egg temperature; the frequency of 'shivering' is inversely proportional to ambient temperature (Harlow & Grigg 1984; Charles, Field & Shine 1985; Slip & Shine 1988b). In contrast, non-brooding female and male pythons are ectothermic, and behaviourally thermoregulate by basking and selecting suitable thermal environments (Slip & Shine 1988e).

Preferred Body Temperature

Laboratory preferred body temperature measured using an artificial thermal gradient, requires no cost and may not reflect a preferred field body temperature of a squamate experiencing various survival 'costs' of body temperature regulation (for example, predation, feeding, reproduction, metabolic cost of locomotion and territorial defence). In addition, laboratory and field preferred body temperature can vary between sexes, at different times of the day or year, and with physiological state (for example, when digesting, or incubating eggs). Nevertheless, laboratory and field preferred body temperatures are generally well correlated and some phylogenetic trends are evident (see Heatwole & Taylor 1987; Greer 1989). Preferred body temperature tends to be high for dragons and goannas, but low and variable for skinks and snakes. Nocturnal, fossorial and aquatic species generally have low preferred body temperatures.
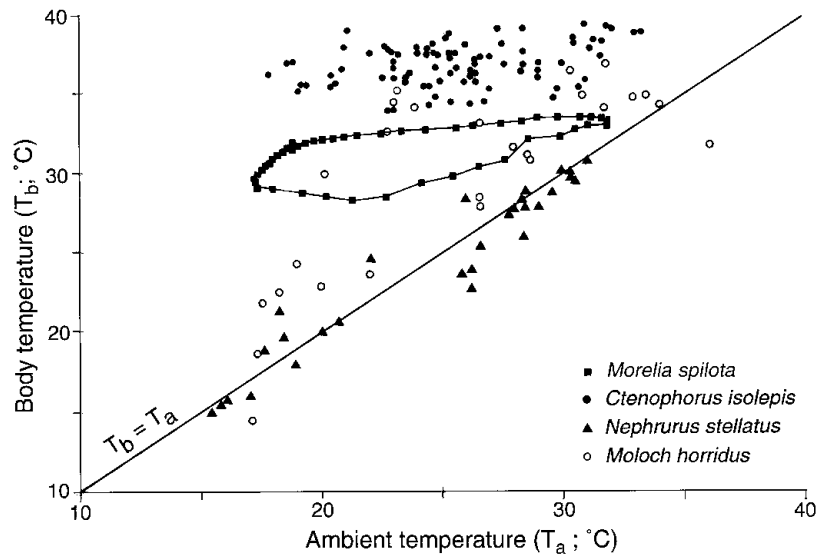
Figure 24.16 Relationship between body temperature and ambient temperature for the thermoconforming, nocturnal gecko, *Nephrurus stellatus*, the weakly-heliothermic agamid, *Moloch horridus*, the heliothermic agamid, *Ctenophorus isolepis*, and the endothermic brooding python, *Morelia spilota*, during a day-night cycle. (Data from Slip & Shine 1988; Withers unpub. data; Roberts unpub. data)   [W. Mumford]

Geckos are somewhat enigmatic because they often have low field body temperatures when active (being nocturnal) but have relatively high laboratory preferred body temperatures.

The frequency distribution of body temperatures is generally left skewed towards lower temperatures (see Pianka 1969a, 1970c, 1971c). A left-skewed temperature distribution might reflect the dual-setpoint mode of behavioural thermoregulation by squamates (Berk & Heath 1975) or an exponential effect of temperature on physiological rate functions (DeWitt 1967).

Thermal Tolerance Range

The body temperature of lizards and snakes can vary widely. A squamate is 'ecologically' dead below a critical minimum temperature (CT_{min}) at which it is incapable of righting itself, and above a critical maximum temperature (CT_{max}) at which it is incapable of escape. There is generally a voluntary minimum temperature ($>CT_{min}$) below which the animal is inactive, and a voluntary maximum temperature ($<CT_{max}$) above which they are inactive. There are also extreme lower and upper lethal temperatures, at which the animal rapidly dies. The laboratory and field preferred T_b falls between CT_{min} and CT_{max}. For example, the CT_{min} of the skink, *Tiliqua rugosa* is 3.5°C whereas the CT_{max} is 43.0°C. The upper lethal temperature at which *T. rugosa* stops breathing is 45.5°C, the laboratory preferred T_b is about 32°C, and the field T_b is about 34.3°C.

Regulation of body temperature within some preferred range is important because most physiological functions are maximal at some optimal body temperature (Huey 1982, 1991). Thermal behaviour and physiological performance therefore tend to be coadapted (Huey 1982). For example, sprint speed and preferred body temperature are coadapted for skinks with a high preferred body temperature (Huey & Bennett 1987), and the aerobic metabolic

scope is maximal for *T. rugosa* at a body temperature of 33.4°C, which is similar to field (34.3°C) and laboratory (32.6°C) preferred body temperatures (Wilson 1974).

Field and laboratory preferred body temperatures are highly correlated with critical thermal maximum (CT_{max}) but not critical thermal minimum (CT_{min}) (Fig. 24.17). Many geckos, legless lizards and dragons have a high CT_{max}, of 40° to 44°C. Field preferred body temperature is higher for terrestrial heliothermic skinks (25° to 36°C) than fossorial or nocturnal skinks (20° to 26°C). Terrestrial skinks also have a higher laboratory preferred body temperature (29° to 36°C) and higher CT_{max} (40° to 46°C) than fossorial or nocturnal skinks (18° to 27°C and 34° to 44°C). Field and laboratory preferred body temperatures for diurnally active snakes are generally 25° to 34°C, and CT_{max} is about 40°C.
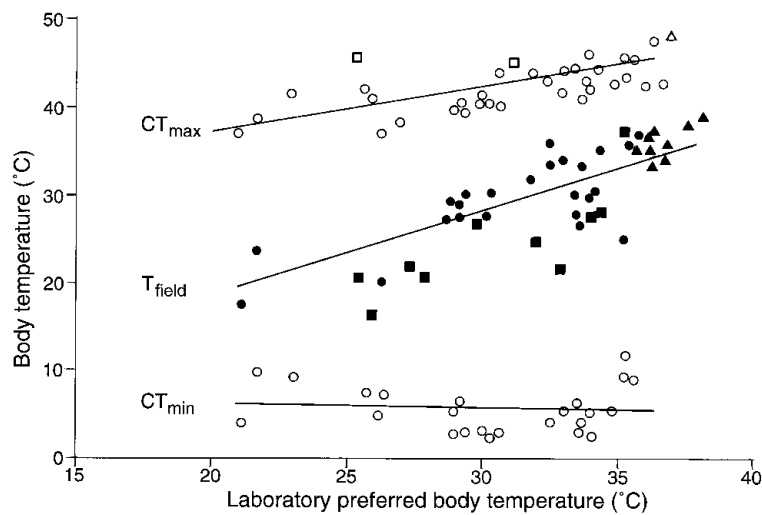
Figure 24.17 Relationship between critical thermal minimum temperature (CT_{min}), field body temperature (T_{field}) and critical thermal maximum temperature (CT_{max}) for a variety of lizards, as related to their preferred body temperature in the laboratory; open circles, skinks; squares, gekkos; triangles, agamids. (Data primarily from Heatwole & Taylor 1987; Greer 1989) [W. Mumford]

EXCRETION

Body Water and Solutes

The total body water content of lizards and snakes is generally about 65 to 75% of body mass (Thorson 1968; Minnich 1982), and is similar for arid and non-arid reptiles (Heatwole & Veron 1977). It is partitioned between the intracellular space (35 to 55%) and the extracellular space (25 to 35%). The extracellular space is further partitioned into plasma volume (about 5%) and interstitial fluid volume (20 to 30%). For example, the total body water content of the agamid, *Ctenophorus ornatus*, is 73.5% of body mass; the extracellular space is 25.5% (5.1% plasma) and the intracellular space is 48.0% (Bradshaw 1970). Some reptiles store water in extracellular fluid compartments, such as bladder, lymph sacs and gut.

Body fluid osmotic concentration is generally 300 to 400 mOsm. Na^+ and Cl^- are the major osmolytes (each at about 140 to 160 mM). Their concentrations can vary dramatically with hydration state for terrestrial species, especially desert reptiles, and are high and variable for marine snakes. Plasma K^+, Ca^{2+}, and Mg^{2+} are generally regulated precisely at 2 to 6 mM. Nitrogenous wastes are present at low concentrations. Intracellular solute concentrations differ substantially from plasma concentrations; the Na^+ and Cl^- concentrations are low and the K^+ concentration is high.

Many squamates tolerate dehydration of up to 30 to 40% loss of body mass. Arid species do not have a higher body water content or greater dehydration tolerance than mesic species (Heatwole & Veron 1977). Tolerance of osmotic and ionic concentration is generally more important than physiological maintenance of normal solute concentrations. For example, many dragons (*Amphibolurus*, *Ctenophorus*, *Pogona*) and skinks (*Tiliqua*) become markedly hypernatremic during drought, with plasma Na^+ levels exceeding 200 mM (Bradshaw & Shoemaker 1967; Bradshaw 1970; Braysher 1971, 1972). Dragons lack functional salt glands and accumulate Na^+ during drought, then excrete it when they rehydrate after rain.

Water Balance

The preformed water content of food varies dramatically, and the physiologically 'available' amount of water is inversely dependent on the ion and nitrogen contents. Many animal and plant food items have a high water content and may be approximately isoosmotic and isoionic to animal body fluids, but some (for example, marine algae and invertebrates, and desert plants and invertebrates) are low in water and/or are hyperionic and hyperosmotic.

Most reptiles drink fresh water when it is available. Some, such as *Tiliqua rugosa*, use their tongue to drink from puddles (Simpson 1973). *Hypsilurus spinipes* has an unusual drinking behaviour, and draws water into its mouth rather than lapping with its tongue (Longley 1943). Snakes drink by a pumping action of the lower jaw, produced by the masticatory muscles. Behaviours may facilitate drinking of rain water in arboreal and sandy environments, which are not conducive to puddle formation. Geckos lap water from moist vegetation, substrates or themselves. *Pogona vitticeps* elevates its body and laps water that drips to its mouth (Fitzgerald 1983). No reptiles have been shown to induce condensation by behavioural actions, such as entering a warm, humid environment (Lasiewski & Bartholomew 1969).

'Blotting paper' skin has been described for a number of lizards, but its role in absorbing water is best understood for the thorny devil, *Moloch horridus* (Bentley & Blumer 1962; Gans, Merlin & Blumer 1982; Sherbrooke 1993; Withers 1993). The surface architecture of the skin transports a water film by capillarity over most of the body surface to the mouth, where it is swallowed. The skin of *Physignathus lesueurii* similarly holds a surface water film, but these lizards apparently do not drink it (Heatwole & Taylor 1987). Some fossorial lizards and snakes absorb water from soil by capillary flow of water into the mouth, or by lapping at the sides of the mouth with the tongue (Krakauer, Gans & Paganelli 1968). Water flux through the skin is significant for aquatic squamates; freshwater species have more permeable skin than marine species (Dunson 1978, 1980; Lillywhite & Maderson 1982).

The biochemical synthesis of water by cellular metabolism can be an important source of water, especially for terrestrial reptiles during prolonged drought or dormancy. The metabolic production of water is greatest for carbohydrates, intermediate for lipids, and lowest for protein (Withers 1992).

A low evaporative water loss (EWL) is one of the major adaptations, or preadaptations, of squamates for terrestriality. Arid species have a lower EWL than semi-arid and mesic species (Heatwole & Veron 1977; Mautz 1982). This might be either genetically-based or acclimational. The EWL depends on body mass; the allometric relationship is of the form EWL m Mass^b, where **b** is about 0.6 to 0.8 (Mautz 1982). EWL increases exponentially with temperature. It also increases during moulting, although at least part of the increase might be ascribed to increased activity during shedding.

Total EWL can be partitioned into cutaneous and respiratory components. For small geckos, dragons and skinks, cutaneous EWL is 40 to 70% of the total at 20°C, and is a lower percentage at 30°C (Dawson, Shoemaker & Licht 1966). For two dragons, cutaneous EWL is 19 to 26% of the total at 35°C (Bradshaw 1970). The evaporative water loss is much lower than the rate of evaporation from a free water surface, reflecting the presence of lipids in the keratinised epidermis rather than the keratin layers *per se* (Roberts & Lillywhite 1980; Lillywhite & Maderson 1982). The keratin layers probably also act as diffusion barriers to water exchange. Scales *per se* do not limit the EWL, as mutant scale-less snakes have a typical EWL (Licht & Bennett 1972; Bennett & Licht 1975).

The eyes can have an exceedingly high EWL (up to 65% of the total EWL) because the corneal surface is essentially a free water film (Green 1969; Mautz 1980, 1982). Some lizards may restrict ocular water loss by partially closing the eyes for example, when basking. Eyelid type is often associated with body size and habitat (Greer 1983a). Some small and/or desert skinks have a transparent window in the lower eyelid, that may reduce ocular EWL without impairing vision. Large and/or non-desert species lack such a window. Snakes, geckos, legless lizards and a few skinks have a fixed and transparent scale (spectacle) covering the cornea. The spectacle restricts EWL from the eye (Mautz 1982), and is also associated with fossoriality, providing physical protection of the eye.

The respiratory water loss of reptiles is low because of their relatively low metabolic rates, and can be further minimised by a high pulmonary O_2 extraction and respiratory nasal countercurrent heat exchange. In addition, nasal salt gland secretion can be used to humidify the inspired air, thus conserving water. For example, the skink *T. rugosa* is often observed with salt encrustations around its nostrils, suggesting such a role of salt gland secretion in humidifying the inspired air.

The water content of the faeces and urine, which are voided together, is determined by the extent of cloacal water reabsorption. The water content of excreta is about 30 to 40% for terrestrial, particularly desert, species and is higher for species with more water available.

The overall flux of water through the body varies depending on the specific conditions at the time of measurement, but is generally lower for xeric than mesic and aquatic squamates. The water turnover rate is also markedly influenced by body mass. For arid and semi-arid zone lizards, water turnover rate (ml day^{-1}) is 20.5 kg$^{0.91}$, in approximate proportion to metabolic rate. In tropical and sub-tropical zone lizards, it is 45.0 kg$^{0.66}$, in approximate proportion to body surface area (Nagy 1982).

Excretory Organs

A variety of organs, including the skin, kidneys, intestine and cloaca, and nasal and lingual salt glands, function directly or indirectly in water and solute balance (Bentley 1976; Dantzler 1976; Dunson 1976; Minnich 1979, 1982).

The paired retroperitoneal kidneys are elongate and lobed organs, usually of equal size, located posteriorly on the dorsal surface of the body cavity; they may fuse posterior to the cloaca. The ureters are short, and an elongate and pear-shaped bladder, with a single ventral opening into the cloaca, is often present.

The kidneys are more elongate and lobulate in snakes and lizards with reduced limbs; the right kidney is often larger and extends more anteriorly in snakes, but there is little or no asymmetry in legless lizards (Underwood 1957; Robb 1960; Shine 1991a). In many snakes the elongate ureters dilate near the openings into the cloaca as a urinary bladder is absent. The embryological origins and development of the reptilian kidney have been reviewed by Fox (1977). The mesonephric kidney is functional in embryonic development, but the metanephric kidney is functional in adults.

The renal vasculature consists of a variable number of renal arteries, a renal portal system arising from various veins (pelvic, caudal, intercostal, cutaneous, spinal), and renal veins. The glomerulus is poorly developed. There are about 500 to 20 000 glomeruli per kidney, depending on body size (Fox 1977; O'Shea, Bradshaw & Stewart 1993). Lizards tend to have smaller glomeruli (50 to 70 mm diameter) than snakes (60 to 120 mm), which also tend to have fewer glomeruli and nephrons with aglomerular diverticula.

The generalised nephron consists of a pavement epithelium (Bowman's capsule) surrounding the glomerulus, a short and narrow partly-ciliated neck, a glandular proximal tubule segment, a fine tubular segment, a distal segment, and a terminal segment leading to the collecting duct. The terminal segment hypertrophies in male lizards and snakes to form a sexual segment. The tubular arrangement of each nephron is a linear array of numerous convolutions, a hair-pin bend, and a termination at right angles into the collecting duct. The total length of the nephron is about 2 to 4 mm.

The glomerular filtration rate (GFR) varies dramatically with hydration state, being highest for water-loaded individuals and lowest for dehydrated or salt-loaded individuals (Dantzler 1976). It also increases with temperature for example, about 10-fold from 14° to 24°C in *T. rugosa* (Shoemaker, Licht & Dawson 1966). The glomerular filtrate is highly modified during its passage through the nephron. Typically, more than 95% of the filtered water is reabsorbed and so ureteral urine is much reduced in volume. Most solutes are reabsorbed from the filtrate, but K^+, H^+, NH_4^+, urate, PO_4^{3-}, and some organic acids are actively secreted. Ureteral urine is isoosmotic or hypoosmotic to plasma; apparently no reptile can produce a hyperosmotic ureteral urine (but see below). The volume and composition of the ureteral urine is subsequently modified in the colon and cloaca.

The colon, cloaca and urinary bladder can highly modify ureteral urine before it is voided (Minnich 1979, 1982). Ureteral urine enters the distal cloaca via the ureteral openings, and it can be refluxed retrogradely into the proximal cloaca and colon, which is the major site of urine storage in most lizards and snakes. Urine can be stored in a urinary bladder, if present, and sometimes is modified before it is voided or returned to the colon/cloaca.

Active solute (especially Na^+; Bentley & Bradshaw 1972) reabsorption by the colon/cloaca, and osmotic water reabsorption, highly modifies the urine and promotes urate precipitation, which further removes solutes (especially Na^+, K^+ and NH_4^+) both as urate salts and as ions trapped within the precipitated urate. Squamates are unable to osmotically concentrate the voided urine to higher than the plasma osmotic concentration by the colonic/cloacal solute-linked reabsorption of water. However, the Lake Eyre Dragon, *Ctenophorus maculosus*, appears to be exceptional in that its voided urine can be more

osmotically concentrated than plasma. The urine is presumably osmotically concentrated by solute-linked water reabsorption in the colon/cloaca (Braysher 1972, 1976).

Salt glands have evolved independently in several lineages of marine, estuarine and terrestrial squamates (Dunson 1976). Salt glands are derived from nasal glands in lizards and lingual glands in snakes. Salt glands are found in some dragons, skinks, goannas and geckos, but their role is most developed in goannas and skinks (Saint Girons & Bradshaw 1987). There are no obvious correlations between nasal salt gland development and geographic distribution, or diet. Salt glands excrete hyperosmotic solutions of Na^+, Cl^-, K^+ and HCO_3^-. The salt glands of an estuarine goanna (*Varanus semiremex*) secrete 460 to 750 mM Na^+, 600 to 800 mM Cl^-, and 35 to 80 mM K^+ (Dunson 1974). The salt glands of marine reptiles secrete primarily Na^+ and Cl^-. *Pelamis platurus* secretes about 650 mM NaCl, but salt glands of terrestrial species excrete high concentrations of Na^+ or K^+ as required.

Nitrogenous Wastes

The primary nitrogenous waste is urate in most squamates (Dantzler 1976; Minnich 1979, 1982). Urate is highly insoluble (Na urate, 6.8 mM; K urate, 12 mM), and solute-linked reabsorption of water from the colon/cloaca precipitates most of the urate present in ureteral urine. Urate precipitation also eliminates ions, particularly K^+ (Minnich 1979, 1982). Ammonium is a significant constituent (2 to 5%) in the precipitated cloacal urine of non-boid snakes and goannas, and significant levels of urea (2 to 5%) are excreted by a few aquatic squamates. Seasnakes excrete primarily uric acid, but *Laticauda colubrina* excretes up to 60 mM ammonia (Schmidt-Nielsen & Mackay 1972).

Water Balance and Excretion in Eggs

Some squamates lay cleidoic, parchment-shelled or calcareous-shelled eggs (Packard, Tracy & Roth 1977; Minnich 1979). Parchment-shelled eggs are typically buried in soil, and absorb water during development by hydraulic/osmotic force. Water absorption appears to be essential for normal development. Selection of a suitably humid environment is important for egg deposition, as the subsequent water balance state of the developing embryo affects hatchling size and hatching success (Muth 1980; Packard & Packard 1988; Tracy 1980; Lillywhite & Ackerman 1984; Somma 1989). The calcareous eggshell of some geckos primarily exchanges respiratory gases rather than water (Bustard 1968a).

Squamate embryos osmoregulate during development. Plasma osmotic concentration and tissue water content are independent of the extent of water absorption by the egg, but hatchling size depends on the magnitude of the water uptake (Vleck 1991). Mineral requirements for embryonic development are derived from the eggshell and especially the egg fluids. The first half of embryonic development in *Pogona barbata* is slow and calcium is mobilised from the yolk, whereas the second half of development is rapid and 40% of the required calcium is mobilised from the shell (Packard, Packard, Miller, Jones & Gutzke 1985).

Developing snake embryos form about equal amounts of ammonia and urea; relatively little uric acid is produced during oviparous or viviparous development (Clark 1953; Clarke & Siskin 1956). Developing lizard embryos produce both urea and urate (Athavale & Mulherkar 1967). Ammonia formation allows gaseous nitrogen excretion across the eggshell as ammonia. Urea accumulation allows osmotic absorption of water from the substrate (insoluble urate formation does not provide an osmotic force for water absorption).

SENSE ORGANS AND NERVOUS SYSTEM

Sense Organs

The principle senses of squamates include mechanoreception (touch, hearing and gravity), chemoreception (taste and smell), photoreception (lateral and median eyes), and thermoreception. These sensory modalities are important in most terrestrial squamates, but are reduced in marine and fossorial species. Goannas and dragons rely primarily on visual stimuli whereas skinks and geckos depend more on a combination of tactile, olfactory and vocal stimuli (Evans 1961). Vision and olfaction dominate the sensory modes for intraspecific communication in snakes (Bellairs 1969).

The epidermis has few external mechanoreceptors, but there are some intraepidermal endings, connective tissue mechanoreceptors lacking Schwann cells, connective tissue receptors with Schwann cells, and Merkel cells (von Düring & Miller 1979). Branched intraepidermal sensory nerve endings in the hinge regions may be stretch receptors. The unencapsulated and encapsulated nerve endings of the dermis may be pressure, stretch and rapidly-adapting mechanoreceptors. Merkel cells in the dermis and epidermis may be slow-adapting mechanoreceptors. Tactile sense organs (touch papillae) are also present, some of which are highly modified to form a tactile area with epidermal bristles, separated from the rest of the scale by a groove. For example, the second infralabial scale of *Delma* is covered by a number of scale organs, some of which bear hairs (Underwood 1957). The joint capsules also contain free nerve endings that convey information concerning joint position and movement.

The auditory system consists of outer, middle and inner regions. The typical external ear is a slight depression situated postero-laterally on the head (Fig. 24.18; Wever 1965; Baird 1970). Some lizards have a deep external ear meatus, which widens to a large tympanic membrane (for example, some geckos and terrestrial skinks). The middle ear cavity is connected to the pharynx by the auditory (eustachian) tube (Fig. 24.18). The extrastapes (extracolumella) and stapes (columella) span the air gap between the tympanic membrane and the inner ear and mechanically transmit sound vibrations. The short extrastapes, which is firmly attached to the tympanic membrane, articulates with the paraoccipital process of the skull, the quadrate of the lower jaw, and the stapes. The medial end of the stapes lies within the opening of the vestibular window of the inner ear. The inner ear consists of a complex membranous system filled by endolymph, and surrounded by perilymph. The saccule and utricle of the inner ear contain sensory maculae which respond to gravity. The three semicircular canals contain maculae which respond to movement of the endolymphatic fluid, thus giving a three-dimensional sensation of movement. The elongate cochlear duct provides auditory sensation and frequency discrimination. *Tiliqua rugosa* has a maximal sensitivity at about 800 Hz, and markedly reduced sensitivity above 2500 Hz (Holmes & Johnstone 1984a). Hearing sensitivity is dependent on body temperature and hydration state, and it increases in spring (Holmes & Johnstone 1984b; Holmes, Fergusson & Johnstone 1984).

The external ear is reduced or absent in a variety of lizards and most legless lizards (Greer 1989). In some burrowing forms, the tympanic membrane is thickened and reduced, the tympanic cavity is reduced, the stapedial footplate is expanded, and the extrastapes articulates firmly with the quadrate. The tympanum and middle ear is almost completely absent in some legless lizards, such as most *Aprasia* (Underwood 1957). These adaptations might reflect the cranial strengthening required by fossorial species, and the transmission of substrate sound vibration to the inner ear by the lower jaw. The inner ear, unlike the external and middle ear, is less modified. For example, the inner ear of pygopodid lizards resembles that of geckos (Shute & Bellairs 1953), to which

they are closely related. In some geckos, parts of the endolymphatic sacs are enlarged for calcium storage, and may even extend through openings in the skull posteriorly along the muscles of the neck.

Snakes have no obvious external ear, and the middle ear lacks a tympanic membrane and cavity, and Eustachian tube. The stapedial footplate is expanded in many burrowing snakes to facilitate sound transmission from the quadrate of the lower jaw to the inner ear.

Chemoreception

Detection of scents from the environment, other animals, and in particular from conspecific animals, is important for many terrestrial squamates (Allison 1953; Parsons 1967; Bertmar 1969; Burghardt 1970; Madison 1977). Odours for communication may be derived from hormones in urine, or faeces, but are commonly produced by specialised integumentary scent glands. The importance of olfaction varies greatly in different squamates. Taste is a poorly developed sense; some taste buds are found in the lining of the pharynx and a few are located on the tongue.

Jacobson's vomeronasal organ is an important chemosensory structure in many squamates, particularly in terrestrial groups, such as goannas, but is poorly developed in arboreal species. The organ in adults is nearly spherical, and the ventral side is invaginated to form a mushroom-shaped body. The hollow space of Jacobson's organ retains its connection (Stenson's duct) to the pharynx. The dorsal and lateral walls are covered by a sensory epithelium that resembles the olfactory epithelium of the nasal cavity. It is widely believed that scent is directly transferred to the ducts of Jacobson's organ by the tips of the tongue, but recent evidence suggests that scent is first transferred from the tongue to the anterior lingual processes, then to the ducts of Jacobson's organ (Oelofsen & van den Heever 1979; Young 1990).
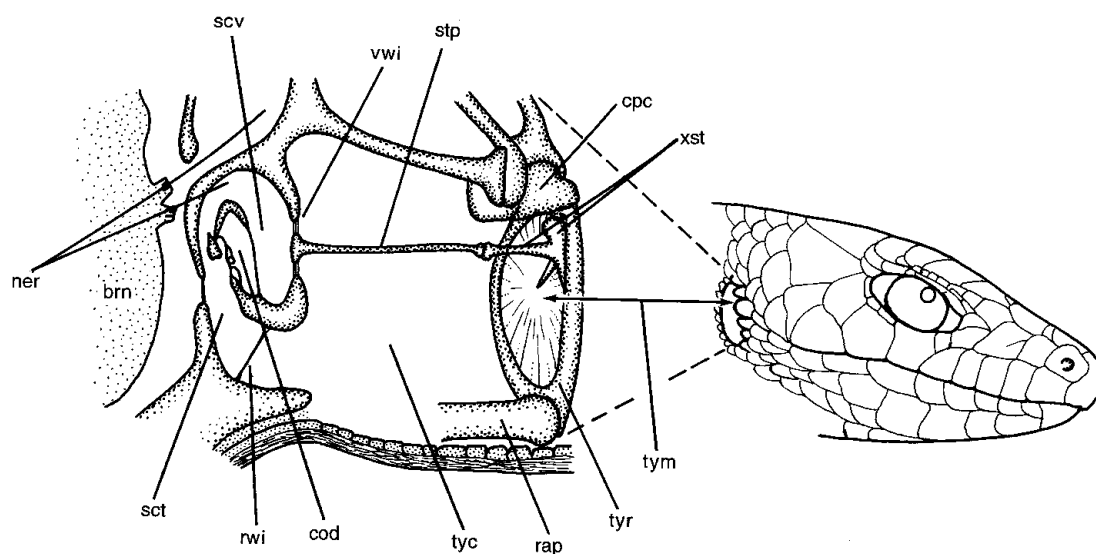
Figure 24.18 Auditory structure of the skink, *Ctenotus grandis*, showing the outer, middle and inner ear of a typical terrestrial lizard. **brn**, brain; **cod, cochlear duct; cpc**, cephalic condyle; **ner**, eighth nerve; **rap**, retroarticular process; **rwi**, round window; **sct**, scala tympani; **scv**, scala vestibuli; **stp**, stapes; **tyc**, tympanic cavity; **tym**, tympanum; **tyr**, tympanic ring; **vwi**, vestibular window; **xst**, extrastapes. (Modified from Storr, Smith & Johnstone 1981; Wever 1965)   [M. Thompson]

Photoreception

Light reception is an extremely important sense for most squamates. The eyes are the primary sensory organs for light reception, although a median (parietal) eye is also present in reptiles and it generally retains a photoreceptive role. The infrared detection by crotaline and boid snakes is also a photoreceptive system, although the actual sensory modality is temperature detection.

The squamate eye generally resembles that of other vertebrates, but there are numerous differences peculiar to squamates and particular modifications in specific groups, especially snakes (Walls 1942; Underwood 1970). Some arboreal species have greater eye mobility but a more limited visual field than terrestrial species.

The large orbits of a typical, diurnal lizard contain the eye, ocular muscles, optic nerve, vascular system, and connective tissues (Underwood 1970). The cornea of the eye is delimited from the sclera by a marked change in radius of curvature (Fig. 24.19A). The sclera contains bony and cartilaginous sclerites which maintain the concavity of the corneal-scleral junction against the intraocular hydrostatic pressure. The clear, soft lens is covered by an epithelial layer which is equatorially thickened as an annular pad. The lens is held in place by zonular fibres extending from the ciliary body, an annular structure located internal to the ring of sclerites. Accomodation (near focussing) is accomplished by radial muscle fibres of the ciliary body (Brücke's and Crampton's muscles) which draw it against the annular pad and squeeze the lens to increase its curvature. Radial and circular muscle fibres of the iris, an anterior extension of the ciliary body, form and control the diameter of the usually circular pupil. The retina consists of an avascular pigmented epithelium, a layer of rod and cone photoreceptors, and layers of neural cells. It extends on the inner surface of the back of the eye from the point of entry of the optic nerve to the ora serrata at the point of inflexion of the sclera. A part of the retina may form a fovea to provide high visual acuity. The retina contains only cone photoreceptor cells in a typical diurnal lizard. The cones contain yellow oil droplets to minimise chromatic aberration by screening out short wavelengths (blue, violet). A highly vascularised conus papillaris, consisting of pigmented neuroglia, may provide nutrients to the eye.

Arboreal geckos have larger eyes than terrestrial geckos (Werner 1969; Pianka & Pianka 1976), possibly because they require a wider visual field. All Australian geckos have a spectacle and a vertical pupil that constricts to form four or five separate pinholes. The retina, which lacks a fovea, appears to contain only rods, but some of these may be derived from cones. The rods may lack oil droplets, have only small oil droplets, or have colourless oil droplets. Pygopodids, like geckos, have a vertical pupil and a spectacle, their retina lacks a fovea, and their photoreceptors lack oil droplets. In *Lialis*, the ciliary body is fairly muscular and the lens has an annular pad. *Delma* has some ciliary muscle, but the lens lacks an annular pad, and *Aprasia* has a markedly reduced ciliary body (Fig. 24.19B).

The eyes of snakes (Fig. 24.19C) and the associated visual parts of the brain are considerably different from those of lizards (Walls 1942; Underwood 1970). These uniquely ophidian structures presumably reflect a reduced eye structure in ancestral fossorial snakes (*cf. Aprasia*), and the subsequent return to terrestrial and arboreal environments required the redevelopment of eye structures. The ophidian cornea and sclera have a similar radius of curvature, and there are no sclerites. The ciliary body is reduced to a non-functional 'ciliary roll'. The nearly spherical, hard lens often has an anterior pad. The lens is yellow in many diurnal species to minimise chromatic aberration. Accomodation is achieved by contraction of circular muscles at the base of the iris, which increases the intraocular pressure in the posterior chamber and forces the lens anteriorly. In

some snakes, accomodation is also accomplished by direct deformation of the lens by the pupillary sphincter muscles. The retina has a blood supply, and some species also have a vascular conus. Ophidian cones have a unique structure, having been derived from the rods of fossorial ancestors. Some diurnal snakes have lost the rods, and only have cones. All ophidian photoreceptors lack oil droplets.

The midbrain of vertebrates has two dorsal outgrowths, an anterior parietal body (parapineal organ) and a posterior pineal body (epiphysis); primitively, both have photoreceptive structures (Eakin 1973; Quay 1979). In lizards, both the parietal body and pineal body develop, to form the parietal eye and the pineal gland respectively. In snakes, the parietal body fuses at an early embryonic stage with the pineal body and only a single epiphysis develops.

The integument over the parietal eye often forms a clear cornea, but may be pigmented (Quay 1979). The parietal eye is typically a simple epithelial vesicle, in which the outer epithelium is modified to form a lens and the inner wall to form a retina; additional vesicular structures may sometimes be present. The retina of the parietal eye is similar in many respects to that of the lateral eyes, but the photoreceptors project towards, rather than away from, the light source.
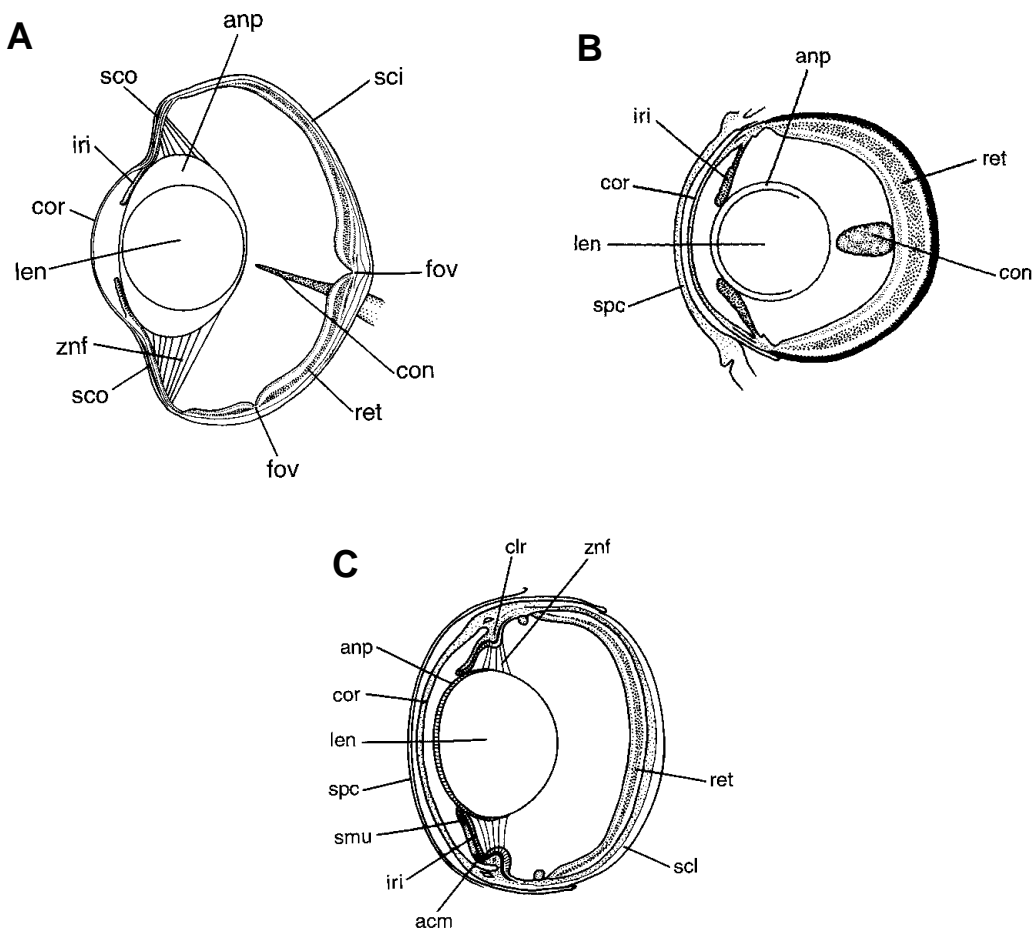
Figure 24.19 Diagrams of eye structure of squamates. **A**, a typical diurnal, terrestrial lizard, *Anolis lineatopus*; **B**, the reduced eye of a pygopodid, *Aprasia repens*; **C**, a snake, *Natrix natrix*. **acm**, accomodation muscle; **anp**, anterior pad of lens; **clr**, ciliary roll; **con**, conus; **cor**, cornea; **fov**, fovea; **iri**, iris; **len**, lens; **ret**, retina; **scl**, sclera; **sco**, scleral ossicle; **smu**, sphincter muscle; **spc**, spectacle; **znf**, zonular fibres. (After A, Underwood 1970; B, Underwood 1957; C, Walls 1942). [M. Thompson]

Functional light reception has been demonstrated by physical, electrophysiological and behavioural means. The parietal eye probably provides photic information for behavioural responses, such as thermoregulation, and endocrine functions, such as reproduction, which are related more to light intensity and to photoperiod than image formation (see Quay 1979).

The parietal eye is reduced and is not externally visible in many nocturnal or crepuscular lizards, such as geckos, legless lizards, a few skinks, and particularly species that live at low latitudes (Gundy, Ralph & Wurst 1975; Quay 1979).

Thermoreception

'Hot' and 'cold' thermoreceptors and pain receptors are present in the skin. Anterior hypothalamic and cutaneous thermoreceptors control themoregulatory behaviour (Berk & Heath 1975). The specialised infrared thermoreceptors of boid and crotalid snakes have been well-characterised (Barrett 1970; von Düring & Miller 1979). Boid snakes have pits sensitive to radiant heat that can be located on the supra-labial, infralabial, rostral and probably the mental scales (Bullock & Barrett 1968; Barrett 1970; Maderson 1970a; von Düring & Miller 1979).

Central Nervous System

The cranium consists of ethmoid, orbitotemporal, otic and occipital regions (Starck 1979). The brain usually lies parallel to the basal axis of the neurocranium (Fig 24.20A), but the forebrain may be inclined in species with large eyes. The shape of the skull is influenced more by feeding apparatus and relative development of the sensory organs, especially the nose, eyes and ears, than brain shape. Brain size is often markedly smaller than the endocranial volume. The size of the brain varies with taxonomic affinity, terrestriality, arboreality or fossoriality, and body mass (Platel 1979).

The brain develops from the neural tube in three main sections, the forebrain (prosencephalon), midbrain (mesencephalon), and the hindbrain (rhombencephalon), which is continuous with the spinal cord (Fig. 24.20A; Senn 1979). The forebrain has an anterior telencephalon and more posterior diencephalon. The telencephalon consists primarily of the olfactory bulbs and lobes, the cerebral hemispheres, and the corpus striatum. The diencephalon consists of the pretectum, the dorsal and ventral thalamus, the hypothalamus, and the epithalamus which connects to the parietal eye and pineal organ. The roof of the midbrain contains the optic tectum and tori semicirculares, and the floor is the midbrain tegmentum. The optic tectum, which can be small and covered by the forebrain, processes optic information. It is large in species which rely primarily on sight, and projects to the surface of the brain between the telencephalon and cerebellum. In contrast, the midbrain of snakes has two nuclei and a torus and paratorus; this difference reflects the ancestral reduction of vision in snakes and the subsequent redevelopment of both eye and visual brain structures. The hindbrain consists of a dorsal cerebellum, ventral tegmentum, and medulla oblongata. The tegmentum consists of the reticular nuclei. The medulla oblongata contains the nuclei of the cranial nerves III–XII.

The organisation of sensory inputs, the brain, and motor outputs is exceedingly complex (see Belekhova 1979; ten Donkelaar & Nieuwenhuys 1979), but an overview is summarised in Figure 24.20B. Olfactory input is via the olfactory bulb and lobes to the corpus striatum. Visual input is via the optic nerve to the midbrain tectum, which also receives inputs from the thalamus and spinal cord. Ascending pathways from the tectum extent to the dorsal thalamus, pretectum and telencephalon, whereas descending tracts extend to the reticular formation

of the brainstem. Auditory information enters the cochlear nuclei of the rhombencephalon, then passes via the torus semicircularis to the thalamus and telencephalon. Equilibrium information enters the vestibular nuclei and passes to the cerebellum, brainstem and spinal cord. Other sensory information from the head enters via the trigeminal nerve to the sensory trigeminal nuclei, then passes to the cerebellum, tectum and motor nucleus of the trigeminal nerve. Sensory information from the body enters the brain via the dorsal sensory nuclei of the hindbrain, and spinal cord. There are numerous ascending spinal pathways to the cerebellum, vestibular nuclei, tectum and dorsal thalamus. The cerebellum receives sensory inputs from the spinal cord, tectum and trigeminal and vestibular nuclei, and has motor output via the vestibular nucleus and red nucleus to the spinal cord. The higher brain centres, especially the telencephalon, have output to the tectum, tegmentum, and ventral thalamus.

The spinal cord extends the entire length of the vertebral canal except the end of the tail (Kusuma, ten Donkelaar & Nieuwenhuys 1979). Its structure reflects the shape and development of the trunk and tail. Limbed squamates have cervical and lumber enlargements of the spinal cord, but these are absent in limb-reduced and limbless forms. The outer white matter of the spinal cord consists of nerve fibres and the inner gray matter consists of the cell bodies of interneurons and motor neurons.
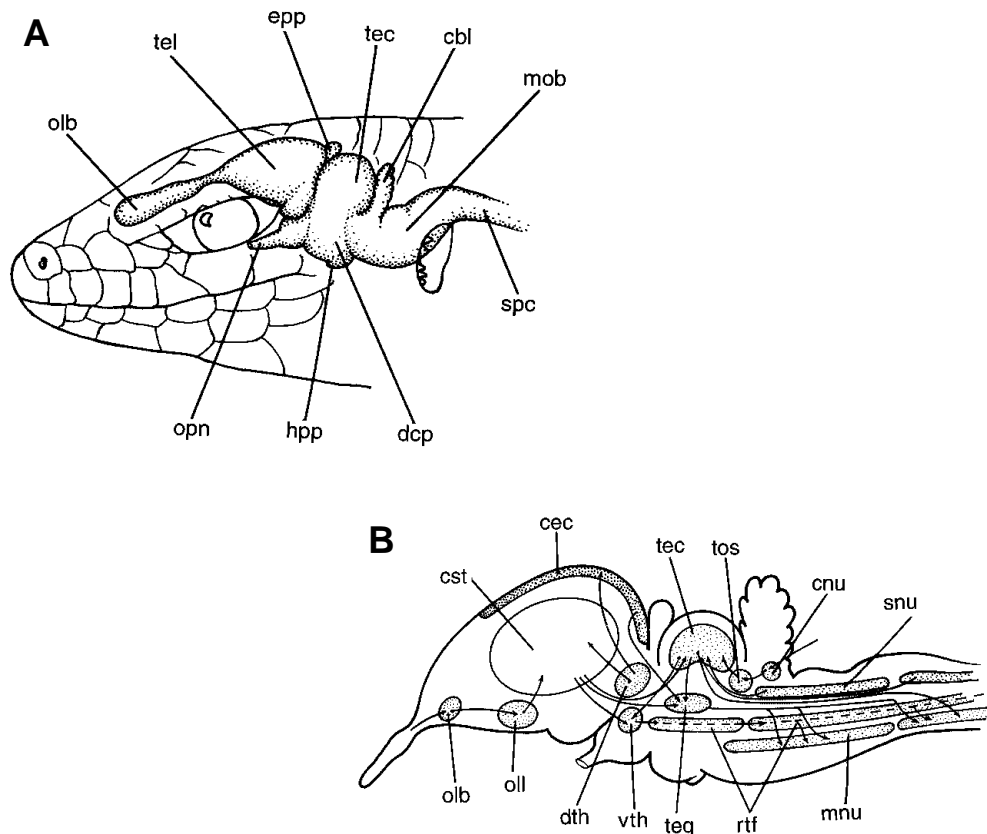
Figure 24.20 Structure of the brain in a typical lizard. **A**, general schema; **B**, schema of the major connections of various brain centres.**cbl**, cerebellum; **cec**, cerebral cortex; **cnu**, cochlear nucleus; **cst**, corpus striatum; **dcp**, diencephalon; **dth**, dorsal thalamus; **epp**, epiphysis; **hpp**, hypophysis; **mnu**, motor nuclei; **mob**, medulla oblongata; **olb**, olfactory bulb; **oll**, olfactory lobe; **opn**, optic nerve; **rtf**, reticular formation; **snu**, sensory nuclei; **spc**, spinal cord; **tec**, tectum; **teg**, tegmentum; **tel**, telencephalon; **tos**, torus semiculares; **vth**, ventral thalamus. [M. Thompson]

Peripheral Nervous System

The peripheral nervous system consists of nerves which enter or leave the brain and spinal cord. The sensory nerves can be divided into somatic nerves carrying sensory information concerning the external environment, position of limbs, and visceral nerves carrying interoceptive sensory information. The efferent nerves can similarly be divided into somatic motor nerves, controlling the voluntary muscles of the body, and visceral motor nerves controlling involuntary muscles and glands.

The parasympathetic and sympathetic branches of the visceral motor (autonomic) nervous system have important effects on the heart, gastrointestinal tract, respiratory system, vasculature, urinogenital system, endocrine and exocrine glands, chromatophores, and the eyes (Berger & Burnstock 1979). Parasympathetic nerves are present in some cranial nerves (III, X and probably VII and IX) and sacral spinal nerves. Their preganglionic and postganglionic neurotransmitter is mainly acetylcholine. The sympathetic system has a thoraco-lumbar spinal nerve organisation with bilaterally arranged ganglia. The preganglionic neurotransmitter is acetylcholine and the postganglionic neurotransmitter is noradrenaline.

The heart is innervated by parasympathetic (vagal) and sympathetic nerves. Vagal stimulation decreases heart rate and force of contraction whereas sympathetic stimulation increases both heart rate and force of contraction. The autonomic nervous system controls motility, secretion and blood flow in the digestive tract; parasympathetic activity generally stimulates these actions. The lungs have an excitatory cholinergic and an inhibitory adrenergic innervation. The parasympathetic innervation contricts the pulmonary artery and increases vascular resistance, and sympathetic innervation vasodilates. The sympathetic innervation of the systemic vasculature regulates peripheral distribution of blood flow, for example during heating and cooling and diving, and contracts the spleen. The parasympathetic innervation of the bladder mediates contraction. There is a sympathetic innervation to the kidney, vas deferens and hemipenes. The thyroid, pancreas and adrenal glands each have a sympathetic and/or parasympathetic innervation. The sympathetic nervous system may affect colour by direct effects on chromatophores and indirect effects on blood flow. There may be autonomic control of the iris, nictitating membrane and glands of the eye.

ENDOCRINE AND EXOCRINE SYSTEMS

Hypothalamus and hypophysis

The hypothalamus and hypophysis (pituitary) are 'master endocrine glands' which enable nervous system regulation of many other endocrine organs. The structure of the hypothalamus-pituitary axis has been described for many reptiles (Saint Girons 1970a). The adenohypophysis consists of the distal and intermediate lobes of the pituitary. The neurohypophysis consists of the neural lobe and median eminence. Neurosecretory cells of the supraoptic and paraventricular nuclei of the hypothalamus, the median eminence and neural lobe collectively form the hypothalamo-neurohypophyseal tract.

The supraoptic and paraventricular nuclei, which lie near the optic tract-diencephalic junction, contain small neurosecretory cell bodies with axons descending along the floor of the third ventricle to the infundibulum and then the neural lobe. This spherical or ovoid extension of the infundibulum is usually located dorsal to the distal lobe of the pituitary. Neurosecretory products of the supraoptic/paraventricular cell bodies are apparent in the neural lobe as colloidal

granules. The median eminence, a vascular swelling of the ventral wall of the infundibulum, liberates hypothalamic releasing factors, which are transported to the distal lobe of the pituitary by the hypothalamo-hypophyseal portal system.

The distal pituitary lobe, which is generally ventral to the neural lobe and postero-ventral to the median eminence, consists of cellular cords of different cell types. The gonadotropic LH (g) cells secrete luteinising hormone (LH). The gonadotropic FSH (b) cells secrete follicle stimulating hormone (FSH). The thyrotropic (d) cells secrete thyroid stimulating hormone (TSH). The function of the alpha (a) cells is unknown. There are also X cells and chromophobic cells. The distal lobe hormones regulate growth, reproduction, the thyroid gland and the adrenal (interrenal) gland. The neural pituitary lobe contains arginine vasotocin (AVT), oxytocin and mesotocin. AVT has important effects on renal function, producing antidiuresis, but the physiological roles of oxytocin and mesotocin are unclear (Bradshaw 1986). The structure of the intermediate pituitary lobe, which consists of external and internal layers, varies considerably. Its hormone, intermedin, disperses melanophore pigment granules.

Thyroid

The lobular thyroid gland is single, bilobed or paired in lizards (Lynn 1970) but is single and elongate in snakes. Spherical follicles of thyroid epithelium (50 to 300 mm diameter) secrete thyroxin (T_4) and tri-iodothyronine (T_3) into the follicular lumen. The thyroid gland incorporates and stores iodine, for synthesis of T_4 and T_3. The thyroid gland is under the control of the anterior pituitary gland, via TSH. It stimulates the reproductive cycle and cellular metabolism. Thyroid activity appears to promote ecdysis in lizards, but inhibits ecdysis in snakes. The thyroid gland also affects other endocrine organs such as the parathyroids and ultimobranchial glands.

In temperate-zone lizards, there is a marked seasonal cycle in thyroid activity, with a peak during summer. Lizards in warmer climates may have the reverse cycle, with greater thyroid activity during winter when feeding activity is maintained, and lower activity during summer when activity is curtailed. Thyroid activity is generally reduced during hibernation or aestivation. Similar seasonal changes in thyroid activity occur in snakes.

Parathyroids

The parathyroid glands are derived from two pairs of pharyngeal pouches (Clark 1970). In most adult lizards, the rostral pair persist, but the caudal pair degenerate. Snakes retain both rostral and caudal pairs. The parathyroids are composed of cords of secretory cells, separated by capillary or sinusoidal channels. They secrete parathormone (PTH, or parathyroid hormone), which elevates blood Ca^{2+} levels by promoting Ca^{2+} mobilisation from bone, Ca^{2+} absorption from the gut, and renal PO_4^{3-} excretion.

Ultimobranchial Glands

The two ultimobranchial glands are located near the heart (the right may be rudimentary or absent). Their hormone, calcitonin, has an antagonistic action to PTH, whereby it decreases blood Ca^{2+} and PO_4^{3-}.

Adrenals

The paired adrenal glands, which are incorporated into the mesentery of the gonads, are typically globular or cylindrical in lizards, but elongate in snakes. The adrenal (interrenal) tissue corresponds to the mammalian adrenal cortex, and the peripheral (chromaffin) tissue corresponds to the mammalian adrenal medulla (Gabe 1970).

The interrenal tissues secrete the corticosteroid hormones, aldosterone and corticosterone (and occassionally cortisol), but their roles in squamates are unclear (Bradshaw 1986). Renal retention of Na^+ and excretion of K^+ by aldosterone, a mineralocorticoid hormone, has been reported in goannas and a water snake. Corticosterone has a similar role in *Varanus gouldii* (Rice, Bradshaw & Prendergast 1982). Aldosterone and corticosterone also affect electrolyte secretion by salt glands.

The chromaffin tissue consists of small cells organised into a dorsal noradrenaline-secreting layer and ventral clusters of adrenaline-secreting cells. Secretion is under sympathetic control (Berger & Burnstock 1979); squamates may be able to independently secrete noradrenaline and adrenaline. Adrenaline and noradrenaline have a variety of actions on the heart, gastrointestinal tract, respiratory system, circulatory vasculature, urinogenital system, endocrine glands, chromatophores, eye and central nervous system.

Pineal Organ

The photosensitive pineal organ arises from the right-side vesicle of the posterior pair of structures of the parietal-pineal complex (Quay 1979). The pinealocytes resemble parietal eye photoreceptors, but their outer (photoreceptive) segments often degenerate. The pineal organ has both sensory (pinealofugal) and autonomic (adrenergic) nerve fibres. The pineal has high concentrations of serotonin, the precursor to the indoleamine melatonin, which affects the reproductive cycle, particularly ovarian activity.

Pancreas

In lizards, the pancreas lies between the stomach and duodenal curve, and has three limbs, one extending towards the gall bladder, one towards the small intestine, and one towards the spleen (Miller & Lagios 1970). The compact pancreas of snakes is often elongate. The pancreatic endocrine tissue consists of numerous islets among the exocrine tissue, mainly in the splenic portion. In lizards, the islets are large, irregularly branched cords of two cell types, but in snakes the cords form more compact structures. The more numerous a cells secrete glucagon, a hormone which increases the blood glucose level, and the fewer b cells secrete insulin, which decreases the blood glucose level.

Exocrine systems

The ducted exocrine glands of the skin, nasal and oral cavities, digestive tract and pancreas have diverse functions in squamates.

The external nasal gland, which lies outside the cartilaginous nasal capsule, is a branched tubular mucous gland that excretes salt in some lizards. Its duct typically enters the nasal vestibulum. Squamates lack a medial nasal gland. In some squamates, the goblet cells of the respiratory epithelium may become concentrated into gland-like structures.

The oral glands are complex in structure and function (Kochva 1978). The gland of Duvernoy of colubrid snakes is located behind the eye and opens via a single duct to a fold of oral mucosa near the teeth. Its secretion is toxic in a number of species. The venom glands of elapid, laticaudid and hydrophiid snakes occupy

the lateral side of the head. The main venom gland may be divided into several lobules, each containing numerous tubules. Venom enters a groove near the base of the fang and travels along a groove to exit near the tip. Envenomation rapidly immobilises prey and commences chemical digestion. Venoms may contain neurotoxic, coagulant, haemolytic, haemotoxic, cytotoxic and myotoxic agents (Gow 1989). Neurotoxins prevent peripheral nervous transmission and paralyse skeletal muscle; respiratory failure is a typical cause of death. The toxicity of venom varies markedly (Elliot 1978; Mebs 1978; Latifi 1978). The LD_{50} varies from 0.01 mg kg^{-1} for the seasnake *Enhydrina schistosa* to over 10 mg kg^{-1} for other species. The toxicity of a snake bite depends on both the LD_{50} of the venom and the volume of venom injected. For example, the inland taipan, *Oxyuranus microlepidotus*, has one of the most dangerous bites because of both the high toxicity and the large quantity of venom injected (Shine 1991a).

The exocrine portion of the pancreas consists of zymogen cells that secrete into the lumen of branching tubules (Miller & Lagios 1970). The secretion contains bicarbonate and enzymes, including amylase, proteases (chymotrypsin, trypsin, carboxypeptidase), ribonucleases, lipases, and chitinase (Skoczylas 1978).

REPRODUCTION

Reproductive Systems

The male reproductive system consists of paired testes, vasa deferentia, the sexual segment of the kidney, and paired hemipenes. In females, there are paired ovaries, and oviducts with uteri. The reproductive tracts open into the central urodeum of the cloaca, often at papillae extending into the lumen. In many male squamates, the ipsilateral vas deferens and ureter fuse near the cloaca and open together at a papilla, but there may be separate vasa deferentia and ureteral openings in some species. Oviducal and ureteral openings are separate in female squamates.

The paired gonads develop into testes or ovaries (Fox 1977). In males, Müllerian ducts transiently develop but they usually degenerate, and Wolffian ducts (the collecting duct of the mesonephric kidney) form the vasa deferentia to convey sperm from the testes to the cloaca. In females, the Müllerian ducts persist as the oviducts and uteri, and the Wolffian ducts degenerate. Rarely, the bisexual potentiality of both gonads and ducts persist to produce a hermaphroditic adult.

The paired ovoid testes are located posteriorly in the body cavity, the right usually extending more anteriorly than the left (Fox 1977). They are particularly elongate in snakes and limb-reduced and limbless lizards. The white connective tissue tunic divides the testes into lobules, containing blind-ending seminiferous tubules, interstitial cells, and vascular and connective tissues. Sustentacular (Sertoli) cells of the seminiferous tubules presumably have a nutritive or phagocytic role. Interstitial (Leydig) endocrine cells are present between the tubules. These numerous, large cells secrete testosterone. The testes have various accessory ducts; the ductuli efferentia lead into the ductuli epididymides and ductus epididymidis, and then into the vas deferens which joins the ureter near the cloaca.

There is often a seasonal sexual cycle during which the gonads enlarge (Duvall, Guillette & Jones 1982; Saint Girons 1985). Interstitial cells become more numerous and active. Spermatogenesis occurs, at least at temperatures above 20°C (Saint Girons 1985). In immature males, the seminiferous tubules are only one cell thick and there are usually no signs of spermatogenesis, but during breeding the tubule diameter increases and spermatids and sperm are abundant in the lumen. The epididymis becomes distended by a milky fluid. The testes

regress during breeding inactivity. The seminiferous tubule lumen decreases in diameter; many spermatogonia and spermatocytes are present but there are few spermatids and sperm. The epididymis is shrunken and empty. Sperm may be stored in the vas deferens during the winter in some snakes, or spermatogenesis may begin in late summer and be arrested at an early stage during winter, to continue in spring. In tropical species, spermatogenesis may be continuous, even though the female reproductive cycle may not.

The paired ovaries are suspended in the body cavity, usually with the right anterior to the left (Fox 1977); they are elongate, sac-like structures in limb-reduced and limbless lizards, and snakes. The ovaries consist of connective tissue stroma, blood vessels, nerves, and ova. They contain two genital beds of oogonia and oocytes in various stages of development. Each oviduct has a thin-walled fallopian tube that terminates in a wide intra-abdominal ostium, and a thicker-walled uterus that is separated from the fallopian tube by a muscle sphincter. The left oviduct is degenerate in some limb-reduced and limbless lizards, and some blind snakes, *Typhlops*, presumably because of 'crowding' by the stomach. However, the right oviduct is lost in *Vermiseps pluto*, which also uncharacteristically has an enlongate right lung (Greer 1989). The oviducts open into the cloaca, separately from the ureters.

Often a seasonal ovarian cycle occurs, influenced by external environmental cues (light, temperature) and internal endocrinological feedback (oestrogen and progesterone). During the inactive phase, immature ova (often two to 20) and some atretic ova are present. Yolk is deposited in the oocytes shortly before ovulation. During oestrus, theca cells of the stroma release oestrogens (Joss 1985). Ovulation may be synchronous from both ovaries, may alternate between ovaries, or only one ovary may be active at a time. After ovulation, corpora lutea are formed, which resemble those of mammals, and similarly secrete progesterone to maintain gestation. The oviducal glands are large during egg-laying but the oviducts regress during inactive periods.

Vitellogenesis is probably less temperature dependent than spermatogenesis, but the high energetic cost of egg formation means that it must be fuelled either by body fat stores or feeding (Saint Girons 1985). Temperate squamates generally have a pronounced seasonal reproductive cycle, but females may reproduce only every second or third year. Even tropical squamates often have a highly seasonal reproductive cycle coinciding with the most favourable time of the year.

In lizards, sperm quickly reach the caudal oviduct after mating (within 1 to 2 days), and remain there for a few days to weeks, until they move to the rostral part of the oviduct before ovulation (Saint Girons 1985). In snakes, mating may preceed ovulation by two to three months, and sperm remain in epithelial crypts of the oviducal funnel until ovulation occurs. Sperm are generally not present in the oviduct after egg-laying (or mid-gestation in viviparous species).

Breeding Cycles

Climatic factors, particularly temperature, influence the seasonal reproductive cycle of squamates (Fig. 24.21). The cycle of female lizards appears to be constrained by temperature, at least in temperate regions. Typically, ovulation occurs in late spring, eggs are laid in early summer, and young are born, or hatch, in late summer (Bustard 1970b; James & Shine 1985; Greer 1989; Saint Girons, Bradshaw & Bradshaw 1992). However, the great diversity in clutch size, offspring size, mating systems, parental care, and timing of mating results in a number of variations in this basic cycle (see Shine 1985b; Greer 1989). The male and female reproductive cycles usually coincide in spring, although the male cycle may be different if females store sperm. For example, female *Hemiergis peronii* are inseminated in autumn and store sperm over winter until they ovulate in spring (Smyth & Smith 1968).
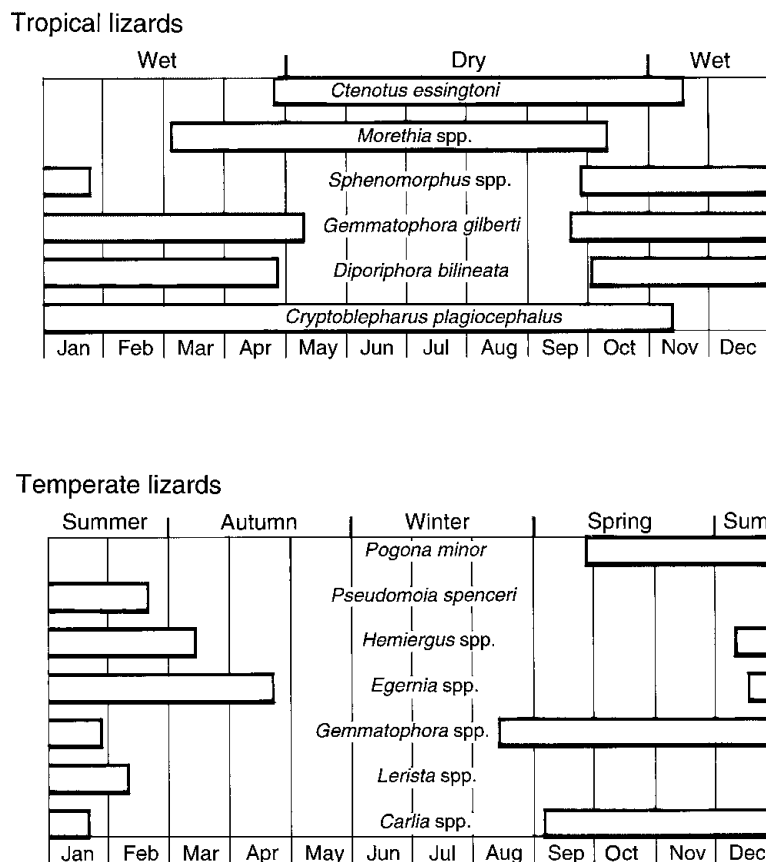
Figure 24.21 Schematic summary of pattern of reproductive cycles in some tropical lizards (above 26th parallel) and temperate lizards (below 26th parallel). (Data from James & Shine 1985)   [W. Mumford]

In tropical lizards, the reproductive cycle may remain seasonal although it varies for different species (James & Shine 1985; Greer 1989). Agamids and terrestrial goannas typically breed in the wet season (November to April), whereas geckos and the dragon *Chelosauria* breed in the dry season (May to October). Aquatic goannas breed in the early dry season. Amongst skinks, most *Ctenotus* breed in the dry season and *Carlia* and *Sphenomorphus* breed in the wet. In contrast, *Cryptoblepharus plagiocephalus* breeds throughout the year in the tropics.

The reproductive patterns of arid-zone lizards are variable. Reproduction may occur in early or late spring, summer, autumn or be continuous during suitable periods (James & Shine 1985; Saint Girons *et al*. 1992).

Snakes also have seasonal reproductive cycles (Duvall *et al*. 1982; Shine 1991a). Females generally ovulate in spring and lay their eggs about a month later, or give birth about three months later, in temperate climates. Males may not be so seasonally constrained, particularly as sperm storage occurs in many species; mating can occur months (or even years) before ovulation. In the tropics, the reproductive cycle may remain seasonal despite continually favorable temperatures, depending more on water availability. However, the precise timing of ovulation by females may vary markedly in different species. Reproductive cycles may be aseasonal or seasonal in seasnakes. For example, female *Aipysurus laevis* ovulate in spring, are gravid during summer, and give birth in autumn (Burns 1985).

Oviparity

Many squamates are oviparous. Most agamids lay more than one clutch; clutch size varies from two to about 30. Geckos and pygopodids lay one, two or more small (one to two eggs) clutches per year. Goannas lay one clutch of about three to 30 eggs per year. Temperate skinks generally lay one clutch of one to eight eggs per year.

Squamate eggs vary from < 0.1 g to over 300 g (Iverson & Ewert 1991). There is a correlation between egg and adult size. Species with large clutches tend to have spherical eggs to maximise oviducal packing, whereas attenuated species tend to have elongate eggs. Incubation time increases with egg size (Vleck & Hoyt 1991). Incubation temperature has many effects on development (Deeming & Ferguson 1991). Elevated temperature decreases the incubation time, but only to a critical temperature above which incubation time increases. Temperature can influence the sex, pigmentation pattern, post-hatchling growth rate, and thermoregulatory and sexual behaviours of the hatchling.

Most eggs have a multi-layered shell membrane that is either a flexible, parchment shell (most squamates) or a rigid, calcareous shell (some geckos; Packard & DeMarco 1991). Flexible-shelled eggs have a thin crust or isolated calcareous deposits, whereas rigid-shelled eggs have calcareous columns attached to the underlying shell membrane. Most oviparous squamates retain their eggs for a period from a few weeks to just before hatching. For example, the skink, *Saiphos*, and the elapid, *Pseudechis*, retain the eggs until a week or so before hatching. Although technically these are egg-laying squamates, they are functionally better classified as live-bearers.

Viviparity

Viviparity<$Viviparity in different taxa> (live-bearing) has evolved numerous times in Australian skinks (see Shine 1985a; Greer 1989). For example, all *Carinascincus*, *Claireascincus*, *Egernia*, *Eulamprus*, *Gnypetoscincus*, *Harrisoniascincus*, *Hemiergis*, and *Tiliqua* are viviparous. Viviparity has evolved independently in some *Anomalopus*, *Lerista*, and *Glaphyromorphus*. *Saiphos equalis* and *Lerista bougainvillii* are oviparous or viviparous in different geographic regions. Numerous terrestrial snakes are viviparous. Some seasnakes (hydrophiids, file snakes and the homalopsine colubrids *Ceberus*, *Fordonia* and *Myron*) are viviparous, but laticaudids are not. Embryonic development is completed within the oviduct and the thin eggshell allows gas and water exchange. A placenta may form to facilitate gas exchange, and even nutrient exchange in some species (Yaron 1985).

Viviparity has evolved in cold-climate squamates (Packard *et al*. 1977; Shine & Bull 1979; Blackburn 1982; Shine 1985a) by physiological modifications for egg retention (Guillette 1985). There is a clear correlation between mean annual temperature and viviparity in skinks and elapid snakes (Shine 1985a). Cold soil temperatures presumably inhibit development or are lethal to eggs, but eggs retained by females are maintained at higher temperatures, at least during the day.

Parthenenogenesis

Parthenogenetic (all-female) reproduction has been reported for about 13 genera of reptiles (Cole 1975; Darevsky, Kupriyanova & Uzzell 1985). The Australian gecko *Heteronotia binoei* is a complex species with two sexual diploid and probably three parthenogenetic triploid forms (Moritz 1983; Moritz & King 1985; Moritz 1991). The origin of pathenogenesis in *Heteronotia* is a hybridisation event between distinct populations, but the meiotic mechanism which maintains the somatic ploidy level is unclear.

Chromosomes

The chromosomes are generally large (macrochromosomes) or small (microchromosomes; Gorman 1973) with a central/ near-central centromere (metacentric) or a terminal/near-terminal centromere (acrocentric).

In lizards, the diploid chromosome number varies from 20 to 56, with $2n=36$ a likely primitive condition. Skinks have $2n=24$ to 32 while goannas have $2n=40$. The diploid number for geckos is 32 to 46 (King 1977c; Moritz & King 1985; Moritz 1991). Pygopodids have $2n=38$, but in *Lialis burtonis* $2n=33$ (females) and $2n=34$ (males) (Gorman & Gress 1970). All Australian dragons are diploid with $2n=22$ or 24.

For snakes, $2n=32$ is a common and perhaps the primitive condition, but varies from $2n=24$ to 50: for pythons, $2n=34$, 36, 40 or 44; for colubrids and viperids, usually $2n=36$; in elapids, $2n=36$, 38, 42 or 44 (or 43 in male *Bungarus caeruleus*). The laticaudid, *Laticauda semifasciata*, has $2n=38$.

Sex differentiation

Sex determination can be either genotypic (genetic) or epigamic (environmental; Bull 1980). Two common forms of genotypic sex determination (GSD) are male and female heterogamety, wherein one chromosome, or chromosomal segment, segregates according to sex. The sex-determining chromosomes may be cytologically indistinguishable (homomorphy) or are cytologically distinguished as sex chromosomes (heteromorphy). In male heterogamety, the possession of two different sex chromosomes determines males, as XY(male)/XX(female); female heterogamety is the opposite, as ZZ(male)/ZW(female). Sometimes, more than one chromosome may segregate according to sex, as $X_1X_2 X_1X_2$ (female)/$X_1X_2 Y$ (male).

The pattern of homomorphy or heteromorphy is complex in lizards, indicating sporadic and multiple origins of heterogamety (Gorman 1973; King 1977c; Bull 1980). Except for legless lizards, heteromorphism is uncommon, and most species do not have sex chromosomes. No dragons have been reported to have sex chromosomes. The heterogametic sex varies in different families, and within families. The heterogametic sex is male in skinks and legless lizards, and female in geckos and goannas.

In snakes, there appears to be a relatively straightforward evolutionary development of sex chromosomes, and the extent of Z-W differentiation increases from primitive homomorphy to a major heteromorphy in W and Z chromosomes. Pythons generally have homomorphic sex chromosomes whereas colubrids have female heterogamety with unequal W and Z chromosomes. The elapid *Bungarus caeruleus* has a multiple Z_1Z_2W sex chromosome system, with $2n=44$ (male) and $2n=43$ (female).

Temperature is the most common factor in epigamic sex determination. Thermal-dependent sex determination (TSD) has been reported infrequently for lizards but not at all for snakes. In species with TSD, the sex ratio is dramatically dependent on the egg incubation temperature. Often a high temperature results in female offspring and a low temperature in males. In both *Eublepharus macularius* and *Agama agama*, the sex ratio increases from predominantly female to male at temperatures above about 28°C (Charnier 1966; Wagner 1980).

Embryology and Development

Squamate eggs have a large yolk mass surrounded by a comparatively small layer of albumen with a surrounding vitelline membrane. The yolk provides the nutritional requirements for the developing embryo, and sometimes for the neonate.

The sequence of development is only well-described for the lizard *Lacerta vivipara* (Dufaure & Hubert 1961) and the snake *Thamnophis sirtalis* (Zehr 1962). Fertilisation begins embryonic development. The first cell divisions of the fertilised ovum are incomplete on one side of the yolk (meroblastic), and produce a germinal disc of comparatively small cells (Hubert 1963). Further cell divisions form a double layered blastoderm, which invaginates during gastrulation to form endoderm and ectoderm. Cells migrate into the space between these two layers to form mesoderm (Hubert 1970). Gastrulation differs slightly in snakes. Lateral folds, formed by the ectodermal cells, migrate and unite ventrally to form a neural tube that is closed anteriorly to form the brain (neurulation). The cells at the margins of the neural tube differentiate and migrate to form the dorsal nerve cord. The mesoderm differentiates symmetrically into a notochord and lateral somites. The notochord is replaced later in development by the axial skeleton. The somites segment antero-posteriorly and split dorso-ventrally to form the segmented body musculature, and form the coelom. The endoderm and part of the mesoderm form the gut. Much later in development, the accessory glands of the digestive tract (pancreas and liver) and the lungs develop from the intestine. The mesoderm also gives rise to nephrotomes, which form the embryonic kidney, and a specialised germinal ridge that forms the gonads.

The endoderm encloses the yolk sac and forms three extraembryonic membranes. The amnion and chorion form first, and extend dorsally to envelop the embryo, which continues its development in the fluid filled amniotic cavity that protects the embryo from shock and desiccation. The chorionic membranes form an extra-embryonic coelom. The final extra-embryonic membrane develops from both endodermal and mesodermal layers behind the stalk of the yolk-sac, and forms the allantois which functions as an embryonic bladder. The well-vascularised periphery of the allantoic and chorionic membranes is the major site of gas exchange. The chorio-allantoic membranes and/or yolk sac may also function as a 'placenta' for nutrient exchange in some live-bearing squamates.

The anterior regions develop and differentiate before the more posterior regions. Rapid growth of the anterior portion of the embryo bends and partially rotates it. Further elongation produces an obvious flexion that is extreme in attenuated forms. The number of somites increases, the pharynx becomes perforated by gill slits (but never develops gills) and the vasculature of the undifferentiated gill arches forms the anatomical basis for the adult vasculature. The eyes, inner ears and olfactory organs begin to differentiate and the heart forms and commences to beat. Two pairs of limb buds form paddle-like anterior limbs, which differentiate discernible digits; these appendicular skeletal components are initially cartilaginous. In snakes and some other limbless squamates, the limb buds initially form then regress (Raynaud 1985). In the final stages of development, the skin differentiates recognisable scales.