FAUNA *of* AUSTRALIA

18. BIOGEOGRAPHY AND PHYLOGENY OF THE CHELONIA

John M. Legler & Arthur Georges

The earliest known turtles, *Proganochelys*, had unspecialised cervical vertebrae (Gaffney 1990) and presumably were unable to retract the head beneath the shell. This innovation was later achieved in two ways. One lineage, the suborder Cryptodira, evolved a mechanism whereby the neck flexes in the vertical plane when retracted beneath the shell. In these forms, the head is still pointed in a forward direction when retracted. The suborder comprises nine extant families, and most of the living species. The majority occur in the temperate region of the northern hemisphere, and in the tropics. The only Australian representatives are the marine turtles, families Cheloniidae and Dermochelyidae, and the freshwater pig-nosed turtle, *Carettochelys insculpta*.

In the second lineage, the suborder Pleurodira, the neck flexes in the horizontal plane so that the head points towards the left or right when retracted. The suborder comprises two families. The Pelomedusidae includes five genera *Erymnochelys*, *Pelomedusa*, *Peltocephalus*, *Pelusios* and *Podocnemis*. Though presently restricted to the South American and African continents, they were once widely distributed across the northern hemisphere. The Chelidae includes five genera *Chelodina*, *Elseya*, *Emydura*, *Pseudemydura* and *Rheodytes* currently found in Australia, New Guinea, the island of Roti (Lesser Sunda Islands, Indonesia), and South America. There are reports of fossil chelid turtles from Europe, North Africa and India, but the diagnosis of these fossils as chelids is either incorrect or has been brought into serious question (Williams 1953, 1954b). There is no well accepted evidence that fossil chelids occur outside the range of extant taxa (Pritchard 1979b; Pritchard & Trebbau 1984). As such, chelid turtles are the only reptile group with clear Gondwanan origins.

DISTRIBUTION

Freshwater turtles are cosmopolitan with breeding populations occurring in suitable habitats in temperate and tropical regions of major continents, large islands, and some oceanic islands. There are epicentres of diversity in the eastern United States of America and southern Asia.

The five extant genera of marine turtles have worldwide distributions in tropical and temperate waters, except for *Natator depressus* which is endemic to the Australian region.

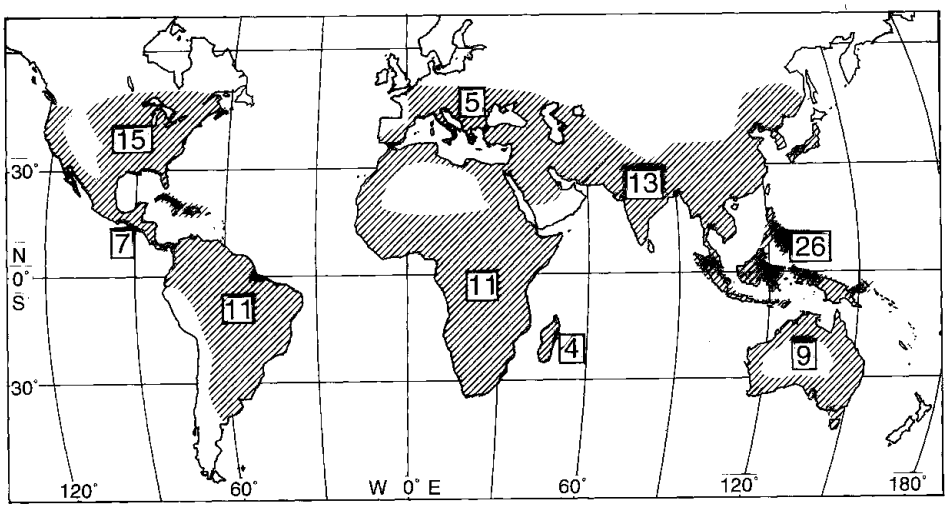


Figure 18.1 Worldwide distribution of the freshwater chelonians. Numbers of genera are indicated for each of eight regions: North, Central and South America, sub-saharan Africa, with Madagascar as a subset, Europe and North Africa, India, South-East Asia, and Australia. [W. Mumford]

Cryptodires are now the only turtles of the Northern Hemisphere, but they occur also in the Southern Hemisphere. Pleurodires now occur only in the Southern Hemisphere. There is a substantial fossil record for pelomedusid turtles in the Northern Hemisphere, but there is no evidence that chelids ever occurred there.

Cryptodires exhibit extremes in geographic range. Painted turtles (*Chrysemys picta*) and snapping turtles (*Chelydra serpentina*) of Canada have the most northerly distribution (about 52°). These turtles probably occur at or near the northern limits for oviparous reptiles. This distribution is equalled only by a few oviparous snakes (*Opheodrys*, *Pituophis* and *Storeria*) (Conant 1975). *Geochelone chiliensis*, a terrestrial tortoise has the most southerly distribution, and occurs at 43°S in Argentina. The emyidid, *Pseudemys scripta*, ranges from 42°N to 36°S, a total of 78° of latitude, possibly the widest breeding range of any freshwater turtle (Legler 1990). Sea turtles may range widely to the north and south of their breeding ranges. *Dermochelys coriacea* has the largest latitudinal range of any known turtle, from the north coast of Iceland to 47°S, a total latitudinal range of 113°.

Most chelid turtles occur in temperate or tropical latitudes. There is a varied fauna of pelomedusids and testudinid tortoises at or near the southern tip of Africa (*ca.* 35°S). *Phrynops geoffroanus* is the southern-most South American chelid (30°S). Australian chelids occur to the latitudinal extremes of the continent, but have epicentres of diversity between 23° and 25°S in eastern Queensland (see Chapter 21).

Limiting Factors

All extant Australian chelids are aquatic. Their geographic distribution is generally limited by the presence of permanent water or its seasonal yet predictable occurrence in natural drainage systems (Anon. 1967; Leeper 1970) as discussed in Chapter 21. A notable exception is *Chelodina steindachneri*, which occurs in water courses that fill unpredictably and which may be dry for well over one year.

However, in well-watered temperate regions, temperature is probably a limiting factor in its effect on the incubation of eggs and the digging of nests. Turtles are oviparous and must rely on a warm season long enough for nesting and at least partial embryonic development. Overwintering of eggs and hatchlings is known (Carr 1952; Ernst & Barbour 1972; Ewert 1979). Turtles seem to prefer microhabitats in which they can voluntarily move into different temperatures. Temperatures of approximately 25°C are probably close to optimum, but there is evidence to suggest that temperate aquatic turtles (including chelids) can move about comfortably, eat, mate, and nest at body temperatures of 15°C or lower (see Chapter 16). Southern Hemisphere turtles in general, and chelids in particular, never experience the vicissitudes of temperature of a boreal winter. Water seems to be a far greater limiting factor in the Southern Hemisphere.

Substrata which do not permit the digging of nests may limit distribution in various areas of otherwise favourable habitat. In streams draining to the Murray-Darling system from the New England Tableland, there is usually a distinct fauna above falls or cascades and another below. The intervening zone contains few or no turtles and, although the water in this zone is fast, it is probably the lack of nesting sites that excludes the turtles.

PHYLOGENETIC ORIGIN

The oldest known turtle, *Proganochelys quenstedti* from the Upper Triassic of Bavaria, lived approximately 200 million years ago (Gaffney 1990). The species was first described by Jaekel (1914, 1918). More recently, Gaffney (1990) prepared a monograph on a series of six specimens, including some that were

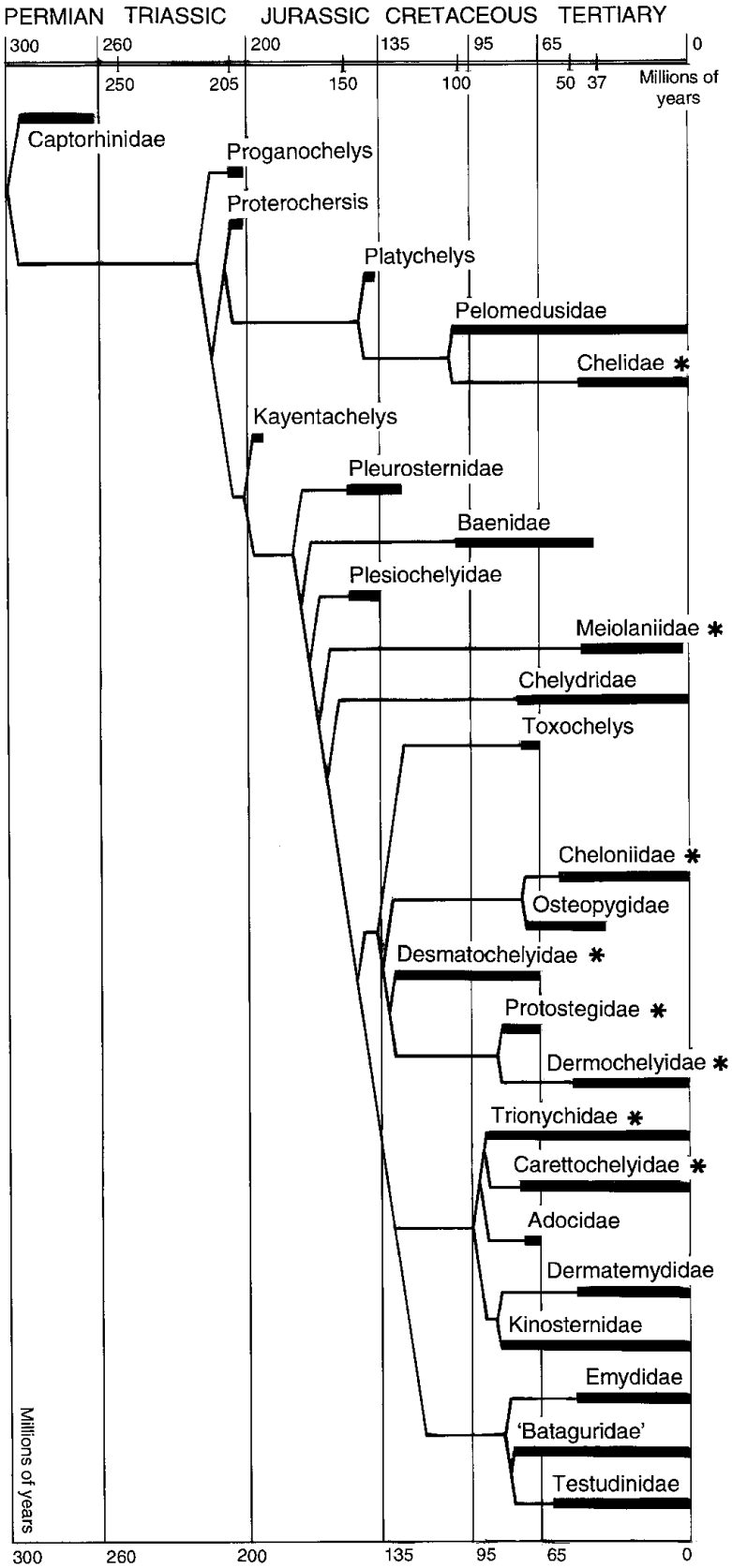


Figure 18.2 Phylogenetic tree showing the relationships of living and fossil turtles. (After Gafney & Meylan 1988) [D. Wahl]

virtually complete skeletons, such that this species is now one of the best known skeletally. Gaffney's restorations and illustrations of *P. quenstedti* suggest an animal with habits, habitat, body form, and general mass similar to the large North American Snapping Turtle, *Chelydra serpentina*. *Proganochelys* has some primitive characters that are absent in living chelonians, but is otherwise quite clearly a *bona fide* turtle. By Triassic times, *Proganochelys* already possessed most of the adaptive modifications that are diagnostic of turtles. In particular, the shell had evolved fully and surrounded the limb girdles.

Unfortunately, *P. quenstedti* provides little or no information about the evolutionary steps leading from the generalised tetrapod body plan to the unique turtle body plan.

The search for turtle ancestry relies heavily on osteological comparisons (usually of the skull) between *bona fide* turtles and groups of reptiles at or near the base of the amniote stock, usually referred to as Stem Reptiles. The two best supported hypotheses of chelonian origin identify different fossil groups of reptiles as the sister group of the Chelonia. Gaffney & Meylan (1988) used the Captorhinidae, a group of anapsids that would necessitate an origin for turtles as early as the early Permian or even late Carboniferous. This hypothetical ancestor would require a gap of approximately 100 million years between the origin of turtles and the oldest material of *P. quenstedti* Gaffney & Meylan (1988) built their hypothesis on four sets of shared, derived characters (synapomorphies) of the cranium, not all of which are unique to the chelonians and the captorhinids.

Reisz & Laurin (1991) invoked the procolophonids, a group of small tetrapod reptiles (or 'parareptiles') from the Permian of South Africa, as the ancestors of turtles. They supported this hypothesis on one postcranial and nine cranial synapomorphies, all of which are unique to the two sister groups. The hypothesis implies an origin for turtles as late as the late Permian, necessitating a much shorter gap in evolutionary history.

Although these hypotheses are of great interest and importance, neither really addresses the matter of the transition from a generalised tetrapod body plan to that of a turtle. Nor does either have an impact on an understanding of chelonian evolution since the Triassic, or of relationships between existing groups within the order Chelonia.

To date, Deraniyagala (1939) has been the only author to suggest and illustrate a body plan (a whole hypothetical organism) that constitutes a stage intermediate between a generalised tetrapod and a pre-chelonian. His 'saurotestudinate' ancestor from the Permian or Carboniferous, although somewhat fanciful, combines many of the characters that most current turtle biologists would predict in an ancestral group (see Chapter 16).

AFFINITIES WITHIN THE CHELIDAE

Morphology has played an important part and, until recently, the only part in the classification of Australian chelids. However, Burbidge, Kirsch & Main (1974) utilised a serological approach to the classification of the Chelidae, and Georges & Adams (1992) recently presented an analysis of relationships within the Australian chelids, based on biochemical data. There is a general congruence between their findings and those of Legler (1981), based on a phenetic analysis of morphological characters (see Chapter 21). Evidence from both studies, together with that from the recent cladistic analysis of Gaffney & Meylan (1988) strongly support the monophyly of the family Chelidae, and the common ancestry of South American and Australian chelids.

The simplest biogeographic scenario to explain monophyly involves the presence of chelids on the large southern continent, Gondwana. The land mass split into South America and Australia-Antarctica during the Palaeocene or

Eocene, 50 to 65 million years ago. Following the separation of Australia and Antarctica, about 45 to 49 million years ago, the Australian plate was completely isolated as it drifted 15° northward, until it collided with the Asian plate about 10 to 15 million years ago (Runcorn 1962; Irving 1964; Dietz & Holden 1970; Doutch 1972; Raven & Axelrod 1972; Tarling & Tarling 1975; Tyler 1979) .

The origin of the longnecked freshwater turtles, *Chelodina* and *Hydromedusa* from a common longnecked ancestor is well supported. *Hydromedusa* is known from the early Eocene of South America (Wood & Moody 1976), probably before the isolation of that continent from Gondwana. The longnecked chelids are, therefore, more likely to be monophyletic (Gaffney & Meylan 1988) than convergent (Pritchard 1984). It seems logical that the longnecked condition is derived; *Hydromedusa* is, therefore, regarded as already too specialised to have been ancestral to both longnecked and shortnecked groups (see also Chapter 21).

The evidence for shortneck lineages is not so clear and is not supported by fossils. Cann & Legler (1993) placed Australian shortnecked chelids in three distinct groups. *Pseudemydura*, which is not closely related to any Australian chelid and might be related to *Platemys* of South America (see also Chapter 21); *Emydura*; and the '*Elseya* complex', containing the *Elseya dentata* group, the *Elseya latisternum* group, *Rheodytes*, and shortneck alpha (see Chapter 21).

Although *Emydura* and the *Elseya* complex almost certainly have a common ancestry, the present authors do not regard the relationship between these two groups to be as close as do some other authors (for example, Gaffney & Meylan 1988; MacDowell 1983), who place them all in the genus *Emydura*.

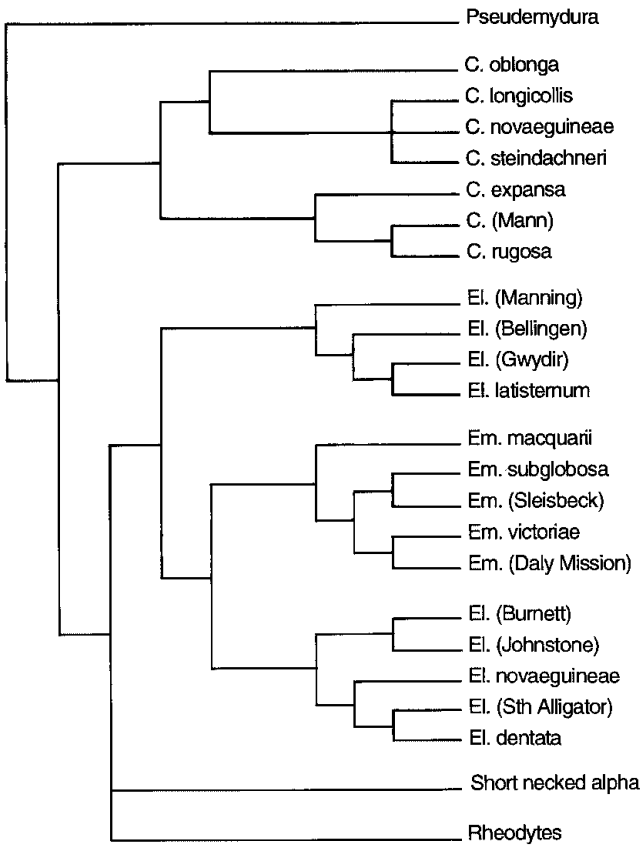


Figure 18.3 Cladogram of relationships within the Chelidae. (After Georges & Adams 1992) [D. Wahl]

BIOGEOGRAPHY

The modern Australian chelonian fauna can be considered in three categories.

The ancient autochthonous fauna includes the chelids, which constitute the dominant continental turtle fauna of Australia. They are the only modern family of turtles common to Australia and South America.

An Asian element of Tertiary origin has entered Australia via the Indo-Australian Archipelago since the Australian and Asiatic plates collided 10 to 15 million years ago. The Australian reptile fauna is predominantly oriental (Tyler 1979), with a large component derived after Australia collided with the Asiatic plate. *Carettochelys insculpta* is probably a part of this oriental group and occurs only in a few river systems in northern Australia and in southern New Guinea. The cryptodiran genus *Pelochelys* belongs in this group if southern New Guinea is considered as a part of the Australian continental plate.

The cosmopolitan element includes the marine turtles of the families Cheloniidae and Dermochelyidae. These occur worldwide and are subject to few or no distributional barriers, with the exception of *Natator depressus*, known only from Australian and New Guinean coastal waters.

FOSSIL RECORD

The Australian fossil record has yielded sparse but identifiable specimens of the Chelidae and Carettochelyidae, two taxa of Early Cretaceous marine turtles included in the Chelonioidea and specimens of the extinct cryptodiran families Meiolaniidae and Trionychidae (Gaffney 1981). The chelonioid fossils are some 110 million years old. Fossils presently not clearly assigned to any higher taxon, such as *Chelycarapookus* of the Lower Cretaceous of Victoria (Chapman 1919), provide tantalising examples of what may yet be discovered in the fossil record. Warren (1969) was unable to determine the suborder, although the species was assigned recently to a new family, the Chelycarapookidae.

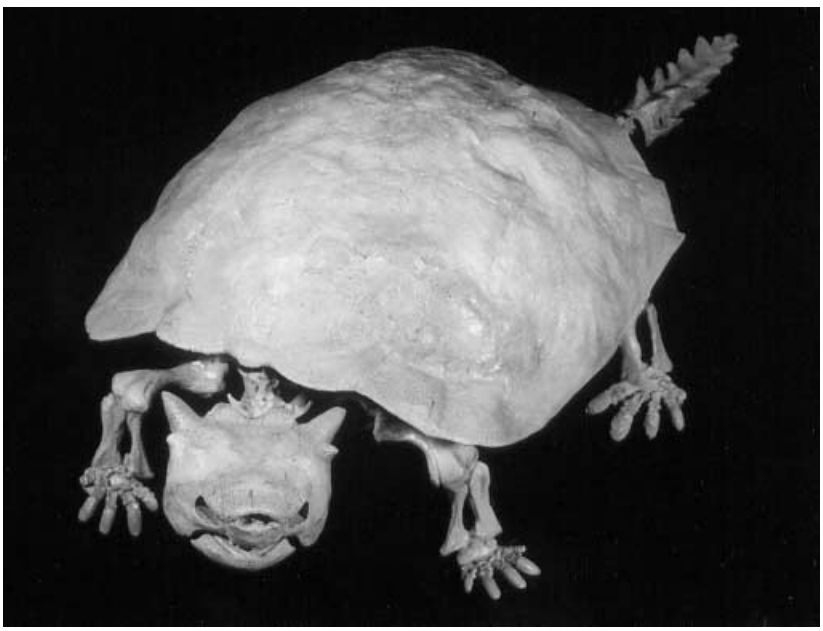


Figure 18.4 Fossil skeleton of *Meiolania platyceps*. [Photo ©Australian Museum]

Meiolaniidae

Meiolaniids are considered to be the only real Australian novelty provided by the fossil record. They occur from the Miocene to the Pleistocene on mainland Australia, in the Pleistocene of Lord Howe Island and New Caledonia, and in the Cretaceous and Eocene of South America (Gaffney 1981).

The best known fossil specimens are of *Meiolania platyceps* of Lord Howe Island. They were large terrestrial turtles with cranial horns and frills, cervical ribs, a bony club at the end of their tails and numerous epidermal ossicles (Gaffney 1983, 1985a). Their bizarre appearance led to much confusion when early palaeontologists endeavoured to identify the fossil remains. Their ecology is unknown, but it is thought likely that they had habits similar to the testudinids of the Galapagos and Aldabra Islands (Gaffney 1985b).

Trionychidae

The trionychids are soft-shelled turtles which occur today in Africa, Asia and North America but not in South America or Australia. *Pelochelys bibroni* of New Guinea probably reached the Australasian region from Asia (Darlington 1957).

Fossil material from Australian deposits is fragmentary, but has been diagnosed as Trionychidae on the basis of surface texture pattern and a natural distal edge to the costals, rather than a suture, suggesting that peripheral bones were absent (Gaffney & Batholomai 1979). Trionychids were widespread through Queensland in the late Cainozoic and possibly as early as the Miocene.

Carettochelyidae

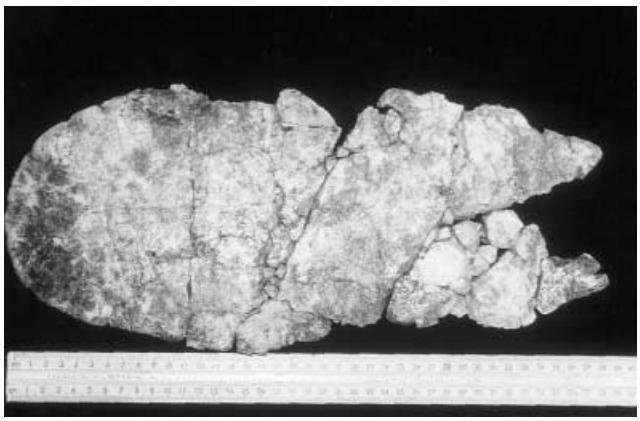
Carettochelys insculpta is found today in the southern flowing rivers of New Guinea and the larger rivers of the Northern Territory in Australia (Cogger 1992). It is the sole surviving species of a family that was widespread in the late Tertiary.The genus is represented in the Australasian fossil record by a specimen from the Miocene of New Guinea (Glaessner 1942). A fossil from Western Australia was misidentified as *Carettochelys* by Goster & McNicoll (1978) (Gaffney 1981).

Chelonioidea

The oldest turtles from Australia with definitive stratigraphic data are the marine chelonioids *Cratochelone* and *Notochelone* from the Early Cretaceous Toolebuc Limestones of Julia Creek (Gaffney 1981, 1991).

Chelidae

The Chelidae dominate the extant freshwater turtle fauna of Australia, and are also the most common and widespread fossil turtles. Chelids are restricted in distribution to Australasia and South America, both as living and fossil forms. They range in age from Miocene to Recent in Australian deposits. Chelids are distinguished from other turtles by the presence of a pelvis that is fused to the carapace and plastron, but in the absence of fossil evidence of this character, Australian material often is assigned to the family if neural bones are absent (Gaffney 1981). Fossil specimens have been assigned to the genera *Chelodina*, *Emydura*, *Elseya* and *Pseudemydura* on the basis of diagnostic scute arrangements of the carapace and plastron (Fig. 18.5; Gaffney 1977, 1981; Gaffney, Archer & White 1989). New insight into the evolution of the chelid fauna awaits discovery.



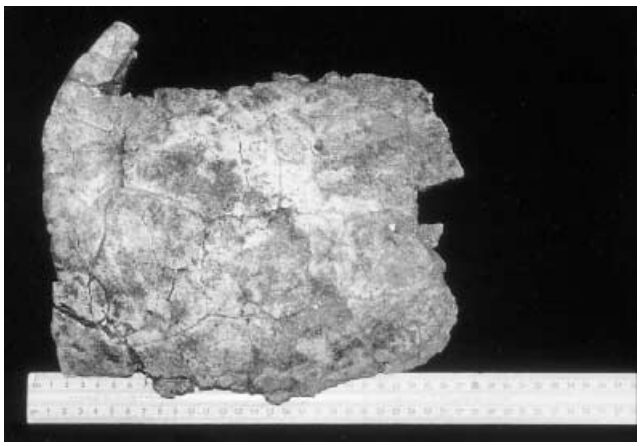


Figure 18.5 Fossil plastron and carapace of *Elseya*. [Photo by J. Cann]

Four of the six extant genera of Australian freshwater turtles are monotypic (*Pseudemydura*, *Rheodytes*, shortnecked alpha, and *Carettochelys*), represented by species that are distinct both morphologically (Ramsay 1886; Siebenrock 1901; Legler & Cann 1980; Cann & Legler 1993) and biochemically (Georges & Adams 1992). Each of these genera arises from lineages of considerable antiquity, as *Chelodina* and *Pseudemydura* may have their closest living relatives among South American forms (Gaffney 1977; Legler 1981). *Carettochelys insculpta* represents an independent lineage of some 40 million years standing (Chen, Mao & Ling 1980). Although today Australia is the driest continent after Antarctica (see Chapter 21), this was not always so. The extant freshwater turtle fauna probably should be considered a relict of a much more diverse fauna of wetter times.

This assertion is not well supported by the fossil record, in part because of little attention having been paid to the turtle elements of Australian fossil collections until recently and, in part, because the morphology of extant forms is poorly known in detail. As Gaffney (1981) pointed out, it is not possible to deal realistically with fossil chelid material at the species level because of the paucity of skeletal material and descriptive work for extant forms. The new taxa described by de Vis around the turn of the century can be diagnosed to family only, and no extinct species can be substantiated at present (Gaffney 1981).