



FAUNA *of* AUSTRALIA



16. MORPHOLOGY AND PHYSIOLOGY OF THE CHELONIA

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Turtles are the subject of some of the earliest accounts of vertebrate anatomy, for example Bojanus (1819). Much of the work on turtle anatomy was done in Europe before 1920. The following important anatomical studies include but do not emphasise Australian turtles. Hoffman (1890) commented on the Australian chelid genera *Chelodina* and *Emydura* and several South American chelids, and Siebenrock (1897) discussed the skull of *Chelodina longicollis*. More recently, Schumacher (1973) described the jaw musculature of *Chelodina longicollis* and *Emydura* species and Walther (1922) presented a thorough anatomical study of a single specimen of *Carettochelys insculpta* Ashley (1955) and Bojanus (1819) described and illustrated typical turtle anatomy (*Pseudemys* and *Emys*), which is applicable to turtles of both suborders. Surveys of anatomy and physiology prepared before the middle of this century are based largely on the common or easily available taxa (for example *Emys*, *Testudo*, *Chrysemys* and *Chelydra*) in Europe, Asia and North America. Australian turtles received attention in direct proportion to their availability in collections outside Australia. The expansion of modern biological studies and especially Australian chelids since the 1950s essentially began with Goode (1967).

Terminology for chelonian shell structures varies. That standardised by Carr (1952) is used here (Figs 16.1, 16.2). Unpublished data and observations, especially for Australian chelids, are drawn from the author's research, and appear in statements which lack citations, unless otherwise indicated.

EXTERNAL CHARACTERISTICS

Turtles range widely in size. Using carapace length as a basis for comparison, the smallest are the North American *Sternotherus* sp. and *Clemmys muhlenbergi*, which mature at lengths of less than 100 mm. *Dermochelys coriacea* (Pl. 3.7, 3.8) is the largest living turtle, with a maximum length of 2.4 m and a maximum weight of 919 kg (Morgan 1989) and ranks with the largest living reptiles. *Chelonia mydas*, largest of the cheloniid marine turtles, can attain a length of 1.2 m (Pl. 3.5). Freshwater turtles are more modest in size, and few attain lengths exceeding 300 mm. Most adults longer than 300 mm considered large. One of these is *Carettochelys*, which grows to about 500 mm in length, and lengths exceeding 400 mm are quite common in Asiatic river batagurids, trionychids and chelydrids. The smallest Australian chelids are *Pseudemydura umbrina* (smallest female 120 mm; Burbidge 1967; Pl. 3.13, 3.14) and male *Emydura* sp. (approximately 100 mm; Cann & Legler 1993). Tortoises attain a moderately large size on islands, such as the Galapagos, but they never reach a size at which they become graviportal.

Adult males of Recent turtles may be smaller or larger than females, or equal in size (Berry & Shine 1980). This range in dimorphism in size is seen in Australian chelids (Chapter 21). In some batagurids and emydids there are some striking sexual differences in colour and pattern, as illustrated by Ernst & Barbour (1989). The sexes of Australian chelids differ mainly in form rather than colour, though the orange head pattern of male *Rheodytes* is characteristic. The shell of females tends to be deeper than that of males, in which the tail is more robust.

BODY WALL

The chelonian shell is an extremely specialised body wall. The shell is *ipso facto* protective, and this must be considered its chief selective advantage. If *Dermochelys* is excluded, the variations seen in fossil and recent turtles are relatively slight and the basic plan and its homologies have not changed. Zangerl (1969) reviewed the structure of the chelonian shell. The shell is a combination of discrete bony and epidermal elements. Some of the former comprise an

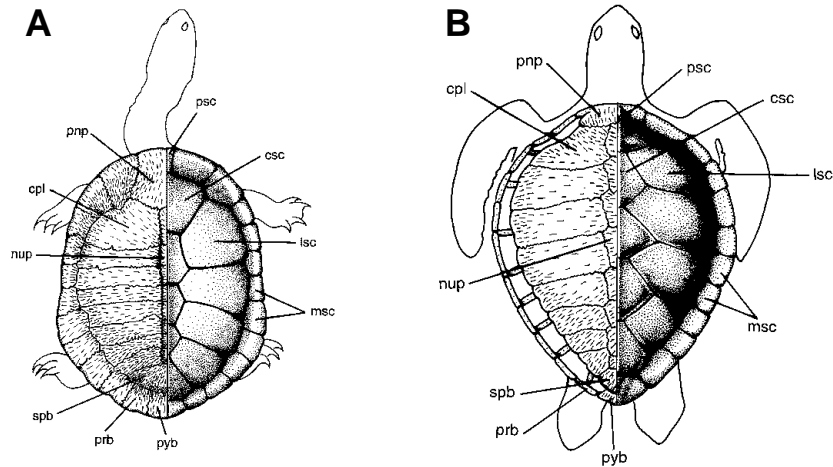


Figure 16.1 Epidermal laminae (right) and bony elements (left) of the carapace. **A**, *Chelodina longicollis*; **B**, *Chelonia mydas*. **cpl**, anteriormost of eight costal plates; **csc**, anteriormost of five central scutes; **lsc**, anteriormost of four lateral scutes; **msc**, marginal scutes; **nup**, neural plate; **pnp**, preneural plate; **prb**, posteriormost of 11 peripheral bones; **psc**, precentral scute; **pyb**, pygal bone; **spb**, suprapygal. Interlaminal seams are shown by solid lines and irregular lines indicate sutures. (After Cogger 1992) [T. Wright]

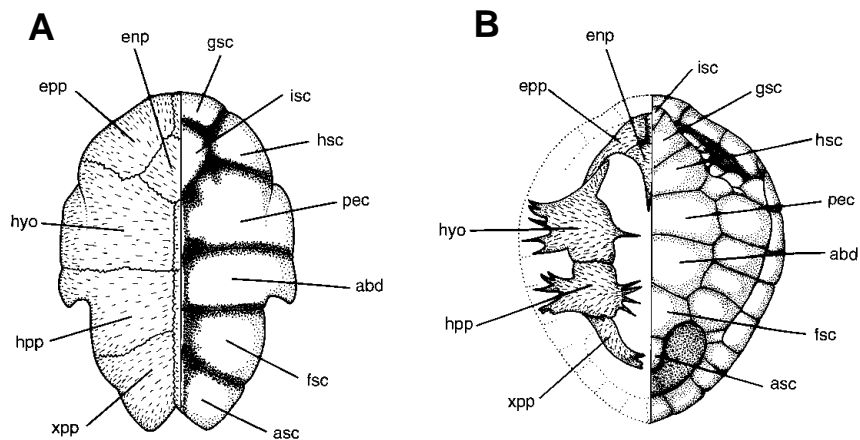


Figure 16.2 Bony elements of the plastron (left) and epidermal laminae (right). **A**, *Chelodina longicollis*; **B**, *Chelonia mydas*. **abd**, abdominal scute; **asc**, anal scute; **enp**, entoplastron; **epp**, epiplastron; **fsc**, femoral scute; **gsc**, gular scute; **hsc**, humeral scute; **hpp**, hypoplastron; **hyo**, hyoplastron; **isc**, intergular; **pec**, pectoral; **xpp**, xiphypastron. Interlaminal seams are shown by solid lines and sutures by broken lines. (After Cogger 1992)

[T. Wright]

internal endochondral element fused to an external dermal element. Endochondral elements have cartilaginous precursors, and dermal precursors ossify in the dermis. The epidermal scutes are normally keratinous, thin, and separated from the underlying bony elements by only a thin layer of soft, vascular, germinative tissue.

The bony elements of the carapace consist of a mid-longitudinal series of neural elements flanked on each side by a lateral costal series, all surrounded by a peripheral series (Fig. 16.1A, B). Fusion occurs between the neural plates and the neural arches of the vertebrae, and between the costal plates and the underlying ribs. The peripheral elements have no endoskeletal component. The bony parts of the carapace articulate suturally via their dermal components, and usually do not co-ossify.

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There are eight costals on each side. The main shaft of the rib is visible only as a slight bulge on the inside of the element, but the head of the rib, which articulates with the vertebral centrum, and the tip of the rib are clearly visible. The tip articulates with a pit or groove in a peripheral bone or between two peripherals. There are 10 dorsal vertebrae, and 10 pairs of ribs. The first and second ribs are fused to the first costal element. The ninth and tenth ribs are fused with the eighth costal element.

The most anterior and posterior of the five to eight neural elements are not associated with vertebrae. The nuchal bone is a large keystone for the anterior end of the carapace. The pygal bone, situated posteriorly, is preceded by a variable number of suprapygals. The number of neurals varies but is usually eight in turtles with a full series. Most Australian chelids lack neurals, though vestiges occur in some (Rhodin 1977), and they are present in South American chelids. In the absence of neurals, the costal elements articulate with each other and with the neural arches along the dorsal midline. There are usually 11 pairs of peripheral bones in recent turtles. The number is reduced in kinosternoids and trionychoids, and there are 10 in the genus *Carettochelys*.

The plastron typically consists of nine bony plates articulated suturally. These are the unpaired anterior entoplastron flanked by the paired epiplastra and the paired hyoplastra, hypoplastra and xiphyplastra. In a few extant pelomedusids and some fossils, a pair of mesoplastra occurs between the hyo- and hypoplastral elements.

The hyoplastral and hypoplastral elements articulate with peripheral bones, usually between the third and seventh, on each side via two vertical or diagonal pillars of bone called the axillary and inguinal plastral buttresses. These buttresses form the bridge, an isthmus of bone between the carapace and plastron. Buttresses are substantial and strong in most Australian chelids. Sutural articulations within the plastron and between the plastron and the buttresses may loosen and become movable joints or hinges that can partly, or completely, close the shell.

The anterior plastral plates incorporate the dermal components of the primitive pectoral girdle. The interclavical fuses to a dermal plate to become the entoplastron, and the clavicles do likewise with the epiplastra. Vestiges of pectoral elements can be seen in the formed plastral elements. The rest of the plastron may be derived from the gastralium, or belly armour.

Superimposed upon the bony shell are epidermal scutes (also termed laminae or shields). These are hardened or cornified layers of the epithelium separated by depressions called seams. Most scutes overlap two or more bony elements and further increase the strength of the shell. The scutes are arranged in series similar to the bones: the median central scutes overlap neurals and costals; the lateral scutes on each side overlap the costals and the peripherals; and a circumferential series of marginal scutes overlaps the peripherals. The precentral is an unpaired anterior scute in the marginal series. Among extant turtles the usual numbers of centrals, laterals and marginals are 5, 4+4 and 12+12, for a total of 38 carapace scutes, including the precentral. There is often an extra scute between the fourth and fifth central scutes in the *Chelodina expansa* group. Extra lateral scutes occur in some marine turtles. Cryptodires with reduced peripheral bones also have a reduced number of marginal scutes. Trionychids and *Carettochelys* have no defined scutes at all (but see Zangerl 1959), and the entire shell is covered by undivided soft skin (Pl. 3.9).

Chelonians typically have 12 or 13 scutes on the plastron (always 13 in chelids): an unpaired intergular plus 6 pairs of large scutes termed the gulars, humerals, pectorals, abdominals, femorals and anals, respectively. Most cryptodires lack an intergular scute. Most aquatic turtles shed scutes periodically as they grow; scutes can also wear away gradually. Moll & Legler (1971) describe the process

of bone and scute growth and scute shedding. The frequency of scute shedding is variable among species of Chelidae (see Chapter 21) and irregular in testudinid land tortoises and terrestrial emydids. In trionychids and *Carettochelys* the epidermal covering of the shell is not divided into discrete scutes and epidermal shedding occurs, presumably by the gradual exfoliation of individual cells.

The skin of turtles is soft, mostly smooth and divided only by shallow grooves. Scales are present on the feet, antebrachium, crus and, to a lesser extent, the tail and head. Many chelids have a well defined, cornified shield on the dorsal surface of the head where soft skin is in direct apposition to the roofing bones of the skull (Pl. 3.14). The head shield is often distinctly coloured and textured.

A variety of integumentary organs occurring in the skin of turtles can be considered in two broad categories: invaginations and evaginations (or integumentary appendages) (Legler & Winokur 1979; Winokur 1982b; Winokur & Legler 1974, 1975).

Integumentary appendages are projections of the body surface which are thought to function as mechanoreceptors. They are used in foraging and perhaps a variety of other tactile ways (see below). Winokur (1982b) recognised three kinds of integumentary appendages in chelonian skin: tubercles, barbels and fimbriae. Each consists of epidermis and a core of dermis and subcutaneum with its blood vessels and nerve twigs, but lacks a glandular, skeletal or muscular component.

Tubercles are usually blunt-tipped, short, conical extensions of the integument (Pl. 3.12, 3.14) that are slightly movable; they may also be cornified and sharp-tipped. Tubercles occur chiefly on the neck and tail and are often arranged in dorso-lateral rows. Gular barbels, also termed mental barbels and chin barbels, are single or paired, usually blunt-ended, elongate cylindrical or conical projections just posterior to the mandibular symphysis. They can be moved easily by contact with a foreign object and probably by water flow. Well-developed barbels occur in the Chelydridae, Kinosternidae, Pelomedusidae and Chelidae and could have evolved independently in these four groups. Murphy & Lamoreaux (1978) described the use of barbels in the mating behaviour of Australian chelids. Fimbriae are elongate extensions of the integument, normally flattened and flexible, and often branched or bearing a complex secondary topography. Fimbriae reach the zenith of their development in the South American chelid, *Chelus fimbriatus*, and in North American Alligator Snapping turtles (*Macroclemys*). In these species the fimbriae play a role in camouflage. Hartline (1967) demonstrated a sensory function for the fimbriae of *Chelus fimbriatus*.

Invaginations of the chelonian integument include mental glands (Winokur & Legler 1975), rostral pores (Winokur & Legler 1974) and follicular tubercles (Legler & Winokur 1979). Rostral pores are invaginations of various depths and complexity in the epidermis of the narrow band of skin between the nostrils. They may be large and melanistic or cryptic. They occur in all families of turtles except the marine turtles and the Carettochelyidae. In longitudinal sections the epidermal invaginations may be simple and cylindrical or highly branched. Dead cells from the stratum corneum tend to fill the lumen of the pore and sometimes form a projecting plug of waxy to keratinous tissue. The dermal papillae associated with rostral pores are highly innervated. Rostral pores may facilitate deep mechanical stimulation of the dermal papillae via the dense core of keratinised tissue. A follicular tubercle is essentially a neck tubercle containing a deep invagination similar to a rostral pore. Follicular tubercles have been observed only in the *Elseya latisternum* group. A follicular tubercle would combine the sensory functions of a barbel and a rostral pore.

Mental glands are paired integumentary glands (or glandular vestiges) on the anterior throat skin. They occur in the Emydidae, Bataguridae, Platysternidae, and Testudinidae. They are highly specialised pheromonal structures in some testudinids, but are usually cryptic and only marginally secretory in the other families. There are no mental glands in chelids. Mental glands and rostral pores may be vestiges of glandular structures in primitive amniotes that have lost their original function but have been re-exploited in groups where the primordia persist.

Musk glands are located within the shell, between the buttresses, in the angle formed by the peripheral bones. They develop from ectodermal invaginations that migrate internally before the shell forms. During ontogeny the ducts develop a *tunica muscularis* of striated muscle and are innervated by the posterior rami of the inner intercostal nerves (Ogushi 1913; Stromsten 1917; Vallén 1944). Their ducts go to orifices near the union of the marginal scutes and the soft skin anterior and posterior to the bridge. The ducts usually pass through osseous foramina or grooves in the buttresses. Musk glands occur in all turtles except the Testudinidae and the *Chrysemys* complex of the Emydidae. The taxonomic occurrence of musk glands suggests that they are primitive structures and that their absence in testudinids and most emydines is a derived condition.

Ten morphological patterns of glands, ducts, and orifices were recognised by Waagen (1972). Chelids have a 'pattern 3' type in which there is a gland at each end of the sternal cavity on each side and ducts pass through osseous canals in the buttresses. Orifices lie between the third and fifth, and eighth and ninth marginal scutes. This pattern also is found in most pelomedusids and in all cheloniids, except *Lepidochelys*. In *Carettochelys* there are three glands: an anterior gland at the third rib tip, with its orifice at the anterior edge of the fourth peripheral bone; a doubled axillary gland at the fourth rib tip, its two ducts anastomosing on a single orifice at the fifth and sixth peripheral bone; and an inguinal orifice at the eighth without any glandular connection (one specimen dissected). Zangerl (1941) described and illustrated musk glands in *Chelydra*.

The formation of musk is probably holocrine. Eisner, Jones, Meinwald & Legler (1978) isolated the following compounds from the musk of *Chelodina longicollis*: oleic acid, linoleic acid, palmitoleic acid, palmitic acid, stearic acid, citronellic acid and beta-ionone. *Chelonia mydas* produces PAS-positive, protein-rich nonacidic musk. In *Sternotherus odoratus*, droplets of free lipid are present in the musk (Ehrenfeld & Ehrenfeld 1973). Studies on the function of the odiferous musk of *Chelodina longicollis* are inconclusive, although it is suspected of being a deterrent to predators (Kool 1981; Dorrain & Ehmann 1988; see Chapter 21).

SKELLETAL SYSTEM AND MUSCULATURE

The pectoral girdle is distinctive and tri-radiate. The scapula is L-shaped, and its contribution to the glenoid cavity lies at the angle. One of its rod-like limbs extends dorsally to the inside of the carapace and the other arm, the acromion process, extends antero-medially at right angles. The coracoid bone joins the scapula at its angle and contributes to the glenoid cavity. It extends postero-medially, in the same plane as the acromion. The arms of the pectoral girdle therefore bear a nearly rectilinear relation to one another (as do the three edges in one corner of a box), and the glenoid cavity lies at the outside apex.

The pelvis is mobile and free of direct shell attachments in cryptodires. In pleurodires, the pubis and ischium fuse to the xiphylastron, and the ilium fuses with the eighth costal element. The top of the ilium in pleurodires is robust and triangular in cross section at the iliocostal interface. The joint contains soft tissue and may be a partially mobile symphysis. The plastropelvic joints are sutural. All the bones of the pelvis contribute to the acetabulum. In turtles the

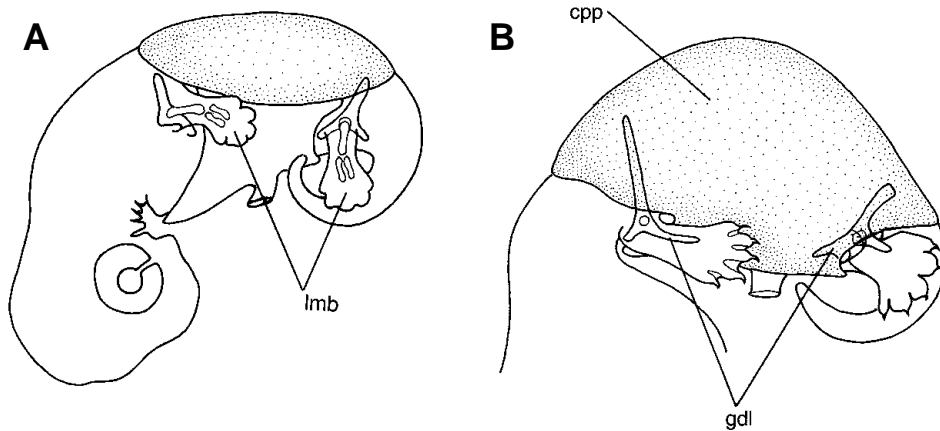


Figure 16.3 Relationship of the carapace primordium to the limbs and girdles in *Chelydra* embryos. **A**, at 10 mm; **B**, at 20 to 25 mm. **cpp**, carapace primordium; **gdl**, girdle; **lmb**, limb. (After Ruckes 1929) [T. Wright]

pubis and ischium do not have a substantial lateral exposure (as in other reptiles), but are folded ventro-medially, with most of the lateral face directed ventrally.

The extreme modification of the tetrapod body plan, resulting in the shell and internal position of the girdles, must have been tremendously advantageous; the shell may be reduced but it is never lost. In features other than the shell, turtles have remained remarkably generalised in most skeletal and visceral structures. These generalised traits are primitive and support the idea that turtles could be the closest living relatives of prototypic amniotes.

It was once thought that the limb girdles had migrated to the inside of the rib cage, both ontogenetically and phylogenetically (Wagner 1922; Ewert 1985). This has been disproved by developmental studies. Turtle limb buds appear on a typical, tubular vertebrate embryo. The carapace and plastron primordia then appear as circumferential ridges above and below the limb buds. The carapace primordium is oriented in the frontal plane and the ribs, which appear slightly later, are short, straight and horizontal. The precursors of the limb girdles probably do not move at all as the carapace primordium radiates and overgrows the girdle rudiments before turning ventrally and actually enclosing them. During this process the characteristic widening of the body occurs (Ruckes 1929; Ewert 1985).

The chelonian skull is anapsid and toothless. Roofing of the temporal region over the mandibular adductor muscles ranges from complete to nil, but there is no true fenestration as there is in other reptiles. The edges of the temporal roof are emarginated from behind, from below or both. Posterior emargination interrupts the parietosquamosal contact and, when coupled with at least slight ventral emargination, creates a lateral temporal arch ('zygomatic' arch) formed by combinations of the quadratojugal, jugal and postorbital (Fig. 16.4E, F). Posterior emargination is typical of most cryptodires and of the pelomedusids among the pleurodires. In some cryptodires the lateral arch has been lost entirely. All chelids show a substantial ventral emargination which eliminates the quadratojugal and leaves no bony bridge between the quadrate and the posterior rim of the orbit (Fig. 16.4A, B). The emargination is least in *Pseudemydura*, leaving a dorsal roofing that is extensive. In other Australian shortnecks the emargination is greater, leaving a posterior temporal arch of moderate width. Ventral emargination is complete in both groups of *Chelodina*,

contact with the sesamoid bone is synovial. In pleurodires the trochlea is formed by a lateral process of the pterygoid bone and the lubricated surface is formed by an evagination of the mouth lining (*ductus angularis oris* of the buccal mucosa).

The usual, and probably primitive, phalangeal formula of the manus and pes of turtles is 2,3,3,3,3 (or 2). All Australian chelids have the formula 2,3,3,3,3 for both manus and pes. Modifications in the flippers of marine turtles and *Carettochelys* result from elongation of phalanges (Romer 1956).

Intercostal spaces are filled with dermal bone in turtles, and the intercostal musculature has become obsolete. There is some evidence that striated muscle lies directly on the lung and is homologous to the intercostal muscles of other reptiles (George & Shah 1954). The homologues of the lateral belly muscles, *m. obliquus abdominis* and *m. transversus abdominis*, remain beneath the skin of the inguinal pockets and function in respiration (see Respiration).

LOCOMOTION

Locomotion is constrained in turtles by the rigid vertebral column, by the extent of the bridge and, in pleurodires, by the fusion of the pelvis to the plastron. Trunk movements of any kind are impossible and locomotion is achieved entirely by limb movements. All turtles can move on land and in water to some extent and most, including chelids, are rather efficient at both. Terrestrial and aquatic gaits in turtles have been analysed in substantial detail (Walker 1973, 1979; Zug 1971), but only the latter are described here.

Freshwater turtles swim with alternate movements of the front and hind feet. The forelimb and hindlimb on opposite sides provide propulsive force while their contra-lateral counterparts recover. At times, only the forelimbs are used and the hindlimbs act as balancers or rudders. Marine turtles and *Carettochelys insculpta* each show convergent modification of the front limbs as flippers; they are used simultaneously in a 'flying' motion for forward propulsion (Pl. 3.9).

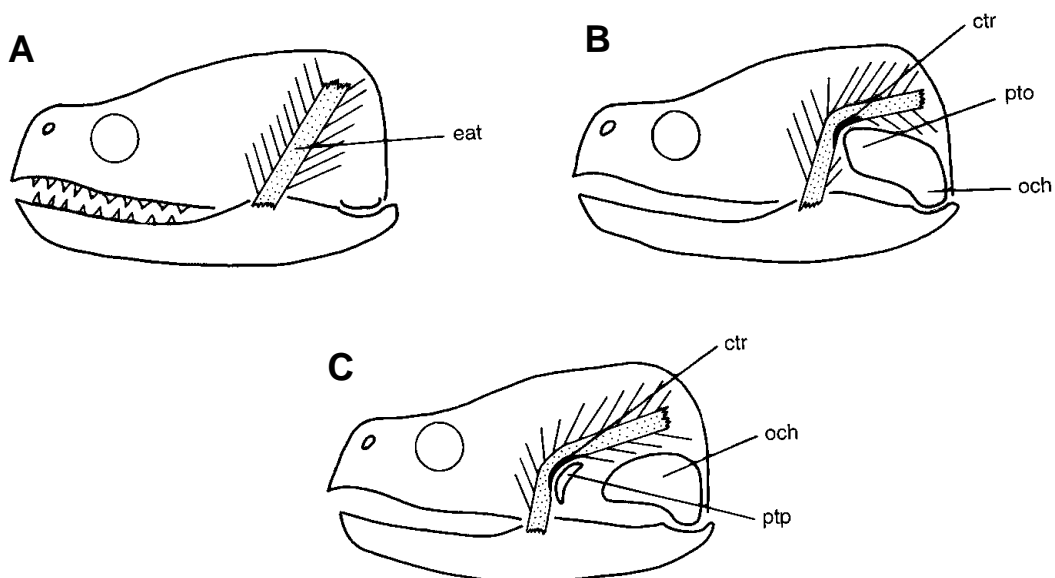


Figure 16.5 The course of the mandibular adductor tendon. **A**, non-chelonian reptiles; **B**, cryptodires; **C**, pleurodires. **eat**, external adductor tendon; **ctr**, cartilago transiliens; **och**, otic chamber; **pto**, processus trochlearis oticum; **ptp**, processus trochlearis pterigoidei. (After Gaffney 1975) [T. Wright]

When chased, however, *C. insculpta* swims rapidly by moving the flippers alternately and coordinating them with the hind feet in a trot-type swimming gait.

Freshwater turtles typically escape towards the bottom in a long, curving path which is banked as 'tight' as the turtle can make it at top speed. At the bottom the turtle usually pauses momentarily, turns its body by obtaining purchase on the substrate, and swims off again at speed, usually in the opposite direction. This 'terminal reverse behaviour' has been observed in most freshwater turtles, including all Australian chelid genera except *Pseudemydura*.

Turtles seldom move rapidly in nature; movements are generally slow and deliberate with frequent pauses for rest, circumspection and feeding. Rapid movements are brief, quite obvious, and normally associated with feeding, aggression, or mating. Chelid turtles probably have no reason to swim long distances, unlike marine turtles which require greater precision and economy of energy.

FEEDING AND DIGESTIVE SYSTEM

Knowledge of natural diet of chelonians has accelerated since the development of stomach flushing (Legler 1977; Legler & Sullivan 1979). Most freshwater chelonians are opportunistically omnivorous as discussed in Chapter 17. The typical feeding behaviour of aquatic omnivores is quiet, unhurried prowling near the bottom, grazing on aquatic vegetation, investigating 'windfalls', and opportunistic lunges at small invertebrates.

Freshwater turtles employ two basic feeding techniques. In inertial feeding, the prey is grasped with the jaws, either deliberately or with a fast strike. After the prey is reorientated by repeated regrasping, it is gradually moved backward into the mouth by rapid forward movements of the head and neck. When the prey or food item is too large to swallow, all freshwater turtles will turn the head to one side and use the claws of one forelimb to tear the prey into more manageable fragments.

Suck and gape feeding involves a fast strike at the food object, depressing the hyoid apparatus, opening the mouth, and drawing the object into the mouth and pharynx, together with a substantial volume of water. The hyoid movements rapidly and substantially increase the volume and reduce the relative pressure of the combined mouth and pharynx. *Chelus*, *Hydromedusa*, and the Australian longnecks use gape and suck feeding almost exclusively to ingest live animals small enough to pass into the mouth. In *Chelodina expansa* and *Chelus* the entire strike and initial ingestion phase is much too fast to follow with human vision. The action slows perceptibly when the mouth closes and swallowing begins. *Chelus* is significantly faster than any of the longnecked chelids. Stomach flushings from *Chelodina expansa* suggest that prey is selected on the basis of length. Objects of an appropriate size therefore may pass into the mouth without touching the jaws and they reach the stomach whole, undamaged and occasionally alive.

Some turtles have been observed to gather and swallow particulate matter by moving slowly at the surface with the mouth open. This behaviour (neustophagia) has been observed in *Podioconemis* (Belkin & Gans 1968) and in *Emydura* (Legler 1976).

Parsons & Cameron (1977) reviewed the general internal topography of the gut and Luppá (1977) the histology and histochemistry. Jacobshagen (1920) presented a substantial study of the gut. The gut consists of a continuous tube connecting the mouth to the cloacal orifice. The internal topography of the gut is seldom simple and smooth. The various folds and ridges of the intestinal mucosa increase the internal surface area for secretion and/or absorption and act as

distensive pleats. The major pattern of ridging and folding is usually longitudinal. Less commonly it is transverse or oblique, for example, in trionychids. The longitudinal folds probably allow free passage of food through the lumen whereas food would be impeded by transverse or oblique folds (Parsons & Cameron 1977).

Some mechanical breakdown is accomplished by the tomial edges of the jaw sheaths and any accessory alveolar ridging within the mouth. This usually has more of a crushing than a chopping effect and is of little use for fragmenting muscle tissue. Long blades of vegetation can be ingested whole by scoring them and then folding them repeatedly into masses that can be swallowed (Legler pers. obs.).

The tongue of chelids is smooth and simple and appears to have little function in feeding. Chelids and many other aquatic chelonians cannot, or do not, swallow out of water.

The oesophagus is a distensible tube of transmission from the pharynx to the stomach. Food travels through the oesophagus either whole or in large chunks. The tube has no known digestive function. Its lining consists typically of longitudinal folds. *Lissemys* is unusual in having transverse or oblique folds (Parsons & Cameron 1977). In marine turtles there are long, sharp, keratinised papillae, directed posteriorly. All Australian chelids possess uniquely developed oesophageal glands which are discussed in Chapter 21.

The stomach is sac-like and distinctly larger than adjacent parts of the gut. The *tunica muscularis* imparts thickness and firmness to the gastric wall. Most turtles have many broad, rugose, longitudinal folds in the gastric mucosa. *Lissemys punctata* and *Platemys platycephala* lack any trace of folds. The stomach is a holding vessel that receives, churns and partially digests materials passing into it from the oesophagus (Parsons & Cameron 1977).

The small intestine of all turtles is similar. Longitudinal folds form a zigzag pattern, which probably disappears as the tube is distended. Various smaller oblique and transverse cross-connections form a net-like pattern between the major folds. This pattern is most complex in the duodenum and becomes simpler and lower towards the colon, as the angles on the zigzags change from acute through obtuse angles to simple longitudinal folds near the end of the ileum. Trionychids appear to be an exception; *Lysemys punctata* lacks folds, and those in *Apalone spiniferus* are low and oblique. All trionychids have a single large fold near the pylorus and smaller transverse folds near the end of the ileum (Parsons & Cameron 1977).

Parsons & Cameron (1977) found little uniformity in colonic structure except for a large lumen, generally reduced internal topography, and thin walls. They attribute some of the variation to different degrees of distension.

CIRCULATORY SYSTEM

The oval, nucleated erythrocytes make up 20 to 30% of blood volume and carry about the same amount of haemoglobin as mammals. Erythrocyte life span is 600 to 800 days in the cryptodire, *Terrapene* (Bellairs 1969; Dessauer 1970). The chelids *Chelodina longicollis* and *Emydura krefftii* have 508 to 583 erythrocytes/mm³ x 10⁻³, representing a packed cell volume of 21.0 to 29.5%. Erythrocytes are 17 to 22 μm long and 9.6 to 12.8 μm wide. Freshwater species have larger and fewer erythrocytes than terrestrial ones (Frair 1977). Dessauer (1970) presented a detailed and informative summary of plasma electrolytes, packed cell volume and organic constituents of the blood.

Turtles are remarkably tolerant to anoxia, exceeding that of all other tetrapod vertebrates (Dessauer 1970). Some *Chrysemys picta* have lived for three to four months underwater at 1.5° to 3.5°C. Anoxia tolerance for various turtles studied by Belkin (1963) ranged from 114 to 1980 minutes. The only chelid turtles sampled had values of 360 and 570 minutes. Aquatic turtles can spend the entire winter underwater (Musacchia 1959). *Chelonia mydas* spends the winter underwater at 15°C in the Gulf of California (Felger, Clifton & Regal 1976) and *Caretta caretta* hibernates underwater off Florida (Carr, Ogren & McVea 1980/1981).

Lymphatics occur almost everywhere in living body tissues but are difficult to observe. They begin as blind lymph capillaries in the interstitial spaces and constitute an accessory drainage system. The lymphatic vessels of reptiles are larger than those in mammals and reptiles lack lymph nodes and valves. The confluence of the lymphatic vessels with veins is usually close to the jugular–subclavian vein anastomosis. Reptilian lymphatic systems were first described by Panizza (1833a). Bojanus (1819) provided a reasonably detailed account for *Emys orbicularis*. A pair of macroscopic lymph hearts just internal to the posterior part of the carapace beat at a frequency of 3 to 45 times per minute. Ottaviani & Tazzi (1977) provided a detailed account of lymphatic systems in reptiles which included several cryptodires.

THERMOREGULATION

Temperature of the circulating blood probably is registered in the hypothalamus (Bellairs 1969; Rodbard 1948). Like other reptiles, turtles are ectothermic heliotherms and derive heat chiefly by moving into the sun or into a warmer medium (see Chapter 21). The chelonian shell is probably better insulation than the non-bony dermis of other reptiles.

Turtles can acclimate to a wide variety of environmental temperatures. The preferred temperature range in most turtles is 25° to 33°C (Hutchison 1979), and critical maxima range from 39° to 42°C (Bellairs 1969). A large *Pseudemys* warmed by basking can maintain a deep-core body temperature above ambient water temperature for several hours after re-entry (Moll & Legler 1971). Activity is reduced but possible at low temperatures. *Terrapene* can copulate at 15°C (Legler 1960b) and North American *Pseudemys* may court under ice.

The optimum water temperature for Australian chelids is between 25° to 28°C. In the Tweed drainage of northern New South Wales, *Emydura* species and *Elseya latisternum* are lethargic at water temperatures of 15° to 17°C but nevertheless will attempt to escape from a diver. *Emydura* sp. in the Macleay drainage, New South Wales, is slow but active throughout the winter at temperatures of 4° to 8°C, and some individuals caught in winter have filamentous algae in the stomach. Under these conditions, aquatic turtles with alternative respiratory mechanisms, such as *Elseya latisternum* (King & Heatwole unpub. data), probably can pass the winter without breathing air.

Dermochelys coriacea feeds as far north as the Arctic Circle and can maintain deep core temperatures of up to 18°C in ambient seawater temperature, by virtue of their large size, use of peripheral tissues as insulation and counter-current exchange in the limbs (Frair, Ackman & Mrosovsky 1972; Greer, Lazell & Wright 1973; Paladino, O'Connor & Spotila 1990; Standora, Spotila, Keinath & Shoop 1984).

RESPIRATION

The lungs of all turtles are functional in pneumatic air breathing. No species is known to have lungs with reduced lung capacity or efficiency, though many aquatic turtles have evolved alternative respiratory structures analogous to gills. The useful comparisons of lung morphology by Gräper (1931), and information on all Australian chelids, except *Pseudemydura* (University of Utah unpub. data) form the basis for this description of lung structure and function.

The basic lung plan found in unspecialised cryptodires and in all chelids examined, consists of eight distinct subdivisions or lobes. Four of these are small, medial and almost cubic in proportions and four are lateral, larger and significantly wider than long.

The pulmonary hilus lies ventro-medially, between the first and second medial lobes. The primary bronchus passes through the hilus and between the median and lateral lobes. The bronchus communicates with the lobes via separate baffled openings. At the hilus, the pulmonary artery bifurcates into a superficial, ventral trunk and a deep trunk, which penetrates the lung and then runs superficially along the dorsal surface. Each trunk has major branches to each of the lobes, forming a collateral arterial supply. A single venous trunk runs parallel to the bronchial passageway ventrally, receives blood from a major vein from each lobe and exits at the hilus. This arrangement represents the 'Grundplan 4' of Wolf (1933). Gräper (1931) showed cross sections through the lungs of several pleurodires, including *Chelodina longicollis*.

Specialisations of the lung result from subdivision of the eight basic lobes. In marine turtles and trionychids the intermediate septa are complete and the resulting subordinate lobes are ventilated individually. The lobes are divided incompletely in *Carettochelys* and kinosternids. The eight lobes in the large, thin-walled lungs of testudinids have minimal interlobular subdivision. In *Rheodytes leukops* there may be a slight reduction in secondary chambering and total internal surface area but, in comparison to other shortneck species, these differences are slight, and not of the magnitude that one might expect in a gill breather.

In cryptodires the lungs may be attached to the dorsal peritoneum, to some of the anterior respiratory muscles, to the aponeurosis of the m. transversus abdominis, or to an extensive connective tissue 'diaphragm' ventral to the lungs (Gans & Hughes 1967; Gaunt & Gans 1969a). In Australian chelids examined, the lungs are attached to the peritoneum only by their dorso-medial edges and seem to be free of visceral attachments. They often are completely collapsed in preserved specimens (Legler pers. obs.).

The definitive modern works on lung ventilation are based on the testudinid *Testudo graeca* and the aquatic turtle *Chelydra* (Gans & Hughes 1967; Gaunt & Gans 1969a). No detailed studies have been published for chelids but useful extrapolations can be made from studies on cryptodires.

The lungs lie just beneath the carapace and are about half the length of the carapace when deflated. They extend between the pectoral and pelvic girdles and occupy the dorsal part of the visceral space. As such, they permit easy surgical approach from the dorsal side of the body and are vulnerable to dorsal puncture wounds.

The coelomic cavity of turtles, like that of most reptiles, is divided into a pericardial cavity around the heart and a common peritoneal cavity for the remaining organs, including the lungs. There is no diaphragm, though partial division of this cavity by a sheet of connective tissue between the lungs and all ventral viscera occurs in some testudinids (Gans & Hughes 1967).

While terrestrial chelonians can breathe at will, except perhaps while burrowing, aquatic turtles must coordinate breathing with times when the nostrils are above water. In deep water, this necessitates swimming to the surface. In shallow water, longnecked chelids may merely extend the neck to reach the surface, and require no limb activity at all.

Turtles can vary intracoelomic pressures and volumes by pulling in the limbs, head and neck. More subtly, this can be achieved by simple rotations of the pectoral girdle and by contractions of the highly modified belly muscles. A dramatic example of this, particularly in cryptodires, is the rapid withdrawal of appendages when a turtle is picked up or startled, accompanied by a hiss of air escaping from the glottis and the expulsion of fluids from the cloaca.

The *m. transversus abdominis* constitutes a contractile sling running beneath the peritoneum and the posterior viscera and attaching to the inner surface of the carapace on each side. When it contracts it lifts and compresses the visceral mass and indirectly exerts pressure on the lungs. The *m. obliquus abdominis* lies beneath the subcutaneous tissue of the inguinal pocket and attaches to the edge of the carapace above and the plastron below. When contracted, it flattens the inguinal depression and decreases intracoelomic pressure. In Australian chelids, these two sheet-like muscles are attached to one another by an aponeurotic patch corresponding to the deepest part of the inguinal pocket. Not only are they antagonistic, but when one contracts it pulls the other with it. The *m. diaphragmaticus* is an anterior analogue of the *m. transversus abdominis* and helps to lift a common aponeurosis in *Chelydra* (Gaunt & Gans 1969a). The *m. transversus abdominis* lifts the 'diaphragm' of tortoises, which achieves further coelomic compression by inward rotation of the pectoral girdles (Gans & Hughes 1967).

At the water surface, lung ventilation in Australian chelids could be satisfactorily explained by operation of only the *m. transversus abdominis*, *m. obliquus abdominis* and hydrostatic pressure. However, observations of captive shortnecked chelids, except *Rheodytes*, show a rapid ventilation of lungs during the first few seconds at the surface. Muscular activity associated with this behaviour has not been analysed, but movements of both inguinal pocket and anterior limbs have been recorded.

The nostrils are at the tip of a long proboscis in *Chelus*, *Carettochelys* (Pl. 3.9) and trionychids, permitting cryptic surface breathing. Erectile tissue and well-defined masses of smooth muscle occur in the snouts of chelids, *Carettochelys* (Winokur 1982a), and in marine turtles (Parsons 1971). In all of these, the two sets of smooth muscles surrounding the nasal canals seem to be nasal dilators. The erectile tissue may act as an antagonistic nasal constrictor, thereby providing a degree of control over water passing in or out of the nostrils. Such control may be important in closing the nostrils during sleep or controlling the flow through the nose for olfactory purposes. An additional mass of smooth muscle, *m. arrector rostri*, controls the angle of the proboscis-like snout in *Carettochelys*, and probably positions it optimally when the animal is buried in bottom silt with only its snout protruding.

Ward (1970) demonstrated experimentally that virtually the entire gut of turtles has the ability to extract oxygen from water. However, the two primary regions involved with accessory, or gill respiration are the buccopharyngeal region and the cloacal bursae. The buccopharyngeal region accounts for 49% and the cloaca and its bursae for 33% of non-pulmonary oxygen uptake by *Elseya latisternum* at 20°C and 30°C (King & Heatwole unpub. data). Aquatic turtles using gill respiration are vulnerable to fish poisons, derris and rotenone (Bellairs 1969; Rosen pers. comm.).

Cloacal bursae are dorso-lateral diverticula of the cloaca and are unique to some groups of turtles, including the Chelidae. They are absent in the Trionychoidea, Kinosternoidae, Testudinidae, the two families of marine turtles, the African pelomedusids, and in some (usually terrestrial) members of the Emydidae and Bataguridae. The bursae are probably a primitive chelonian character and absence is a derived condition. In general, cloacal bursae are better developed in aquatic than in terrestrial turtles.

Cloacal bursae have been known for more than two centuries and Pickel (1889) reviewed the early literature. Interest in cloacal bursae was renewed with the discovery of *Rheodytes* (Legler & Cann 1980; see Chapter 21). King & Heatwole (in press) examined the cloacal bursae of *Elseya latisternum* and found extensive modification consistent with a respiratory function.

Smith & Nickon (1961) suggested that bursae only have a respiratory function in cold, inactive turtles surviving under water. The contrary is true, however, in *Rheodytes* and *Elseya dentata*. These animals swim at top speed in water of 25°C or warmer with the cloacal orifice widely dilated. Chelids have not been observed surfacing to breathe when chased, in contrast to *Apalone* species and *Chelydra*, which can be forced to breathe under such circumstances.

The cloacal bursae probably assist in buoyancy control, as air can be expelled from the lungs without placing the animal in respiratory jeopardy. Before an escape dive, many Australian chelids, particularly shortnecks, expel air from the mouth. This air presumably originates from the lungs. Captive *Rheodytes* are always negatively buoyant. They walk on the bottom with ease, and regularly release large bubbles of air from the mouth. This suggests a release of accumulated gas from the lungs and may be a factor in maintaining negative buoyancy.

The cloacal bursae are retroperitoneal and lie internal to the inguinal pocket. Two layers of striated muscle lie lateral to the bursae at this level. The *m. transversus abdominis* muscle girdles most of the peritoneal cavity, and the *m. obliquus abdominis* muscle lies immediately below the subcutaneous tissue of the inguinal pocket. These sheets of muscle curve away from each other and

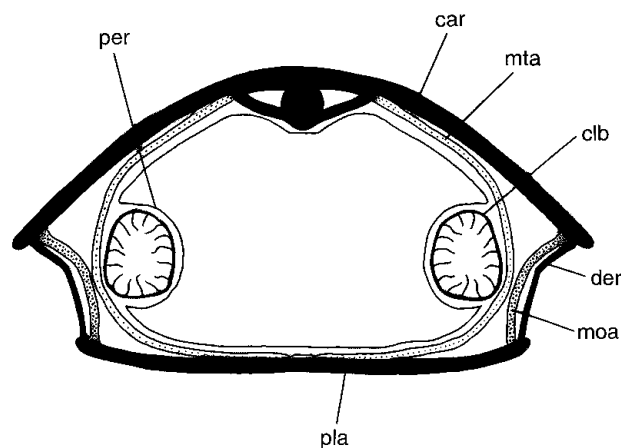


Figure 16.6 Schematic transverse section of a young *Rheodytes leukops* at the level of the inguinal pocket (posterior one-third of body), showing the relative positions of the *m. transversus abdominis* and *m. obliquus abdominis* muscles, the cloacal bursae, and the shell. The *m. obliquus abdominis* lies just below the skin of the inguinal pocket and attaches by its inner surface to the *m. transversus abdominis*. **car**, carapace; **clb**, cloacal bursa; **der**, skin; **moa**, *m. obliquus abdominis*; **mta**, *m. transversus abdominis*; **per**, peritoneum; **pla**, plastron. (Modified from a drawing by Mark T. Nielsen, University of Utah) [T. Wright]

Urinary nitrogen values for *Chelodina oblonga* and *C. steindachneri* demonstrate that both species excrete ammonia and urea when hydrated, but produce urates when dehydrated (Burbidge 1967). This change is more pronounced in the latter species, as discussed in Chapter 21. Apparently aquatic turtles absorb little water through the skin. If excess water enters via the gut, it can be voided in dilute urine (Bellairs 1969).

Chelonians can store water in the urinary bladder, in the cloacal bursae and probably as coelomic fluid. These reserves can be reabsorbed if necessary, as shown for *Chelodina oblonga* and *C. steindachneri* (Burbidge 1967). It is common for aquatic turtles and tortoises of all kinds to squirt varying amounts of water from the cloaca when handled, probably from the urinary bladder and/or the cloacal bursae.

Water comprises about 65% of body mass in turtles (Bellairs 1969). Freshwater turtles live in a low-sodium environment. The converse is true of marine turtles. Plasma osmolarity is variable, and ranged from 278 to 400 mOs/l in seven testudinid species and 258 to 436 mOs/l in *Chelodina oblonga* and *C. steindachneri* (Burbidge 1967); values for the chelids related with the state of hydration of the turtles. Marine turtles (*Chelonia* and *Caretta*) are able to live in fresh water. The osmolarity of a specimen of *Caretta* kept in fresh water for three years dropped from above 350 to 211 mOs/l. This change involved a decrease in sodium and chloride. Estuarine turtles (*Malaclemys*) survived after 14 days at 3.3% saline followed by 10 days at 6.6% saline. Over this period, plasma sodium rose to about 170 mEq/l in the hypertonic environment. The terrestrial emydid, *Terrapene*, survived only four days in 3.3% saline (Dessaur 1970).

The primary osmoregulatory strategy in freshwater turtles appears to be the production of dilute, low-sodium urine. *Apalone spiniferus* has special cells in the pharynx that can absorb sodium from water containing as little as 5 mM/l. Marine turtles and some estuarine turtles (*Malaclemys*) secrete excess salts in tears (Fig. 19.2) via enlarged lachrymal glands. The tears of *Caretta* have a concentration of 810 to 992 mM chloride (732 to 878 mM sodium) compared to 470 mM sodium in normal sea water (Bellairs 1969; Dessaur 1970; Dunson 1976).

SENSE ORGANS AND NERVOUS SYSTEM

The degree of encephalisation in turtles is similar to that in crocodiles and ranks between that of lizards and snakes. Brain weight expressed as a percentage of body weight in a very small sample of cryptodires ranged from 0.008% to 0.19% (Platel 1979).

The eye has a generalised structure, similar to that of other amniotes, and functions well under a variety of conditions. The reptilian eye, and details of retinal structure and function were reviewed Underwood (1970), Peterson (1992) and Granda & Sisson (1992). The pupil in turtles is always round. The surrounding iris may be dark, or pale (golden, yellowish, or greenish) in sharp contrast with the pupil. Often a bright metallic-coloured ring is present on the rim of the pupil. The visible part of the eyeball surrounding the iris is usually dull coloured. Blotches of melanin may disrupt a brightly coloured iris, and blend with the pupil to form a stripe, which sometimes corresponds to a lateral head stripe. An uncamouflaged bright iris is very evident under water.

The supportive layer of the eyeball contains a ring of 6 to 13 scleral ossicles (Underwood 1970). All amniotes focus light on the retina by modifying the shape of a flexible lens. The muscular ciliary body surrounds the lens and, in

middle ear. Its distal part is the cartilaginous extrastapes, an expansion of which is attached to the inner surface of the tympanic membrane. The extrastapes joins the stapedial shaft which passes through a foramen or an open notch in the quadrate, traverses the recessus cavi tympani and expands into a vertically oval footplate articulated to the vestibular or oval window (fenestra ovalis).

Part of the stapedial footplate abuts a fluid-filled sac, the paracapsular sinus. The shaft of the stapes lies upon the sinus and indents it dorsally. The sinus occupies most of the recessus cavi tympani and its posterior part lies against the lateral surface of the periotic sac. According to Baird (1970) the paracapsular sinus is a dampening mechanism unique to turtles and has no homologue in other reptiles.

The vestibular part of the osseus labyrinth is similar to, but simpler than that of lizards. The cochlear recess lies posterior to the vestibule rather than ventral. The vestibular window and stapedial footplate are almost vertical rather than horizontal. The utricle and semicircular ducts are like those of lizards. The saccule lies ventral to the utricle, as in *Sphenodon*, and is rounded but may be extended posteriorly (Baird 1970).

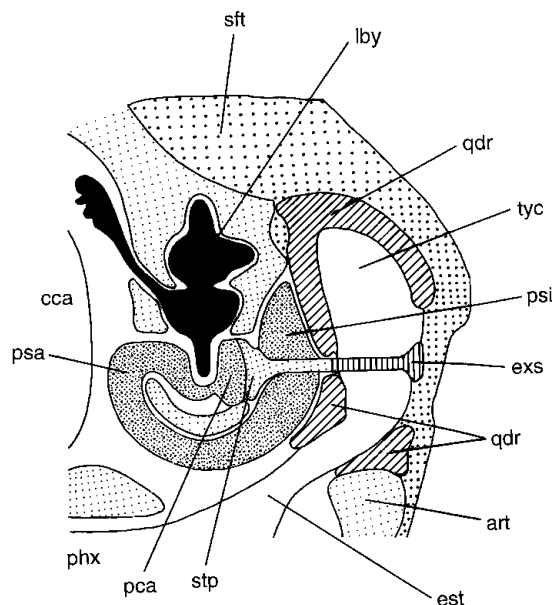
The auditory sensitivity of turtles is inferior to that of crocodylians and lizards, especially above frequencies of one to two kHz, and the ears of *Testudo* and *Terrapene* are responsive to sounds of about 110 Hz. The sensitivity of *Clemmys insculpta* for tones of up to 500 Hz is good, but declines rapidly above one kHz (Bellairs 1969). Some tortoises vocalise when mating and a few aquatic turtles make hissing or piping noises while breathing, but it has not been demonstrated that hearing these sounds is important to other turtles.

The nasal passages between the external nares and the internal nares in the roof of the buccal cavity are used in three basic ways—for normal aerial breathing, for olfactory purposes in the water and air, and for aquatic respiration. Most aquatic turtles practise buccopharyngeal pumping, during which water passes through the nose.

Of all reptiles, turtles have the most distinctive nasal anatomy, which Parsons (1970) considered to be primitive. Immediately inside the external naris is an expanded vestibule, which is linked to the expanded main nasal chamber by a short, narrow passageway. The roof of this chamber is lined with olfactory epithelium and Bowman's glands. The nasopharyngeal duct leads from the nasal chamber to the internal choanae. The length of this terminal choanal tube is directly related to the length of the secondary palate. The nasopharyngeal duct contains no olfactory epithelium (Parsons 1970; Romer & Parsons 1977).

Figure 16.7 Schematic section through the middle ear and inner ear of a turtle. **art**, articular bone of lower jaw; **cca**, cranial cavity; **est**, eustachian tube; **exs**, extrastapes; **lby**, membranous labyrinth, shaded black; **pca**, perilymphatic capsule; **phx**, pharynx; **psa**, perilymphatic sac; **psi**, perilymphatic sinus; **qdr**, quadrate; **sft**, soft tissues; **stp**, stapes; **tyc**, tympanic cavity. (After Romer 1956)

[T. Wright]



Most turtles have widely scattered taste buds in the buccopharyngeal region (Winokur 1988). The olfactory epithelium is concentrated in the nose. The vomeronasal (Jacobson's) organ discriminates olfactory sensations from substances in the mouth (Romer & Parsons 1977). The vomeronasal region is not well separated from the rest of the nose in turtles, and there is controversy about its occurrence and homology in turtles.

SECRETORY ORGANS

The unpaired, almost spherical thyroid gland is situated ventral to the trachea and immediately anterior to the heart (Lynn 1970). A detailed account of thyroid anatomy in *Emys orbicularis* and *Testudo graeca* can be found in Naccarati (1922).

Clark (1970) illustrated the positions of the parathyroids, the thymus and the thyroid relative to the trachea and heart. Turtles do not respond dramatically to parathyroidectomy. The parathyroid, as in mammals, seems to regulate the calcium and phosphate concentration in body fluids. There are two pairs of parathyroids. The anterior pair is embedded and hidden in the tissue of the thymus. The posterior parathyroids lie near the arch of the aorta in close association with the left ultimobranchial body.

Gabe (1970) illustrated the adrenal glands in *Pseudemys scripta* and their relationship to the ventral surface of the kidney. The adrenal gland is closely adpressed to the ventral surface of the kidney, and comprises the interrenal cords, derived from coelomic epithelium, and the adrenal cells, originating from the neural crest. The histology of the adrenal organ resembles that of other vertebrates (Gabe 1970).

The brief review of pancreatic anatomy by Miller & Lagios (1970) includes Australian chelids. Illustrations of two cryptodires (*Lissemys punctata* and *Pseudemys scripta*) and one pleurodire (*Podnocnemis unifilis*) show the relative positions of pancreas, spleen, tubular gut and major arteries. The pancreas always lies in the loop formed by the duodenum and the pyloric end of the stomach, but the position of the spleen varies.

REPRODUCTION AND DEVELOPMENT

The gonads of both sexes lie immediately ventral to the kidneys. The testis is situated ventro-medially to the anterior half of the kidney. Testes are normally oval but may become elongate during the cycle of enlargement. The efferent ducts consist of a long coiled epididymis, and a short vas deferens which enters the dorsal wall of the cloaca just medial to the ureter. All male chelonians undergo a seasonal testicular cycle of hypertrophy and regression. Stages of spermatogenesis can be approximated by the degree of enlargement (Moll 1979). Fertilisation is by sperm produced in the preceding year. Mature sperm are produced after ovulation and oviposition have occurred. Engorgement and pallidity of the epididymides is an accurate indicator of motile, mature sperm.

The ovary is a sheet-like organ. Presumptive follicles are detectable as pale surface granules in juveniles. The oviducts lie ventral to the ovaries and enter the cloaca ventro-laterally. The proximal portion of the oviduct, nearest the ostium, is flattened and folded like a concertina, whereas the distal end, which communicates with the cloaca, is rounded, thicker walled and unfolded.

Most anatomical drawings show a neat arrangement of these structures in the dorsal posterior half of the coelomic cavity, but when the ovary bears large follicles and the oviduct is laden with oviducal eggs, these structures take up most of the available coelomic space and impinge upon other coelomic organs, including the lungs.

At puberty, presumptive follicles in each ovary accumulate yolk (vitellogenesis) and enlarge to ovulatory size at the beginning of each annual cycle, reaching a diameter approximating that of the mature egg. A follicle consists of the thinly-stretched ovarian wall surrounding a yellowish ovum. At ovulation the follicular wall ruptures and releases the ovum into the coelomic cavity. Ovulation of all follicles in a size group seems to be simultaneous in most turtles that have been studied. The empty follicle collapses and becomes a distinct, cup-shaped corpus luteum about 15 to 25% of the diameter of the mature follicle, and each has a bloody orifice where ovulation occurred. Corpora lutea begin to regress almost immediately but remain visible throughout the breeding season (and sometimes into the next). Their presence is evidence that ovulation has occurred. Corpora lutea are present in different stages of regression if more than one set of ovulations occur in one breeding season. Multiple ovulations can be predicted from detectable size groups in enlarging follicles. The annual reproductive potential can be calculated from the sum of all enlarged, preovulatory follicles and the number of corpora lutea of all stages.

Depending upon environmental factors, ovulation of all preovulatory follicles may not occur, and the reproductive potential may not be realised. Follicles not ovulated in a given season become dark and flaccid, or atretic, and are reabsorbed. Atretic follicles are usually identifiable late in the season.

Postovulatory ova lie free at least momentarily in the coelomic cavity. Extra-uterine migration is common, and ova from one ovary may go into either oviduct (Legler 1958). This may involve coelomic migration of ova, movement of the oviducal ostia or both. As the ovum passes through the oviduct, the clear albuminous material around the yolk, the shell membrane and the hard part of the shell are added to it in a series of layers. Coating proceeds quickly to the stage of a thin shell. The shell then thickens more gradually over a period of days. The rapidity of this process is indicated by the rarity of any stage earlier than a thin-shelled egg in the oviduct or the coelom in thousands of specimens examined (Legler pers. obs.)

Multiple layers of fibres orientated in different directions in the shell membrane impart a felt-like appearance under magnification. A variable number of layers can be separated mechanically. The configuration of the fibres determines whether the membrane will tear transversely, longitudinally or spirally at hatching. The mineralised layer consists of a single layer of shell units, each of which is a multi-sided inverted polyhedron with its apex attached to, or abutting, the shell membrane. Eggshell units begin as crystallisation nuclei (Ewert 1985) on the shell membrane and grow to final size by the addition of thousands of aragonite crystals. Initially the shell units are almost conical in shape, and become polyhedral as they abut on one another. The crystallisation nucleus becomes a hollow space near the apex of each shell unit

Eggshells range from thin and flexible to hard and brittle (Ewert 1985; Legler 1985), the condition being characteristic of particular taxonomic groups. The shell may thicken in long-retained eggs. Under normal circumstances there is a single layer of shell units. Shell strength, rigidity and thickness depend on the height of the shell units and the extent of their fusion to one another (Fig. 16.8A, B).

Flexible-shelled eggs are rather rigid at laying. They become flexible and turgid as they absorb water and swell during incubation. This swelling necessarily involves movement between the shell units. Even hard-shelled eggs of medium shell thickness eventually expand, for example, in both groups of *Chelodina*, but not without cracking and flaking of part of the hard shell. The hardest-shelled eggs, such as those of *Elseya dentata*, have the thickest shells and do not expand at all. Thick-shelled eggs tend to have well-defined pores which are formed at points common to three or four shell units. Thin-shelled eggs usually lack pores.

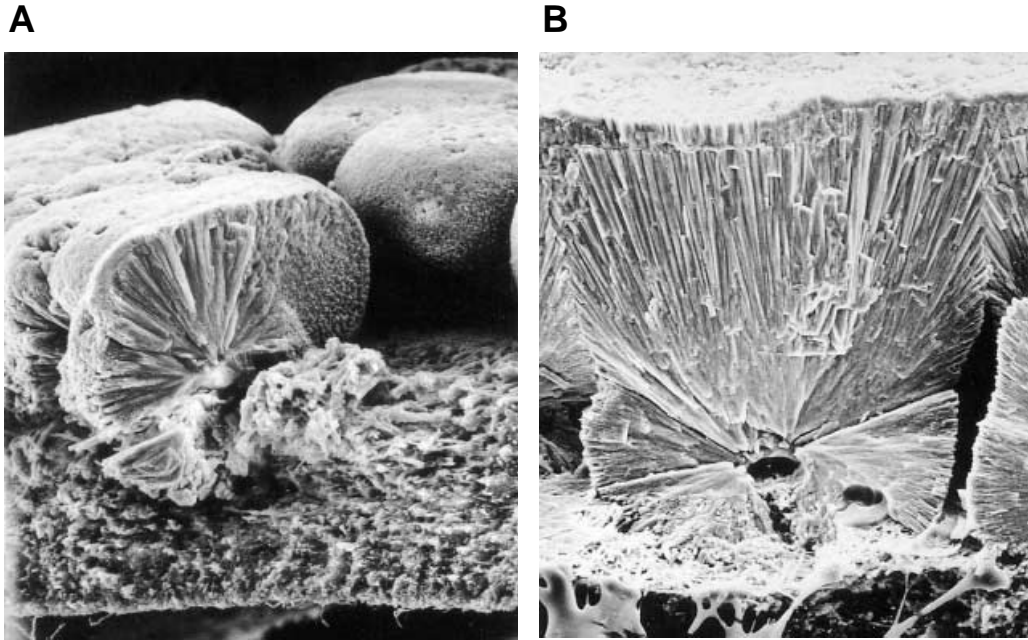


Figure 16.8 Scanning electron micrographs of oviducal egg of *Euseya dentata*, with the external surface of the eggshell at the top. **A**, a thin, undeveloped shell of specimen from Barramundie Creek, Northern Territory. Three rounded shell units are shown resting on a shell membrane. The broken shell unit in the foreground shows crystals radiating from the crystallisation nucleus. Note that shell units barely touch one another. **B**, a normally developed, thick shell from a specimen from Edith River, Northern Territory. Note hollow centre of crystallisation nucleus and potential zone of fracture passing through it. Flaking of the shell in late incubation may occur at this zone. Parts of other shell units are shown to the sides. Shell membrane and amorphous adhesive are shown below. [Photo by J. Legler]

Fully-shelled eggs normally are held in the oviduct until environmental conditions are suitable for laying. Development stops at the gastrula stage and does not proceed further until laying. This pre-ovipositional developmental arrest has been well-documented, but its causes have not been explained (Ewert 1985). Whatever the mechanism, it has a high selective advantage in permitting the nesting female to judge the suitability of conditions for nesting and therefore to determine the time that postgastrulatory development begins.

All living turtles are oviparous, and usually lay their eggs in nests dug in earth or sand near water. Australian freshwater turtles typically lay white ellipsoidal eggs. Eggs of *Carettochelys insculpta* are spherical. The eggs of marine species are spherical and soft-shelled, as the calcareous layer is much reduced (Miller 1985). There is no evidence of the development of viviparity in turtles. Lack of viviparity or the inability to evolve viviparity has been discussed eruditely but never satisfactorily explained (Packard, Tracy & Roth 1977; Tinkle & Gibbons 1977; Shine 1985a). The chelonian body plan is remarkably preadapted as a protective enclosure for development, but the habits of most turtles do not favour temperatures that are high enough to facilitate optimal developmental rates. Even the marine turtles that are endothermic, for example, *Dermochelys coriacea*, make long journeys to deposit eggs. Viviparity would impair the tremendous fecundity of turtles by limiting or preventing multiple clutches. To evolve viviparity, turtles would have to retain eggs without developmental arrest, limit the formation of the eggshell, and redirect the distribution of calcium and nutrients to the embryo.