



FAUNA *of* AUSTRALIA



21. FAMILY CHELIDAE

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Pl. 3.10. A Western Australian *Emydura* species.

[Cann]



Pl. 3.11. *Chelodina longicollis* showing characteristic, elongate neck; carnivorous; in wetlands of eastern Australia.

[Cann]



Pl. 3.12. *Rheodytes leukops* occurs in fast flowing waters of the Fitzroy River system, eastern Queensland. [Cann]



Pl. 3.13. *Pseudemydura umbrina*, Australia's most endangered reptile; one or two ponds in Western Australia; head covered with solid shield. [Cann]



Pl. 3.14. *Pseudemydura umbrina*, Australia's most endangered reptile; one or two ponds in Western Australia; head covered with solid shield. [Cann]



Pl. 3.15. *Eseya dentata* lives in large rivers and lagoons of northern Australia.
[Cann]

DEFINITION AND GENERAL DESCRIPTION

Chelids are all aquatic or semi-aquatic freshwater turtles. In Australia, the presence of distinct ankle joints and webbed feet, each with four or five claws, readily distinguishes this family from marine turtles and *Carettochelys*, which have flipper-shaped limbs. The posterior parietosquamosal arch is usually present (absent in *Chelodina*), but the quadratojugal is absent. The vomer is always present and usually separates the palatines. The presence of nasal bones (except in *Chelus*) is diagnostic for the family Chelidae, if living forms only are considered (Gaffney 1979). A splenial bone is present.

Chelids are typical pleurodirans in respect of features associated with the mechanism of head withdrawal. The cervical vertebrae have strong lateral processes, closely juxtaposed or fused postzygopophyses, and well developed central articulations which are never double (Williams 1950). The trochlear processes of the pterygoids are well developed, to accommodate the pleurodiran arrangement of the external adductor tendon (Gaffney 1979).

Horny scutes overlie the bony shell. The plastron is made up of nine bony plates, covered by 13 plastral scutes. A mesoplastron is lacking. The carapace is bordered by 11 pairs of peripheral bones covered by 12 marginal scutes, and a precentral scute is present in all but the genus *Elseya*. The pelvis is fused to both the carapace and plastron, which are joined by a rigid bridge. Neural bones are frequently reduced or absent. The fifth and eighth cervical centra are biconvex and there are never any saddle joints.

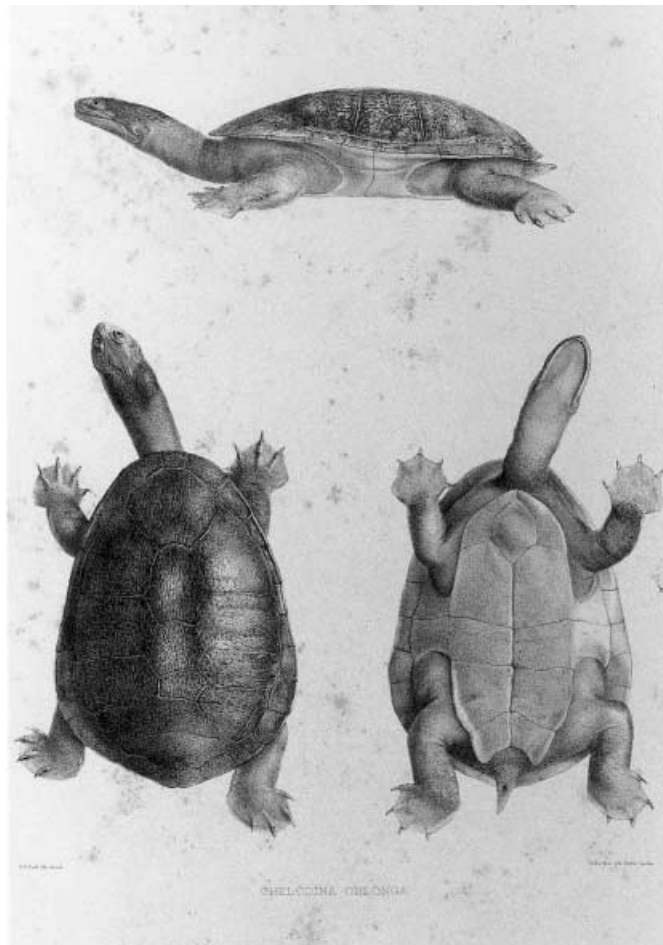


Figure 21.1 *Chelodina oblonga*, described by Gray in 1841, is one of only three species of freshwater turtles known from Western Australia. (After Gray 1856) [Photo ©Australian Museum]

Australian chelids are often considered in the categories of ‘shortnecks’ and ‘longnecks’. These useful terms are seldom defined. In a live chelid, the neck can be bent gently to the side that so it arcs continuously from its joint with the first thoracic vertebra. In longnecks, the tip of the snout will reach to a point somewhere on the posterior quarter of the plastron (*Chelodina longicollis* group), or beyond the posterior edge of the carapace (*Chelodina expansa* group). In shortnecks, the snout tip extends at most to the middle of the bridge.

The chromosome number in the Chelidae ranges from $2n=50$ to 64 (96 in triploid *Platemys*), and is $2n=50$ in Australian shortnecks or $2n=54$ in Australian longnecks (Bull & Legler 1980).

In Australia, the family is represented by the five named genera, *Chelodina*, *Elseya*, *Emydura*, *Pseudemydura* and *Rheodytes* (Pls 3.10–3.15). Three additional genera are yet to be described (Legler unpub. data). Useful illustrated references on Australian chelids are those of Cann (1978), Goode (1967) and Worrell (1963b). More comprehensive references include those of Pritchard (1967), Pritchard & Trebbau (1984) and Ernst & Barbour (1989).

HISTORY OF DISCOVERY

The first described Australian chelid turtle *Chelodina longicollis* (Pl. 3.11), collected by Sir Joseph Banks from the east coast of Australia on Cook’s first voyage in 1770. The species was formally described as *Testudo longicollis* by Shaw (1794), and transferred to the genus *Emys* (Schweigg, 1814) before it was considered distinct enough to be placed in the new genus *Chelodina* (Fitzinger, 1826). As the Australian continent was explored, more genera of freshwater turtles became known. *Emydura macquarii* was collected by the French explorers and naturalists Lesson and Garnot in 1825 and described by Gray (1830), and *Elseya dentata* (Pl. 3.15), named for the collector, Dr J.A. Elsey, who was surgeon and naturalist on Gregory’s expedition from the Victoria River of northern Australia to Moreton Bay in Queensland (Goode 1967).

The description of many species from single, isolated specimens of vague geographic origin which were shipped to European museums, often led to considerable confusion. For example, *Pseudemydura umbrina* (Pls 3.13, 3.14) was first described in 1901 from a specimen found in 1839 (Siebenrock 1901). In 1953, a specimen was discovered in the possession of a schoolboy and taken to the Western Australian Naturalist’s Club annual Wildlife Show. The specimen was described as a new species *Emydura inspectata* by Glauert (1954), but Williams (1958) showed that it was in fact, *Pseudemydura umbrina*, described over 50 years earlier.

Many discoveries of Australian turtles are much more recent. *Rheodytes leukops* (Pl. 3.12) of the Fitzroy River in Queensland was first described in 1980 (Legler & Cann 1980). Perhaps the most perplexing is the species unofficially called ‘shortneck alpha’ or the petshop turtle. For more than two decades, it was known to science only from petshops in Victoria, and the source of the specimens could not be discovered, despite thorough investigative work by Cann, Legler and others. An electrophoretic study by Georges and Adams showed that it was not a petshop hybrid, as it had many unique alleles. Finally, in 1990 the species was found by Cann in its native habitat of the Mary River, Queensland (Cann & Legler 1993).

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Australian chelids are small to moderate in size. As adults, they range in size from *Pseudemydura* (carapace length of smallest female 120 mm; Burbidge 1967) and males of *Emydura* from some eastern coastal drainages (carapace length approximately 100 mm) to a maximum of 485 mm in *Chelodina expansa* (usual range 250 to 350 mm). *Elseya dentata* and shortneck alpha attain lengths close to 400 mm. Most specimens of *Emydura*, *Elseya latisternum* and *Rheodytes* are intermediate in size (Cann & Legler 1993).

Though the sexes are difficult to distinguish by external characters before sexual maturity, the development of secondary sexual characteristics at puberty simplifies this process in adults. The form of adult size dimorphism is variable in Australian chelids. Males are larger in *Pseudemydura*, the sexes are of equal size in *Rheodytes*, and males are smaller than females in all other genera. The hypothesis proposed by Berry & Shine (1980) that larger male size is associated with forcible mating, whereas larger females are able to select their mating partner, has yet to be corroborated for Australian chelids. The tendency for shells of females to be deeper and more commodious than males would be adaptive in facilitating the periodic storage of eggs. The precloacal part of the tail, which accommodates the penis, is almost always deeper, longer and in general more heavily developed in males than in females.

Australian chelids tend to be drab in colour and unpatterned. The young are generally more brightly coloured than the adults. Hatchlings of *Chelodina longicollis* have a bright orange and black plastron. Bright yellow, orange, pink markings, alone or in combination, mark the head and neck of adults in some populations of *Emydura victoriae*, *E. subglobosa* and *Elseya latisternum* and pale areas of the plastron and ventral soft skin may be suffused with pink. In juveniles of some populations of *E. latisternum*, melaninistic marks on the plastron contrast brightly with yellowish or pinkish colour.

Chelids show little colour dimorphism, except for males of *Rheodytes*, in which the head is characteristically orange in colour.

Skeletal System

The sutural articulations which firmly join elements of the carapace and plastron may co-ossify in old adults. The only Australian genus to show any reduction of the rigid joints in the shell is *Pseudemydura*, in which the articulation between carapace and plastron contains fibrous connective tissue, or is syndesmotomic, and is at least slightly movable. The adaptive significance of these slight modifications is unclear, though they may permit the animal to lay a relatively large hard-shelled egg.

The skull roof is complete, feebly or not emarginate posteriorly, but with variable emargination between the orbit and the tympanum. Emargination is least in *Pseudemydura*, resulting in extensive dorsal roofing. Greater emargination in other Australian shortnecks leaves a posterior temporal arch of moderate width. Ventral emargination is complete in both groups of *Chelodina*, in which parietosquamosal contact has been lost completely.

Feeding & Digestive System

Usually, the mandible is lightly constructed and the dentary bones are unfused medially. Jaw structure is correlated with diet. The occlusal surfaces of the jaws consist principally of the maxillary bones above and the dentary bones below.

The palatine and premaxillary bones make a variable and minor contribution to the upper member. The occlusal surfaces are covered by the cornified epithelium of the jaw sheaths.

Each jaw ramus bears an outer, vertical tomial ridge and an inner, horizontal, triturating (crushing) surface. The mandibular tomium occludes with the inner surface of the maxillary tomium to form an efficient shearing device. This is used for general initial feeding movements, for shearing or scoring of vegetation too large to swallow whole and for grasping objects to be torn apart by the foreclaws. *Rheodytes* uses the tomial apparatus to scrape food off submerged rocks. Slightly modified tomia and triturating surfaces are characteristic of generalised, opportunistic omnivores, such as the *Elseya latisternum* group and most *Emydura*.

Three basic adaptive modifications to the jaw structure are found in Australian chelids. Secondary alveolar ridging may be present on the triturating surfaces, the tomium and triturating surfaces may be reduced in those chelids that use the suck and gape mode of feeding (both groups of *Chelodina*), or the opposed triturating surfaces and associated osseous structures are developed extensively to form a crushing plate. This last form is associated with megacephaly, as described later in this section.

The *Elseya dentata* group are the only Australian chelids with median alveolar ridging. Such ridging provides additional shearing or crushing planes. The median alveolar ridge of the lower jaw fits closely inside its counterpart on the upper jaw. Another ridge, here termed the 'secondary maxillary ridge' develops variably on the extreme medial edge of the maxillary triturating shelf, and serves to deepen the groove into which the dentary alveolar ridge fits. Alveolar ridging is an adaptation associated with herbivory. It has evolved convergently several times within the order, for example, in *Chelonia* (Cheloniidae), *Pseudemys* (Emydidae), *Batagur* (Bataguridae) and *Dermatemys* (Dermatemyidae).

Megacephaly is a phenotypic state in turtles in which the head is normally but often grossly enlarged (Figs 21.2, 21.3). Megacephaly is arbitrarily defined in *Emydura* as a head width greater than or equal to 18.6% of carapace length. Increased head size results from hypertrophy of the mandibular adductor musculature and compensatory modifications of the cranium and mandible. The condition is associated with the crushing of hard food, almost always molluscs (Worrell 1945; Legler 1981, 1989b). Megacephaly provides the ability to utilise molluscs as a food source over and above the typical omnivorous opportunistic diet.

As head size increases, the secondary palate and the mandibular symphysis extend posteriorly as crushing surfaces. These skeletal modifications shorten the effective load arm of a class III lever system and increase mechanical advantage between the posterior edges of the crushing plates. As the turtle grows in size, and gape increases, it is capable of eating larger molluscs. As individuals graduate to larger sizes of molluscs, the tomial edges of the jaw sheaths become worn and are broken frequently. This damage is never repaired and in older individuals the anterior parts of the jaw sheaths no longer occlude (Legler 1984).

Megacephaly occurs convergently in the Chelidae, Pelomedusidae, Kinosternidae, Trionychidae and Emydidae (Dalrymple 1977; Legler pers. obs.). Among Australian chelids, megacephaly is common in *Emydura* and occurs also in *Chelodina novaeguineae*.

Objects of an appropriate size may pass into the mouth without touching the jaws and be found in the stomach whole, undamaged and occasionally alive. Stomach flushings from *Chelodina expansa* suggest that individuals select prey of a given length (Legler pers. obs.). When a part of the prey object protrudes from the mouth, inertial movements are used to move it inward and backward. The jaws of *Chelodina* are weak.

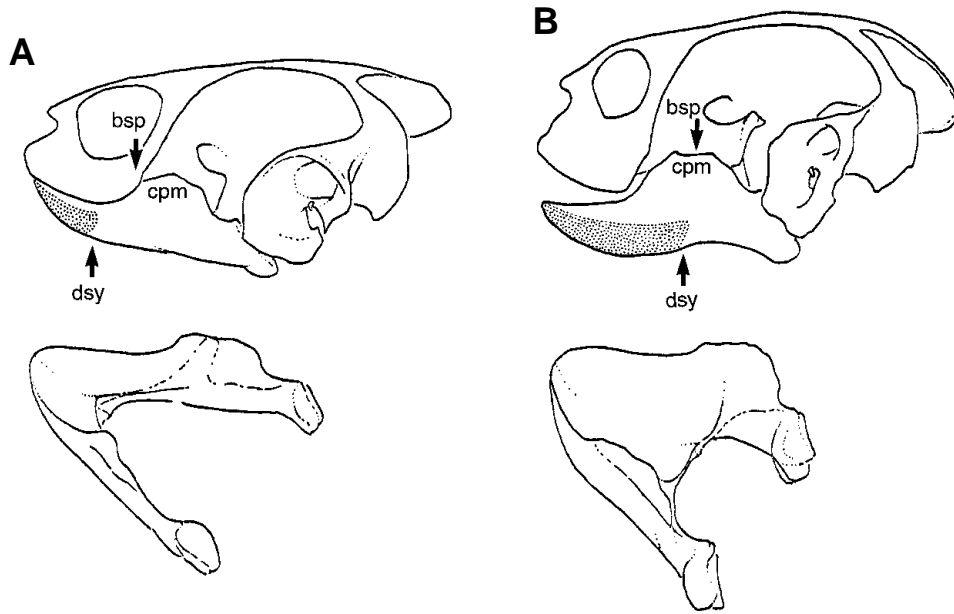


Figure 21.2 Lateral view of skull, and oblique view of mandibles of female *Emydura victoriae*. **A**, small, young adult, showing basic proportions of palate and dentary symphysis present at hatching; **B**, large, old megacephalic adult, showing extreme megacephaly, especially in the development of the dentary symphysis. **bsp**, posterior extent of bony secondary palate; **cpm**, coronoid process of mandible; **dsy**, posterior extent of dentary symphysis (shaded). [J. Legler]

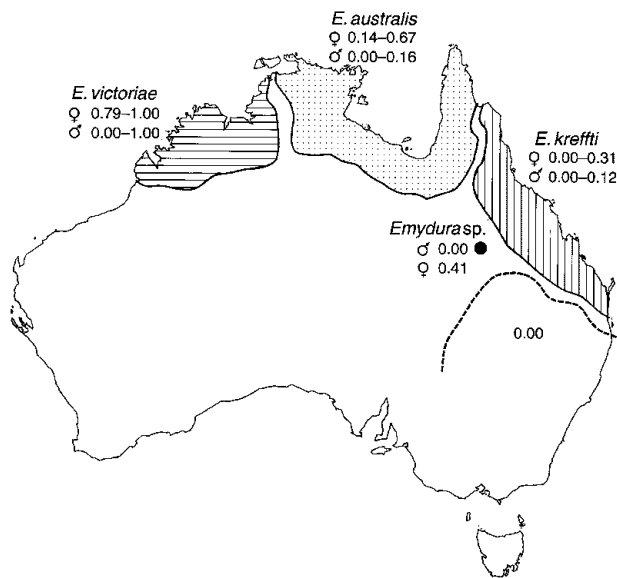


Figure 21.3 Distribution of *Emydura victoriae*, *E. australis*, *E. krefftii*, *E. macquarii* and a distinctive, unnamed species of the Cooper's Creek drainage, illustrating the percentage frequencies of megacephalic adults in various subpopulations. The broken line indicates the southern limit of megacephaly, which includes the entire range of *E. macquarii* and several distinctive coastal populations in southeastern Australia. (From Legler unpub. data) [W. Mumford]

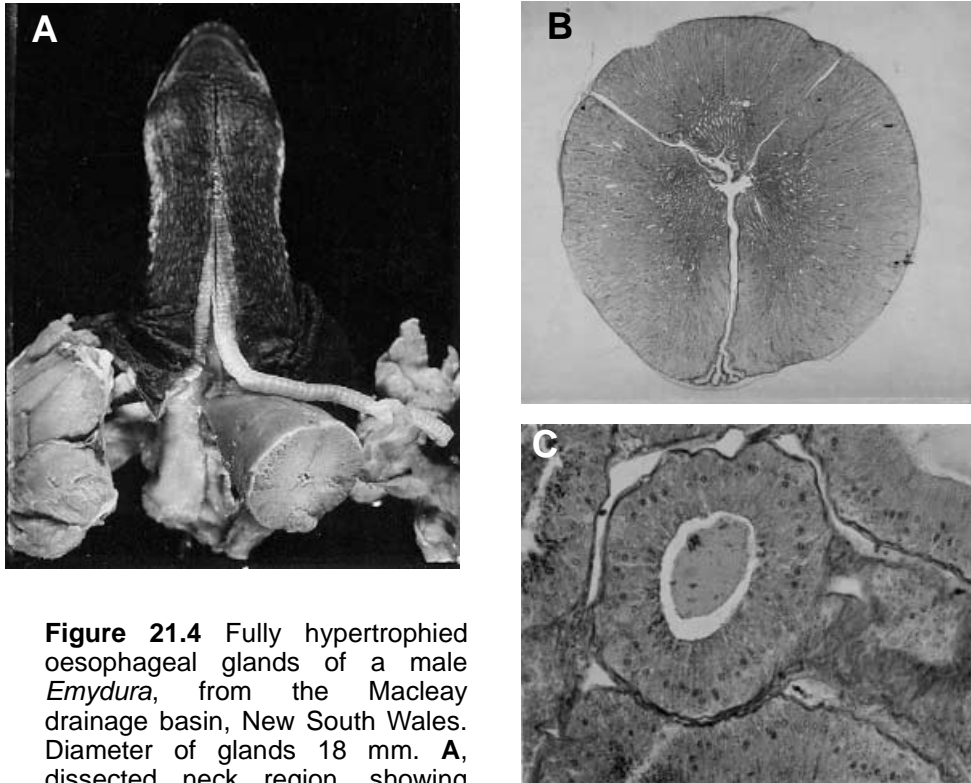


Figure 21.4 Fully hypertrophied oesophageal glands of a male *Emydura*, from the Macleay drainage basin, New South Wales. Diameter of glands 18 mm. **A**, dissected neck region, showing transverse section of the exposed oesophagus. Pale tissues on either side are muscles of the axillary region; **B**, transverse section through oesophagus, showing the single dorsal lobe, two lateral lobes and compressed oesophageal lumen. Collecting ducts from the glands converge on the lumen at the apex of each lobe. The stretched *tunica muscularis* and *tunica externa* are barely visible on the oesophageal periphery. H&E stain; **C**, transverse section of a single secretory tube. H&E stain.

[Photos ©J. Legler]

The oesophagus is normally regarded only as a tube of transmission in chelonians. However, large intrinsic glands are present in the submucosa of the cardiac oesophagus in all Australian chelids studied so far (Hoffmann 1890; Legler pers. obs.). The glands are present in various forms and sizes in *Chelus fimbriatus*, in several emydids and in both families of marine turtles (Hoffmann 1890). They seem to be homologous with the deep oesophageal glands of mammals (Bloom & Fawcett 1975).

At maximal development in *Emydura* the glands swell the oesophagus to the diameter of the neck and compress its lumen to a narrow vertical slit, though eating continues during this period. The oesophageal enlargement is a cylinder tapered at each end with visible and palpable longitudinal lobes. It lies immediately dorsal to the trachea. Most of the enlargement lies anterior to the bifurcation of the trachea and all of it lies within the confines of the shell (Fig. 21.4).

In *Emydura*, *Elseya latisternum* and *Elseya dentata* the glandular tissue forms three longitudinal lobes—a dorsal lobe and a lateral lobe on each side (Fig. 21.4A, B). The trachea usually indents the ventral oesophageal wall between the two lateral lobes. The internal surface of each lobe bears a longitudinal series of approximately 25 clusters of pores. Most observations have been made on eastern *Emydura*. The lateral lobes are subdivided in some genera. There are five lobes in *Chelodina longicollis* and seven in *Chelodina rugosa* and *Pseudemydura umbrina*.

The glands are of the branched tubular type and drain to longitudinal collecting ducts which parallel the pores (Fig. 21.4B, C). Unstratified columnar epithelium lines all parts of the system and is the only layer in which the glands are convoluted. In more peripheral parts of the system, the underlying stratified epithelium seems to be non-secretory. The columnar cells have a distinct nucleus and secretory granules. The secretory granules accept an Azocarmine stain and appear to be eosinophilic. At full development the glands stretch the *tunica muscularis* of the oesophagus virtually beyond recognition as smooth muscle (Fig. 21.4B). The secretion is brownish, odourless, tasteless and has no noticeable effect on humans. Other turtles will eat the glandular tissue and appear not to react to it in any unusual way (Legler pers. obs.). Specimens held for several days in captivity develop white, comma-shaped secretory plugs which can be squeezed from the orifices.

The glands are sexually dimorphic and seasonal in their development in the few species studied. Glandular hypertrophy has been observed only in adult males. Homologues of the gland are evident in females and immature stages but only by microscopic examination. Development of esophageal glands complements the gonadal cycle. They are largest at the beginning of the breeding season when testes are smallest and wane to minimal size by January when testes are largest and most active.

Locomotion

Aquatic turtles must leave the water to nest. Usually this involves only a short round trip from water to land, and aquatic turtles are rarely seen on land. Terrestrial locomotion in Australian chelids resembles that of most aquatic cryptodires, and is a slow, deliberate trotlike gait in which the contralateral front and hind limbs propel, while the other two recover for the next stroke (Walker 1973, 1979; Zug 1971).

Thermoregulation

Australian chelids thermoregulate primarily by basking, either whilst floating at the water's surface, or on solid substrata. During aquatic basking, turtles float near to the surface for extended intervals, with the snout and sometimes the top of the carapace exposed and the rest of the body submerged (Chessman 1987). The limbs are usually spread and a slow, paddling action is common. The turtles are presumably taking advantage of direct exposure to solar radiation in addition to conductive uptake of heat from the warm surface layers of the water.

Basking out of water is a common activity among shortnecked species of *Emydura* and *Elseya*, but rarely observed in the *Chelodina* (Webb 1978). During aerial basking, the turtles climb from the water onto the shore, exposed banks, logs and tree roots to expose their bodies to the sun (Chessman 1987). Typically the legs are spread and the head and neck are extended upward. In the latter stages of basking, tears may be wiped over the head with the forelimbs, or the animal may dip its forefeet into the water then wipe them over the head (Webb 1978). The head, neck and limbs may be withdrawn periodically beneath the carapace and the animal may gape.

These behaviours have led to the suggestion that the turtles experience discomfort during the latter stages of basking, but persist with the activity so as to raise body core temperatures even though temperatures of the extremities may be uncomfortable. Elevated core temperatures are probably important for rapid and effective digestion, especially in omnivorous species, though other functions of basking have been suggested (Neill & Allen 1954; Boyer 1965; Pritchard & Greenwood 1968; Chessman 1987).

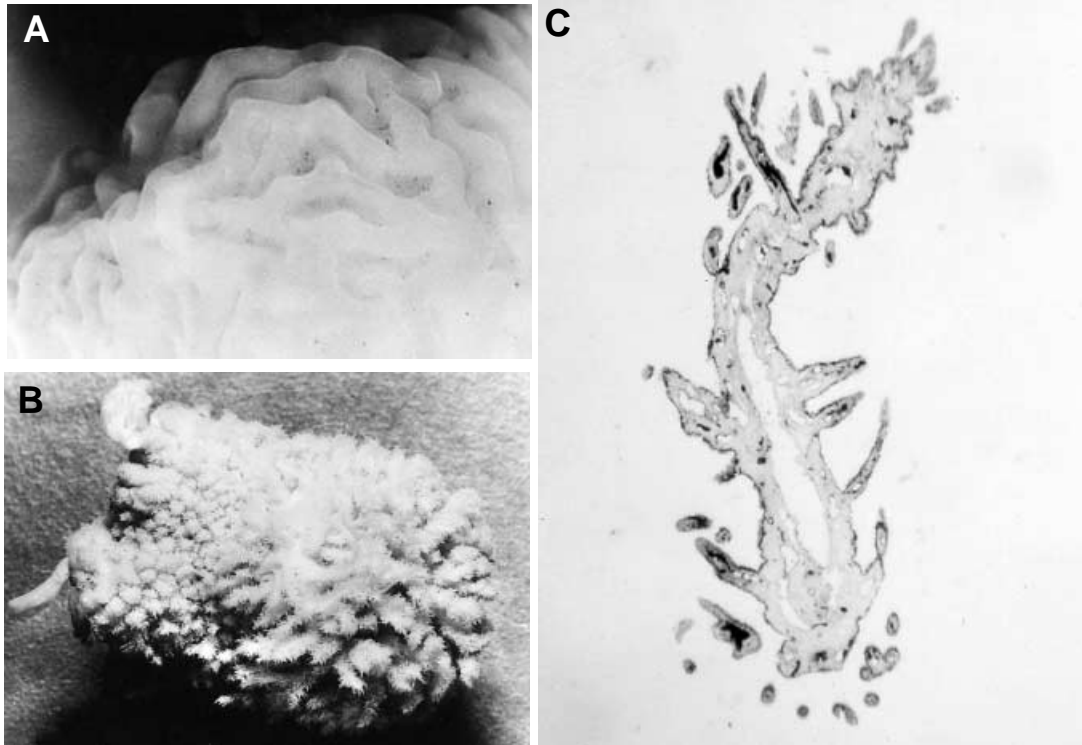


Figure 21.5 Structure of cloacal bursa lining. **A**, *Chelodina expansa*, showing series of simple rugosities in the lining; **B**, the lining of *Rheodytes leukops* is covered with branched papillae. The longest of these were ≈ 15 mm before fixation; **C**, longitudinal section through a single branched papilla of *Rheodytes leukops*. The central lumen, and blackened lumina in the bases of the branches are vascular. Blackened capillary networks are discernible just beneath the epithelial covering of the papilla. Smooth muscle occurs in the main walls of the central stem. [Photos ©J. Legler]

Respiration

All Australian chelids have functional lungs of similar eight-lobed structure, that are much like those of generalised cryptodires (see Chapter 16). All can rely indefinitely on the lungs for respiratory function where air breathing is possible. Observations of captive shortnecked chelids (except *Rheodytes*) show a rapid ventilation of lungs during the first few seconds at the surface, as evidenced by the rise and fall of the body in the water. Muscular activity associated with this behaviour has not been analyzed, but movements of both inguinal pocket and anterior limbs have been noted (Legler pers. obs).

All chelids can also augment pulmonary respiration with gaseous exchanges through accessory respiratory structures. These consist of the buccal and pharyngeal mucosae and the cloacal bursae. Buccopharyngeal respiration is considered in Chapter 16.

Cloacal bursae have a vascular lining and the degree of respiratory exchange that can take place is chiefly a surface phenomenon. Surface area is increased by modifications of the lining. The simplest bursae in Australian chelids have a rugose lining (*Chelodina* of both groups, *Pseudemydura*, and some *Emydura*). Most *Emydura* and *Elseya latisternum* have a rugose lining with elongate papillae only near the orifice. The bursae of *Elseya dentata* are completely lined with elongated ribbonlike papillae, each of which may bifurcate several times. Shortneck alpha has a dense aggregation of flattened papillae near the bursal orifices and is structurally intermediate between *Elseya dentata* and the genera which are only partly papillose.

Cloacal bursae reach a quintessence of development in *Rheodytes*. The volume of a relaxed bursal sac equals that of a lung (measured by filling with water) and the entire bursa is lined with highly vascular, cylindrical papillae which have multiple branches. The papillae are richly vascularised with small, spirally arranged blood vessels and capillaries. Bursae are lined with non-ciliated, pseudostratified columnar epithelium. The apices of these cells stain densely with Alcian blue, but no specialised mucus cells occur. There are large numbers of eosinophilic granulocytes and lymphoid nodules.

Nielsen & Legler (unpub. data) present approximate figures for internal surface area of cloacal bursae in terms of increase in surface area over a theoretical smooth area. A value of 2.5 (for example, *Chelodina expansa*) means that the topography of the mucosal lining increases the surface area by 2.5 times that of a smooth area. Surface increase values for Australian chelids range from 1.4 to 16.1. In *Chelodina* (both groups), *Pseudemydura*, *Emydura* and the *Elseya latisternum* group, the figures vary from 1.4 to 6.2, but average between 3.5 and 4. The upper range is represented by the *Elseya dentata* group (10.0) and by *Rheodytes* (16.1).

In general, the physical diffusional barrier decreases as surface area increases. At its extreme, in *Rheodytes* this barrier consists of the endothelium of a blood capillary and as few as two epithelial cells. Papillae contain smooth muscle, suggesting that flow of blood into a papilla can be regulated. This smooth muscle contracts on fixation, and greatly reduces the length of the principal papillae. The bursal wall has an intrinsic *tunica muscularis* of at least two layers, in which contractile units are orientated almost perpendicular to one another.

All Australian chelids can acquire oxygen, and probably dispose of carbon dioxide, via the cloacal bursae. Captive *Rheodytes* seldom breathe air and we have never observed heads at the surface in the wild. It has been demonstrated that captive animals diving voluntarily can obtain all of their necessary oxygen from the bursae (Gatten & Legler unpub. data). *Rheodytes* has seemingly achieved the greatest emancipation from air breathing of any aquatic chelonian.

Excretion and Osmoregulation

Burbidge (1967) compared the physiology of two chelids in south-western Australia. *Chelodina steindachneri* occurs in temporary water in severe desert, and *Chelodina oblonga* spends most of the year in permanent fresh water. The former is apparently adapted to a desert environment; it has a lower desiccation rate, increased ability to store water using cloacal bursae and an enlarged urinary bladder. It has the ability to convert ammonia to urates more effectively than *C. oblonga*, is able to maintain blood volume during dehydration, and has a higher critical thermal maximum.

Sense Organs and Nervous System

Australian chelids are well-endowed with a variety of integumentary organs on the head and neck, which are thought to function as mechanoreceptors (see Chapter 16). The nictitating membrane is absent or vestigial in all Australian chelids. Its absence is probably a derived condition (Legler & Cann 1980; Legler & Bruno unpub. data; Legler pers. obs.). Most Australian chelids have a translucent to transparent lower eyelid, through which the turtle's eye is visible. Brief mention of eyelid translucency was made by Walls (1942) and Gadow (1901).

Eyelid translucency occurs to a variable extent throughout the order Chelonia but tends to be greater in taxa that lack a nictitating membrane. The lower eyelids of young *Chelodina* of both groups and various shortnecked chelids can be virtually transparent. The transparency lessens with age but usually at least

some detail of the eyeball can be discerned. Certainly perception of light is proportional to translucency, and probably an image can be formed in instances of transparency without opening the eye. Translucent eyelids may therefore serve in lieu of nictitating membranes. Captive chelids close their eyes when they sleep and usually wake when there is movement in front of the aquarium. Integumentary appendages and transparent eyelids are probably adaptations for dark and turbid aquatic environments.

Some chelids can achieve a high degree of stereoptic vision. Members of both groups of *Chelodina* and *Hydromedusa* provide the best examples but there is some stereopsis in *Rheodytes* and other shortnecks. In longnecks, stereopsis facilitates an accurate strike at moving prey.

Secretory Organs

Australian chelids all have well-developed musk glands (see Chapter 16). Captives accustomed to handling usually secrete only under traumatic circumstances. Members of the *Chelodina longicollis* group are perhaps the most odiferous turtles in the world. Each gland may store as much as 2.5 ml of yellowish secretion. This can be squirted for a few centimetres, but usually it is just smeared on the surface of the turtle. While the odour of widely diffused musk is interesting and distinctive, concentrated musk is unique and powerful. It makes some persons nauseous, and may irritate the mucous membranes of the eyes, nose, and pharynx (Legler pers. obs.). Eisner *et al.* (1978) isolated the several compounds from the musk of *Chelodina longicollis*, including oleic acid, linoleic acid, palmitoleic acid, palmitic acid, stearic acid, citronellic acid and beta-ionone.

The function of musk is unknown. Kool (1981) was unable to demonstrate that the musk of *Chelodina longicollis* deterred various native predators. Dorrian & Ehmann (1988) have presented data that suggest that some predators are repulsed by musk from *C. longicollis*. They tested various sympatric freshwater fishes (eels, catfish, murray cod, and lungfish) and freshwater crocodiles with normal food and food to which musk had been applied. Musk-tainted food was avoided by eels and crocodiles.

Dorrian & Ehmann (1988) observed that some *C. longicollis* hatchlings turned on their backs in the presence of eels and also that some orientated the bright orange and black plastron towards a fish while floating at the surface. This sparse information suggests a possible warning colouration/noxious taste combination in young *C. longicollis*.

Reproduction and Development

Egg volume (ml) and egg weight (g) are roughly equal (Legler pers. obs.). Weight is a valuable descriptor for egg size but unfortunately is not available uniformly in studies of turtle eggs. However, the volume can be estimated with reasonable accuracy from egg measurements, using the formula for an elliptical spheroid, where:

$$V(ml) = \frac{4}{3}(\pi B^2 A) \quad \text{where } A = \frac{1}{2} \text{ length and } B = \frac{1}{2} \text{ breadth}$$

Most of the comparative data are presented by Ewert (1979). Egg volume varies substantially within and between Australian chelid species (Table 21.1). The largest eggs are those of *Elseya dentata* and *Chelodina expansa*, which range from 20 to 26 ml, and 12 to 20 ml, respectively. The smallest Australian chelid eggs are those of *Emydura* in several southeast coastal drainage basins (3.75 to 5.3 ml) and of *Chelodina longicollis* (4.0 to 6.7 ml).

Table 21.1 Egg size and weight (mean \pm one standard deviation and sample size) for the eight genera or generic groups (indicated by parentheses) of Australian chelid turtles. Length and breadth are simply the largest and smallest dimensions of each egg.

Genera	Length (mm)		Breadth (mm)		Weight (g)	
	Mean \pm SD	N	Mean \pm SD	N	Mean \pm SD	N
<i>Chelodina (expansa)</i>	39.16 \pm 3.40	304	27.51 \pm 2.41	304	17.08 \pm 3.46	169
<i>Chelodina (longicollis)</i>	30.87 \pm 2.88	282	20.00 \pm 1.86	282	6.65 \pm 1.47	57
<i>Elseya (dentata)</i>	50.21 \pm 2.14	72	28.84 \pm 1.75	72	24.49 \pm 4.22	39
<i>Elseya (latisternum)</i>	33.06 \pm 2.76	300	21.55 \pm 1.55	300	9.41 \pm 1.84	194
Shortneck Alpha	34.20 \pm 1.26	120	22.40 \pm 0.68	120	10.10 \pm 0.72	119
<i>Rheodytes</i>	29.37 \pm 1.51	234	21.04 \pm 0.80	234	7.40 \pm 0.89	208
<i>Emydura</i>	34.06 \pm 3.06	127 8	19.96 \pm 1.65	127 9	8.66 \pm 2.29	489
<i>Pseudemydura</i>	36.64 \pm 1.43	8	19.70 \pm 0.51	8	8.47 \pm 0.35	3

Egg shape can be expressed simply as W/L. The eggs of most chelonians are ellipsoidal spheroids (0.5 to 0.7). The eggs of some populations of *Chelodina rugosa* are closest to spherical (0.809 to 0.858) of the Australian Chelidae.

Hatchling sizes and weights for seven Australian chelid genera are summarised in Table 21.2. There is a general direct correlation of hatchling size with egg size in all turtles (see Ewert 1979 for comparative data).

Table 21.2 Selected data on carapace length and weight of hatchling Australian chelid turtles. Mean, one standard deviation and sample size (N) are given for each datum. All hatchlings were measured and weighed between 3 and 14 days of age, which avoided anomalous measurements caused by shell distortion immediately after hatching and precluded most early growth.

Species	Length (mm)		Weight (g)	
	Mean \pm SD	N	Mean \pm SD	N
<i>Chelonia expansa</i>	35.3 \pm 4.9	3	8.6 \pm 1.1	4
<i>Chelodina longicollis</i>	30.0 \pm 1.7	87	4.6 \pm 0.5	83
<i>Elseya dentata</i>	46.8 \pm 0.8	21	14.8 \pm 0.9	21
<i>Elseya latisternum</i>	31.8 \pm 2.1	32	5.1 \pm 1.0	8
Shortneck Alpha	34.8	4	–	–
<i>Rheodytes leukops</i>	29.3 \pm 1.6	20	4.3 \pm 0.5	24
<i>Emydura victoriae</i>	32.6 \pm 0.7	15	5.1 \pm 0.3	15
<i>Emydura australis</i>	32.7 \pm 1.7	22	5.6 \pm 0.6	35
<i>Emydura krefftii</i>	29.8 \pm 2.4	66	4.1 \pm 0.7	60
<i>Emydura macleay</i>	26.6 \pm 3.0	48	3.6 \pm 0.8	46
<i>Emydura macquarii</i>	30.1 \pm 0.6	10	5.4 \pm 0.6	7

Incubation times in the laboratory for six genera are summarised in Table 21.3. The longest incubation times are those of those of *Elseya dentata* and *Chelodina expansa*. Legler (1985) demonstrated that incubation time at a given temperature (30°C) is inversely related to southern latitude in wide ranging taxa (*Emydura* sp. and *Elseya latisternum*). Ewert (1985) presents the most comprehensive comparative data on incubation times at controlled temperature. Australian chelids studied to date lack temperature dependent sex determination (Bull, Legler & Vogt 1985; Georges 1988a; Thompson 1988; Palmer-Allen, Beynon & Georges 1991).

Table 21.3 Incubation time (in days) to pipping for genera or generic groups (indicated by parentheses) of Australian chelid turtles, at controlled laboratory temperatures. Data derived from Legler (1985) and Ewert (1985) for *C. longicollis* and *E. latisternum* at 25°. N represents number of eggs for *Chelodina expansa* and number of clutches for all other taxa.

Genera	Incubation temperature (°C)	Mean ± SD (days)	N
<i>Chelodina (expansa)</i>	30°	126 ± 2.0	3
	28°	150 ± 17.4	26
	25°	163 ± 16.8	22
<i>Chelodina (longicollis)</i>	30°	69 ± 4.7	8
	28°	65 ± 0.0	1
	25°	81 ± 0.0	3
<i>Elseya (dentata)</i>	30°	77 ± 0.0	2
	28°	85 ± 0.0	1
<i>Elseya (latisternum)</i>	30°	59 ± 4.8	15
	28°	56 ± 0.4	2
	25°	75 ± 0.0	3
<i>Emydura</i>	30°	46.6 ± 4.4	54
	28°	51.8 ± 0.9	6
	25°	72.8 ± 1.6	9
Shortneck Alpha	–	56	–
<i>Rheodytes</i>	30°	46 ± 2.2	10

NATURAL HISTORY

Life History

Two broad reproductive patterns can be identified among the Australian Chelidae. Species of the temperate zone commonly nest in spring and hatch in summer, while patterns of tropical zone chelids can be more variable.

The most common reproductive pattern among Australian temperate zone chelids is one of spring nesting and summer hatching. This pattern is exhibited by *Emydura krefftii* (Georges 1983), *E. macquarii* (Chessman 1978), *Elseya latisternum* (Legler 1985), *Rheodytes leukops* (Legler & Cann 1980), shortneck alpha (Cann unpub. data) and *Chelodina longicollis* (Parmenter 1985). Variations on this theme occur with latitude and altitude. In the more southern

populations, ovarian development and mating activity ceases in winter. The nesting period may begin as early as August (Georges 1982a) in warmer areas and as late as November in colder areas (Vestjens 1969). For each of the above species, multiple clutching is common throughout their ranges (Legler 1981), with the exception of populations of *Chelodina longicollis* located close to the altitudinal limit of their range (Vestjens 1969).

The western swamp turtle, *Pseudemydura umbrina*, must contend with both cold winter temperatures and summer drought near Perth, Western Australia. It inhabits ephemeral clay swamps which are dry for six to nine months of the year, depending upon rainfall (Burbidge 1981). The turtles spend the dry summer period in refugia beneath leaf litter, under fallen branches or in holes in the ground. Ovarian development begins while the turtles are aestivating, and continues throughout winter and spring (Kuchling & DeJose 1989). Ovulation is apparently stimulated by the spring flush in food availability, in the short period when temperatures and availability of free-standing water allow the accumulation of reserves for breeding and aestivation. The turtles copulate when active during winter and spring, and females nest during the early summer, not long before they must aestivate once more. Hatchlings emerge in the late autumn and early winter some 180 days after laying, an event timed to coincide with the winter season rains (Burbidge 1981).

Even greater variation from the typical temperate zone pattern is shown by *Chelodina expansa*, which nests in the autumn and winter (Goode & Russell 1968; Georges 1984; Legler 1985). After an exceptionally long incubation period, the hatchlings emerge in the following autumn. Little development of the eggs can be expected in winter, and overwintering of eggs no doubt contributes substantially to the incubation period of the species. However, eggs of *C. expansa* laid in the autumn still hatch some months after those of *Emydura macquarii* and *C. longicollis* laid in the following spring (Goode 1967). There may be some form of delayed or retarded development in *C. expansa* (Goode & Russell 1968).

The reproductive pattern of *C. expansa* is a curious one for the temperate zones, and more in keeping with the tropical strategy of coping with the seasonal cycles of wet and dry rather than the temperate cycles of hot and cold (Georges 1984; Legler 1985). It may well be that *C. expansa* originated in tropical Australia and that it is a recent arrival in the temperate zones, after a rapid spread through the Murray-Darling system. At the same time, the species may have retained many of the features of a tropical reproductive strategy (Legler 1985).

The need for flexibility in the reproductive patterns of tropical zone chelids is evident in the complex nesting habits of the northern longnecked turtle, *Chelodina rugosa* (Kennett, Christian & Pritchard 1993a; Kennett, Georges & Palmer-Allen 1993b). It is found in the extensive network of floodplains covering thousands of square kilometres (Finlayson, Bailey, Freeland & Fleming 1988), over which rapidly fluctuating water levels limit the availability of relatively dry ground suitable for nesting. In the dry season, the turtles survive by burying in the muddy bottom of the receding waterbody and aestivating underground (Grigg, Johansen, Harlow, Beard & Taplin 1986; Covacevich, Couper, McDonald & Trigger 1990a). If *C. rugosa* has similar preferences to *C. longicollis*, *C. expansa* and other freshwater species for relatively dry nest sites, only a short period would be available for nesting, after the wet season waters have receded but before aestivation becomes necessary.

In itself, this is not an insurmountable problem, as the reproductive cycle could be timed so that nesting coincides with suitable conditions, brief though they might be. *Pseudemydura umbrina* is faced with constraints of similar severity. However, although the wet-dry rainfall cycle occurs reliably each year, there is considerable annual variability in the timing of the onset, the duration, and the

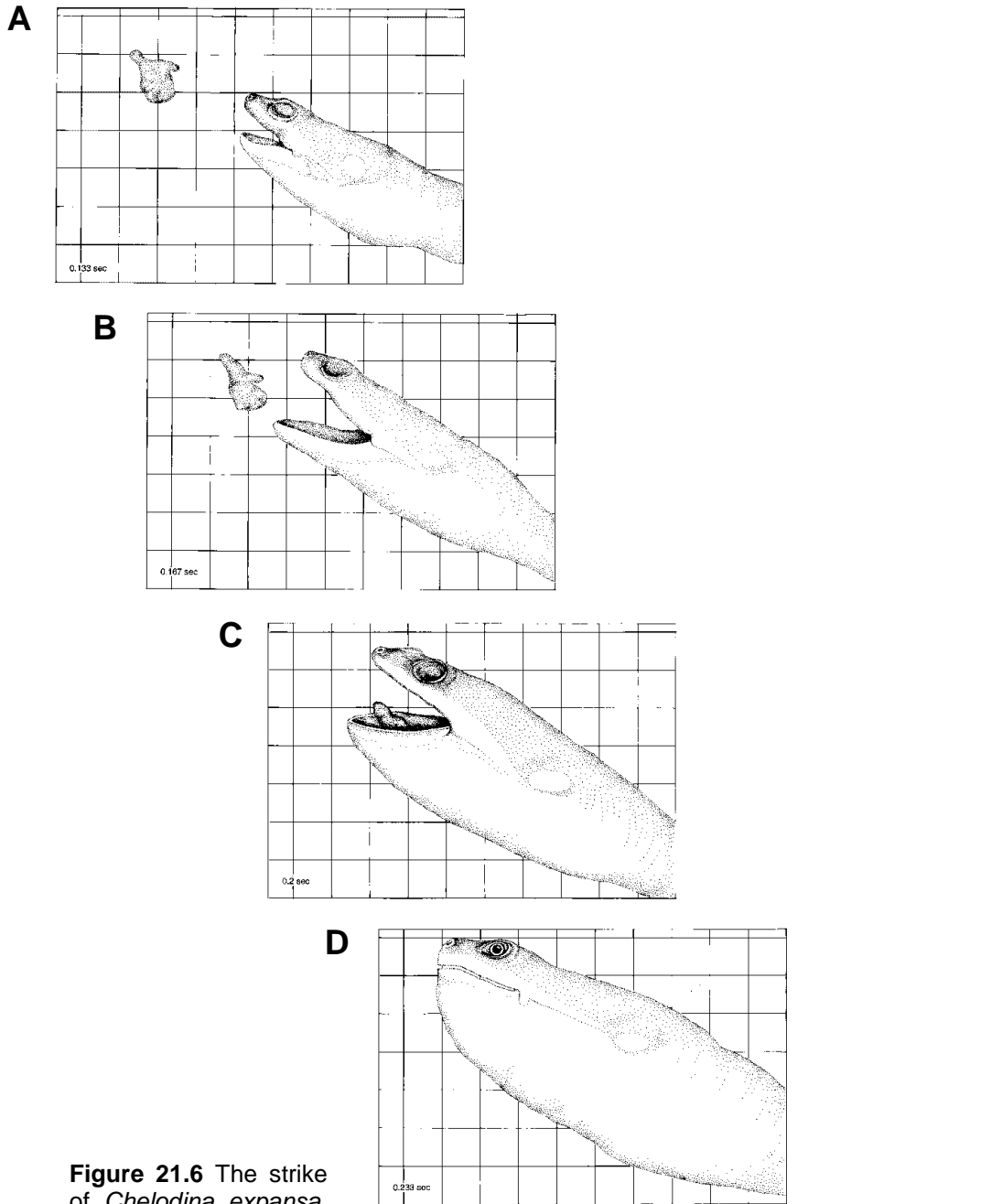
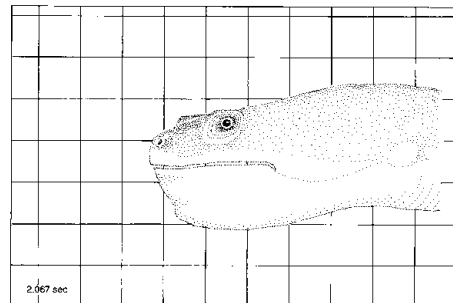


Figure 21.6 The strike of *Chelodina expansa*.

In this experiment, numerals show the time (seconds) elapsed since the bait was dropped into the water. **A**, mouth opening rapidly, hyoid apparatus drawn slightly ventrad, and rapid forward thrust continues, eyes closed; **B**, increasing volume of mouth produces significant negative pressure and food moves toward mouth, hyoid still not fully abducted, eyes closed; **C**, rapid forward strike terminates and extreme hyoid abduction begins, food now in buccal cavity, eyes closed and seemingly retracted; **D**, strike continues to apogee, mouth closes and hyoid maximally abducted, neck retraction follows immediately, food now in pharynx, eyes open; **E**, head tilted back to original position during rapid withdrawal, mouth closed and hyoid expansion maintained, food in oesophagus and swallowing movements evident. (From video by J. Legler)

E



[T. Wright]

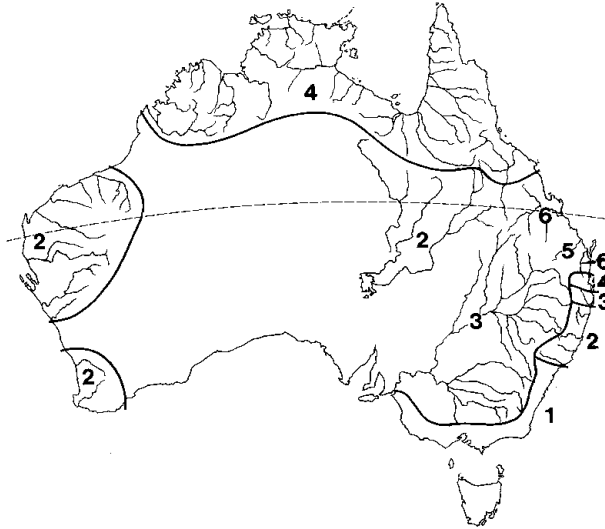


Figure 21.7 Diversity of Australian Chelidae expressed as number of genera in particular regions. Highest diversity occurs in the Fitzroy and Mary drainages of Queensland (four shortnecked, two longnecked genera). Three shortnecked and two longnecked genera occur in the Burnett drainage.

[W. Mumford]

intensity of the wet and dry seasons (Taylor & Tulloch 1985). The combination of the short period suitable for nesting and extreme unpredictability as to when that period will occur would make it very difficult for *C. rugosa* to persist in the floodplains if its nesting requirements are similar to those of other freshwater turtles.

Instead, *C. rugosa* appears to lay its eggs under water or in a saturated soils (Kennett *et al.* 1993a). Development is arrested presumably because of the hypoxic conditions resulting from immersion (Kennett *et al.* 1993b). By nesting underwater, inability to predict the timing of the wet-dry transition is obviated and a more protracted nesting period is made possible. When the ground eventually dries and oxygen reaches the eggs, conditions presumably become suitable for incubation and development proceeds. The incubation period is such that the eggs hatch in time for the onset of the torrential rains of the wet season that follows.

Chelodina novaeguineae also occupies ephemeral waterbodies of the wet-dry tropics, but moves overland to more permanent waters when the floodplain recedes. If permanent water is not available, it will aestivate beneath litter, in burrows constructed by other animals or in flood crevasses and channels (Covacevich *et al.* 1990a; Kennett, Georges, Thomas & Georges 1992). In the Northern Territory, the species nests from April to July (Kennett *et al.* 1992). Apparently breeding is opportunistic, and a protracted nesting season is possible only for turtles successful in finding permanent or semi-permanent water to carry them through the dry season. Such opportunistic nesting has been suggested also for its close relative, *Chelodina steindachneri* (Kuchling 1988).

Elseya dentata occupies permanent water and nests in the early dry season of the Northern Territory and in the winter months in its Queensland range. There are insufficient data on the reproductive biology of this species and many others to speculate on the adaptive significance of the timing of egg laying and hatching.

Ecology

Recent studies have done much to increase knowledge of the diets of Australian freshwater turtles. Species of the genus *Emydura* are typically omnivorous. A broad range of food types is eaten, such as filamentous algae, periphyton, sponges, aquatic macrophytes and macro-invertebrates, terrestrial insects which fall or are blown onto the water, and carrion (Legler 1976; Georges 1982b; Chessman 1986). Highly mobile species such as fish appear to be unavailable to these species except as carrion. The diet of *Emydura* provides much scope for opportunism, and may vary considerably from place to place and with season in response to local differences in the availability of food resources (Chessman 1986). Small juveniles of *Emydura krefftii* (Fraser Island) are principally carnivorous, and become omnivorous as they age (Georges 1982b). The diet of *Emydura macquarii* in the Murray Valley shifts from periphyton to greater reliance on plant material and carrion as the turtles age (Chessman 1986). Variation in diet with size and age can be explained in terms of energetic efficiency and the fact that more robust foods become available to them, as the turtles grow in size and strength.

Chelodina longicollis has a diverse and opportunistic diet that differs little in composition from that of available prey (Parmenter 1976; Chessman 1978; Georges *et al.* 1986). The shortnecked *Pseudemydura umbrina* and *Rheodytes leukops* are carnivorous. *Pseudemydura* will only take live prey, including aquatic crustacea and insects, small tadpoles and an aquatic earthworm *Eodrillus cornigravei* (Burbidge 1981). *Rheodytes leukops* feeds upon insect larvae and freshwater sponges (Legler & Cann 1980). These species lack the specialised morphological adaptations of *Chelodina* and other longnecked chelid turtles (Parmenter 1976; Legler 1978; Pritchard 1984) necessary for securing rapid prey.

Most shortnecked chelids secure their food by active foraging, which consists of slow prowling on the bottom. Neustophagia has been noted (Legler 1976). Food is ingested by inertial feeding movements combined with some suck and gape feeding. Sensory cues in locating edible items seem to be tactile, visual and olfactory. Typical olfactory inspection involves pressing the snout against the object with the neck extended and the head cocked slightly forward. Foraging turtles react to and alter course for movements detected at a distance. Chelids rarely actively pursue prey under water. The jaws of shortnecks are sufficiently powerful to hold objects firmly in the mouth while tearing at them with the foreclaws.

The longnecked chelids combine foraging with a sit-and-wait ambush feeding strategy. All longnecks are capable of executing an accurate strike at a prey target, which may be moving, and engulfing it by suck and gape ingestion. Members of the *Chelodina expansa* group rely more on ambush feeding than members of the *C. longicollis* group. *Chelodina expansa* is sometimes found buried in silt with only the tip of the snout visible (Legler & Cann pers. obs.). It is not known whether this is simple concealment or a part of sit-and-wait predation.

Before striking, *C. expansa* remains virtually motionless and is usually firmly supported on the bottom or in a tangle of underwater brush (Legler 1978). The head and flexed neck are gradually oriented toward the prey. The strike is sudden and explosive and recovery to the flexed-neck position follows immediately. As the head nears the target, the mouth opens rapidly and the hyoid apparatus is depressed, creating an increased volume and negative pressure. The prey target is brought into the mouth with a rush of water. The mouth quickly closes and at least some excess water is expelled by hyoid movements before swallowing begins.

The mode of feeding and associated apparatus preclude chelid turtles from feeding out of water, but within these constraints, dependence on water varies considerably among species. Some require permanent water and typically leave it only to bask or nest (*Emydura* spp.). Others occupy seasonally ephemeral waters and survive dry periods by migrating overland to permanent water refugia (*Chelodina longicollis*, *Elseya latisternum*), by aestivating beneath the muddy bottoms of their once watery abodes (*Chelodina rugosa*) or beneath litter in surrounding terrestrial habitats (*Chelodina novaeguineae*, *C. longicollis*).

Six species of freshwater turtle occur in the Fitzroy-Dawson drainage of Queensland (Legler & Cann 1980). *Rheodytes leukops* prefers fast flowing water and riffle, where it can be found in microsympatry with *Emydura krefftii* and *Elseya dentata*. *Rheodytes leukops* is numerically dominant in riffle. In the deep, slow flowing pools of the main channel, *Emydura krefftii* is numerically dominant, but found together with *Elseya dentata*, *Chelodina expansa* and the occasional *Rheodytes leukops*. *Elseya latisternum* is abundant only in small tributaries off the main channel, and *Chelodina longicollis* is restricted to backwaters. These habitat differences, together with variation in diet, presumably allow these species to co-exist in the same drainage.

In the Murray valley, *Emydura macquarii* and *Chelodina expansa* live in deep, slow flowing stretches of the main river channel and in deep river backwaters and oxbows adjacent to the river (Chessman 1988). *Emydura macquarii* dominates in lentic environments. The third species, *Chelodina longicollis*, is the most common species in oxbow lakes, anabranches and ephemeral ponds, rain pools and swamps.

In the tropics, species in the genera *Emydura* and *Elseya* occupy permanent water only, as their abilities to aestivate or migrate overland are limited. *Emydura victoriae*, *Emydura* sp. aff. *victoriae* (formerly *Emydura australis*), and *Elseya dentata* are riverine species, but their distribution within a drainage may be very patchy. In the dry season, *Emydura victoriae* prefers smaller waterholes and tends to congregate in smaller tributaries than *Elseya dentata*, which predominates in the main channel and larger waterholes (Coventry & Tanner 1973; Georges & Kennett 1989). In the Daly River, which flows continuously in all months, turtle diversity reaches a peak at Policeman's Crossing where the large pools are shared by *Elseya dentata*, *Emydura victoriae* (red face), *Emydura* sp. aff. *victoriae* (yellow face) and *Chelodina rugosa* (Kennett & Georges 1989). A third species, *Emydura* sp. aff. *subglobosa* occurs in the upper reaches of the Daly drainage, above the escarpment. Further to the east in Arnhem Land, *Elseya latisternum* and a species of *Chelodina* with close affinities with the lowland *Chelodina rugosa* occur in sandstone billabongs and washpools above the escarpment.

Many species inhabiting ephemeral waters aestivate during dry periods (*Pseudemydura umbrina*, *Chelodina rugosa*, *C. steindachneri*, *C. novaeguineae*) while others rely upon migration to more permanent water during dry spells. *Chelodina longicollis* is capable of terrestrial aestivation (Chessman 1983b), but unlike *P. umbrina* and *C. rugosa*, it occupies ephemeral environments that may dry unpredictably for several consecutive years (Chessman 1978; Kennett & Georges 1990). Physiological studies indicate that prolonged terrestrial aestivation is unlikely in this species (Chessman 1978).

Behaviour

Basking is a major component of daily activity for *Emydura* sp. and *Elseya latisternum*, whereas *Chelodina expansa* and *Chelodina longicollis* bask only occasionally (Webb 1978). The function of basking in turtles has been debated by Neill & Allen (1954), Boyer (1965), Pritchard & Greenwood (1968) and

Chessman (1978). Aerial basking appears to facilitate scute shedding and general epidermal sloughing in aquatic turtles. All *Emydura* shed whole scutes in the manner described by Moll & Legler (1971) for tropical *Pseudemys*.

Shedding of whole scutes has not been observed in adults of either group of *Chelodina*, in the *Elseya dentata* group, or in *Rheodytes*. In *Elseya latisternum* and in shortneck alpha, scutes are shed in fragments or as a result of wear. In *Rheodytes*, the scutes are not as thick as those of other chelids and the outer layer of the scute sloughs away as a pasty substance when the shell is touched.

There seems to be a close association with the almost completely aquatic mode of life, the absence of basking and scute shedding and the occurrence of autogrooming in *Chelodina expansa* and *Rheodytes*. Grooming is common in captive *Rheodytes* and *Chelodina expansa* and serves to remove the cornified layer of the soft skin wherever the head can reach (Legler 1978 pers. obs.).

The mating sequences of *Emydura macquarii*, *Elseya latisternum* and *Chelodina longicollis* have been described by Murphy & Lamoreaux (1978). In *Emydura macquarii* and *Elseya latisternum*, males approach females with a series of head-bobs, which the females reciprocate. The males then engage in cloacal touching, attempt to align their barbels with those of the females, and begin extensive stroking of the females' barbels, snout and orbital region with the forefeet and claws. The female is then mounted from the rear. This sequence has been confirmed for *Emydura krefftii* (Banks 1987a).

Goode (1965) described the nesting behaviour of *Emydura macquarii*. The cavity is dug with the hind limbs and enlarged through the slow process of inserting one leg then the other into the hole. Dirt is extracted with a cupped foot, while the alternate limb bears the animal's weight. The soil is placed to

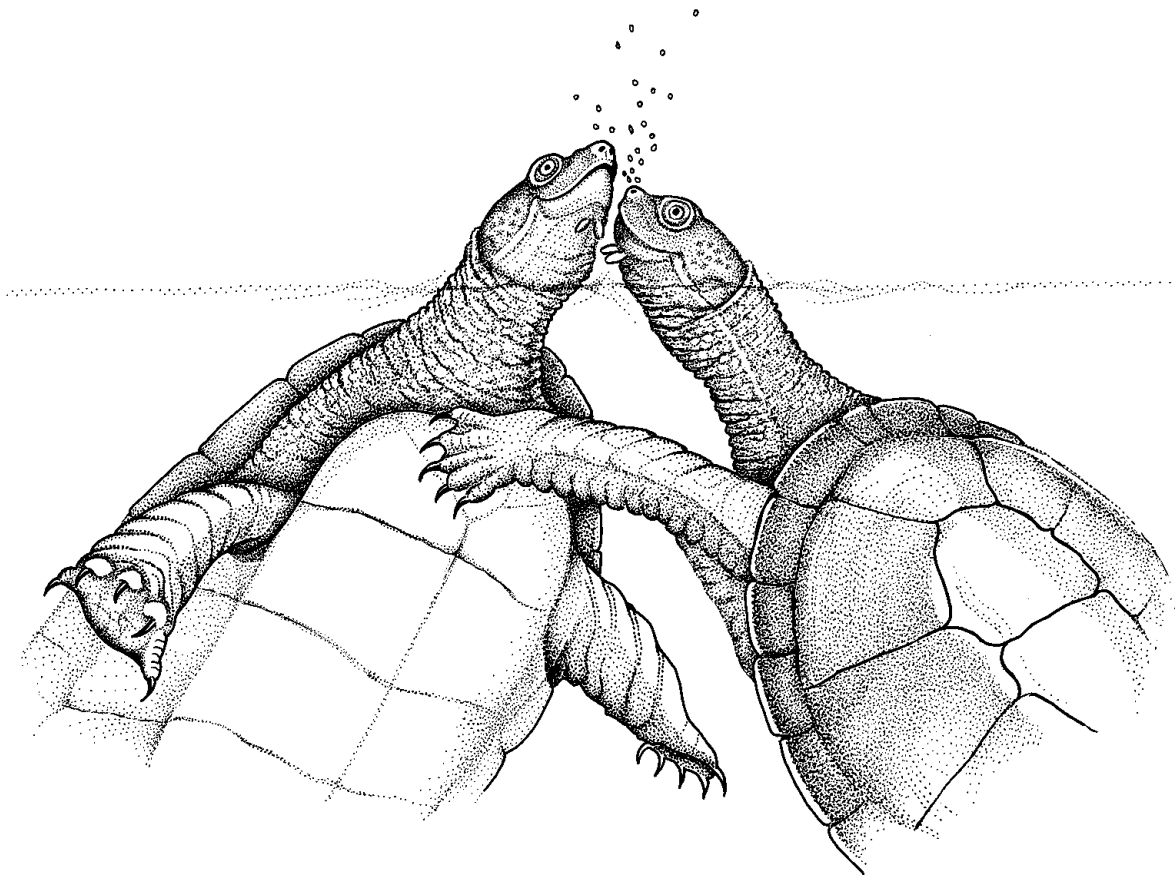


Figure 21.8 Barbel usage in the mating sequence of *Emydura macquarii*.
(After Murphy & Lamoreaux 1978) [T. Wright]

either side and behind the animal. Once the flask-shaped nest chamber is complete the eggs are laid. After each egg is deposited, the hind leg is inserted into the hole to arrange it in position. When laying is completed, the nest cavity is covered. The hind legs are extended until almost at right angles to the spine, the feet are orientated in a backward direction and brought together through an arc, carrying with them the soil from the excavated cavity. This action is repeated until the nest cavity is filled. The turtle then raises itself on all four legs and then drops its shell hard on the ground to compact the soil in the filled nest. This tamping of the soil has been observed also in *Chelodina longicollis* (Vestjens 1969), *C. oblonga* (Clay 1981) and *C. expansa* (Georges pers. obs.).

In the Murray Valley, *Emydura macquarii* tends to nest more frequently in lighter soils, whereas *Chelodina longicollis* and *C. expansa* will nest in any type of soil (Goode & Russell 1968). The latter two species apply copious quantities of cloacal fluid to the soil when constructing their nests (McCooey 1887; Goode & Russell 1968) and *C. longicollis* may 'puddle' its eggs in the mud formed by the cloacal fluids and clay soils. Rain is not necessary for nesting, as *Chelodina novaeguineae* has been observed nesting in the heaviest of clays in the absence of recent rain during the dry season in the Northern Territory, with the aid of cloacal fluids (Georges & Kennett unpub. data; Curtis 1928).

Head-bobbing has been observed in both groups of *Chelodina* (Legler pers. obs.) and is probably a form of communication. Some captives develop the habit and will perform various sequences of rapid head-bobbing in response to a person passing the aquarium or to bobbing motions made with human fingers. Amateur turtle fanciers are very familiar with such behaviour and have observed it in a variety of chelids, chiefly longnecks, but it has never been described or analysed.

Typical defence behaviour out of water consists of tucking in the head and tilting the shell toward the source of danger before turning the body, minimising the exposure of soft parts and maximising exposure of the shell. Defensive snapping and biting are common in shortnecks. Both of the *Elseya* groups, *Emydura*, and shortneck alpha can be savage and can inflict painful wounds. *Rheodytes* seldom bites under any circumstances and, in our own experience, neither group of *Chelodina* bites defensively. Members of the *Chelodina expansa* group often lash the head and neck from side to side in a behaviour that resembles a strike.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

The distribution of Australian chelids is limited by the availability of permanent water or predictably seasonal water. The correlates of this geographic distribution are natural drainage systems. Australia is a relatively dry continent. Total effluent is 345×10^6 megalitres. By comparison, single rivers in other parts of the world discharge almost as much water, for example, 281×10^6 megalitres for the Danube River. Most of Australia's fresh water habitats are in a series of small coastal drainage systems at the periphery of the continent. The Murray-Darling system is the largest external drainage (Anon. 1967; Leeper 1970). Total external drainage is about 47% (by rough estimate) of continental area. The rest is dry by comparison and drainage is internal; water drains to internal basins and/or evaporates. This internal drainage area defines 'The Centre' for purposes of turtles. Turtles occur only in the easternmost part of this internal drainage system, the Cooper's Creek catchment or Lake Eyre drainage. If the Cooper's Creek drainage is included with all other drainage systems in which turtles are known to occur, the rough estimate is maximally 51% of the Australian land mass. Actually, the figure would be much lower because the

upper reaches of many small, well-watered drainage systems are dry much of the time, especially in the north. The *Chelodina expansa* group has the largest distribution of any Australian chelid genus, occurring in most of the external drainage systems and approximately 45% of the continent.

Chelodina longicollis occurs farther south than any other Australian chelid. There are breeding populations at or near the southern tip of Victoria (39°S) and records for King and Flinders Islands in the Bass Strait (Cogger 1979; Iverson 1992). A species of *Emydura* is known from the Miocene of Tasmania (Gaffney 1981, 1991), but no chelid species occur there now. *Emydura macquarii* and *Chelodina expansa* occur in the lower Murray-Darling system at approximately 37°S. *Emydura* (near *signata*) and *Elseya* (near *latisternum*) occur at elevations of about 1000 m on the New England Tableland, equivalent to 34°30' S when corrected for altitude (Legler 1975). Although the extreme southern limits of distribution for Australian chelids may constitute 'harsh' conditions in human or agricultural terms, nowhere do chelids experience what could be termed a severe winter.

Chelids occur commonly on islands near the coasts of Australia and New Guinea, such as for example, Fraser Island, Daru and Stradbroke islands, and islands in the Torres Strait. There is an old record of '*Chelodina longicollis*' on Roti, off the south-western tip of Timor (de Rooij 1915) which has recently been confirmed by Anders Rhodin (pers. comm.) and is currently under study. Thus far there is no evidence that chelids have a natural distribution on oceanic islands but it is possible that they have been introduced in many places, including those mentioned above.

The Fitzroy and Mary drainages of Queensland each support six species of chelids in broad geographic sympatry—two species each of *Chelodina* and *Elseya*, *Emydura* and either *Rheodytes* or shortneck alpha.

Affinities within the Chelidae

Burbidge, Kirsch & Main (1974) made the first attempt to develop a phylogeny for the Australian Chelidae. They undertook a phenetic analysis of morphological and serological data and identified three divergent groups, equally related to each other. These are the species of *Chelodina*, the species of *Emydura/Elseya*, to which Legler & Cann (1980) later added *Rheodytes leukops*, and *Pseudemydura umbrina*. This trichotomy is supported by other studies of morphology (Goode 1967; Gaffney 1977; Legler & Cann 1980), total protein electrophoresis, karyotypes (Bull & Legler 1980) and behaviour (Webb 1978). In his studies of skeletal morphology, Gaffney (1977) refined and extended this phylogeny to incorporate South American forms. From the perspective of Australian forms, Gaffney's phylogeny differed from that of Burbidge *et al.* (1974) in that the divergence of *Pseudemydura umbrina* predated the divergence of *Emydura* and *Elseya* from *Chelodina*.

As chelid turtles are conservative in many morphological features, Georges & Adams (1992) used allozyme electrophoresis as an alternative to traditional morphological approaches to the systematics of the Australian chelids. They added many more species to the phylogenetic tree, some of which are yet to be described. The most striking departure from the phylogeny accepted at the time was the paraphyletic nature of the genus *Elseya*. The closest common ancestor of the living species of *Elseya* has the species of *Emydura* among its descendants. One approach to resolving this paraphyly is to synonymise *Elseya* with *Emydura*, the latter name having precedence, as suggested by McDowell (1983). McDowell's suggestion built upon previous support for the synonymy of the two genera from Gaffney (1977, 1979). Unfortunately, *Rheodytes* and shortneck alpha were not available for study by McDowell. These two monotypic genera could not be placed by the electrophoretic analyses of

Georges & Adams (1992), but several of their analyses placed one or both of these species within the clade containing *Elseya* and *Emydura*. Synonymy of *Elseya* and *Emydura* may have to include the distinctive *Rheodytes* and shortneck alpha, a far less acceptable proposition when genera are erected largely on morphological criteria. Georges & Adams (1992) therefore recommended the preferred option of Legler (1981), who proposed to split the genus *Elseya* into two genera (*Elseya dentata* plus related species, and *Elseya latisternum* plus related species), and of Legler & Cann (1980) who considered that morphological similarities between species in *Elseya*, *Emydura* and *Rheodytes* were sufficient to indicate a common ancestry, but not to warrant lumping of any of the three genera.

Whether or not the Australian and South American chelid faunas each represent monophyletic assemblages is subject to dispute. It is not clear whether the *Elseya–Emydura–Rheodytes*, *Pseudemydura*, *Chelodina* trichotomy arose in Australia independently of lineages in South America. On the basis of a cladistic analysis of skeletal structure, Gaffney (1977) considered the longnecked South American genera *Hydromedusa* and *Chelus* to be the closest relatives of the Australian longnecked *Chelodina*. However, a subsequent analysis by Pritchard (1984) suggested that the similarities in head and neck structure of the South American and Australian longnecked turtles are the result of parallel evolution, in response to a common piscivorous diet. Attempts to relate *Pseudemydura umbrina* to other Australian chelids have failed (Legler 1981), possibly because the monotypic genus has no close relatives in Australia. Gaffney & Meylan (1988) considered *Pseudemydura* so divergent that they suggested placing it in a monotypic subfamily. *Pseudemydura* shares many morphological features with the South American genus *Platemys*, species of which may be the closest living relative of *Pseudemydura* (Legler 1981).

In a non-cladistic analysis using mensural morphological characters, soft anatomy, behaviour and life history, Cann & Legler (1993) place the Australian shortnecked chelids in three distinct groups (*cf.* Legler 1981, 1984, 1989a; Legler & Cann 1980). These are: *Pseudemydura*, which is not closely related to any Australian chelid, and may more closely related to a South American shortneck; *Emydura*; and the ‘*Elseya* complex’, containing the *Elseya dentata* group, the *Elseya latisternum* group, *Rheodytes*, and shortneck alpha.

A multidiscriminate analysis of 39 morphological characters for the *Elseya* complex, including shortneck alpha and *Rheodytes*, showed the four genera of this group clustered almost equidistantly from each other without overlap in a three-dimensional plot, but distantly from all other Australian chelids. Thus the four genera are probably of common origin, and although they differ substantially from each other, are seemingly more closely related to each other than any is to *Emydura*.

Cann & Legler (1993) substantially corroborate the hypotheses of Georges & Adams (1992) on phylogeny and relationships. One of us (JL) however, questions the placement of *Chelodina oblonga* and the genus *Emydura*, and prefers to regard *Emydura* as more distantly related to all members of the *Elseya* complex and to regard *Chelodina oblonga* as a derivative of a *C. rugosa*-like ancestral stock that gave rise to other extant members of the genus. This approach to the genus *Chelodina* has a precedent in the division of *Chelodina*, by Burbidge *et al.* (1974), into the *longicollis* group, the *expansa* group, and a third group comprising *C. oblonga*.

Fossil Record

There are reports of fossil chelid turtles from Europe, North Africa and India, but the diagnoses of these fossils as chelids have been disputed (Williams 1953). There is no well-accepted evidence that fossil chelids occur outside the range of extant taxa (Pritchard 1979b; Pritchard & Trebbau 1984; see also Chapter 18). As such, chelid turtles are the only reptile group with clear Gondwanan origins.