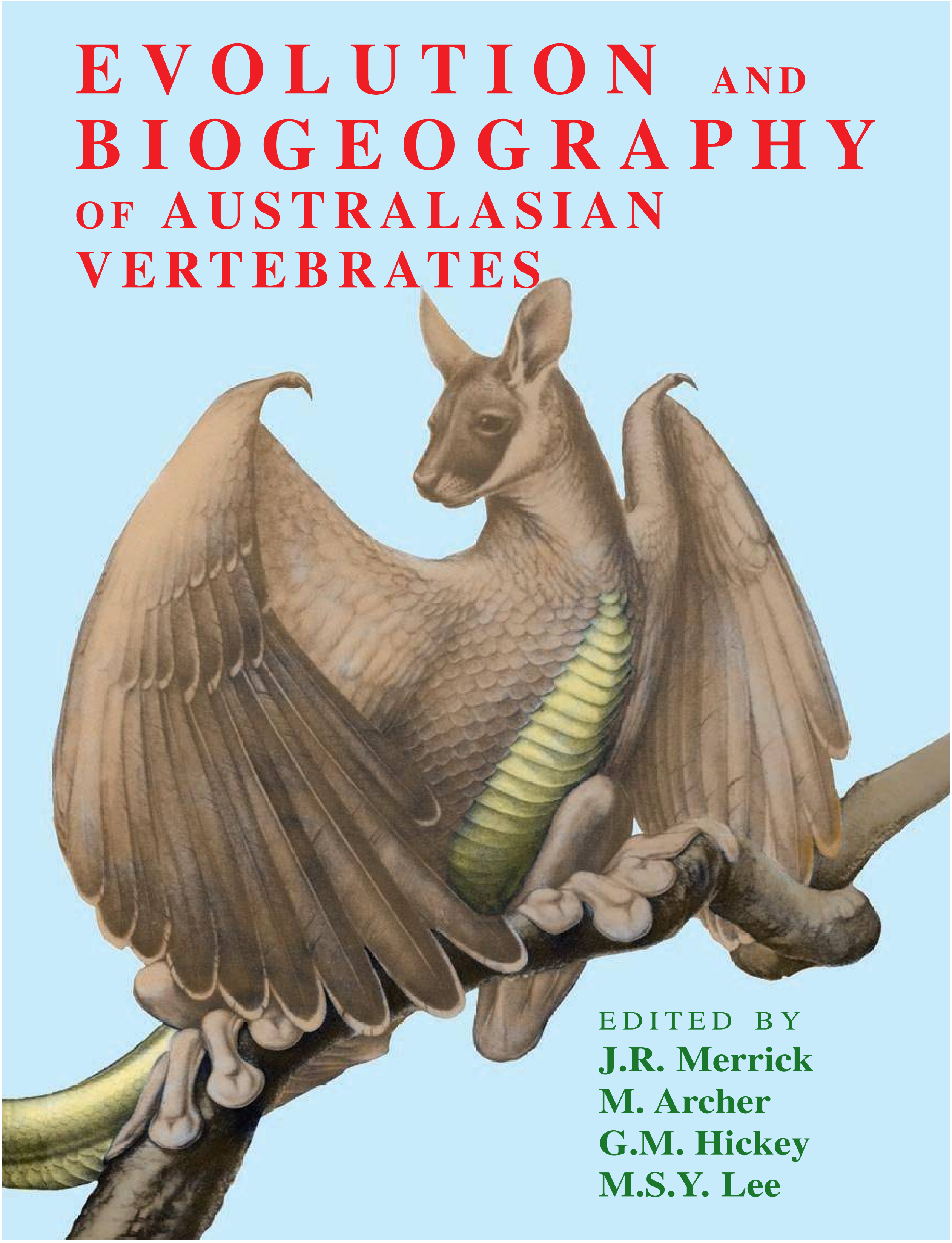
Announcing



EVOLUTION AND BIOGEOGRAPHY OF AUSTRALASIAN VERTEBRATES

EDITED BY

J.R. Merrick
M. Archer
G.M. Hickey
M.S.Y. Lee

A ground-breaking volume of international significance.

An overview of Australasian vertebrates in the extinction crisis!

A reprint from

Evolution and Biogeography
of Australasian Vertebrates

Chapter 16

Evolution and Zoogeography of Australian Freshwater Turtles

auscipub
Australian Scientific Publishing

Reprinted from *Evolution and Biogeography of Australasian Vertebrates* (Merrick *et al.*, Eds. 2006)

First published in 2006

Auscipub Pty Ltd
PO Box 68
Oatlands
NSW 2117
Australia
auscipub@btinternet.com
www.auscipub.com

National Library of Australia Cataloguing-in-Publication data (for original volume)

Evolution and biogeography of Australasian vertebrates
Bibliography.
Includes Index.
ISBN 0 9757790 0 1 (pbk) (now 978 0 9757790 0 2)
0 9757790 1 X (hbk) (now 978 0 9757790 1 9)

1. Vertebrates - Australasia - Evolution. 2. Vertebrates - Ecology.
3. Biogeography - Australasia. 4. Zoogeography - Australasia.
I. Merrick, J.R. (John Rodney), 1944–

596.09

Reprinted from *Evolution and Biogeography of Australasian Vertebrates* (Merrick *et al.*, Eds. 2006)

Chapter 16

Evolution and Zoogeography of Australian Freshwater Turtles

Arthur Georges and Scott Thomson
Applied Ecology Research Group and Cooperative Research Centre for Freshwater Ecology,
University of Canberra, A.C.T. 2601 Australia
E-mail: georges@aerg.canberra.edu.au

TURTLE DIVERSITY AND ORIGINS

The turtle shell is one of the most enduring morphological innovations in vertebrate history. It is the single unifying theme for the great diversity of turtle and tortoise species that have come to occupy our oceans, forests, swamps, lakes, rivers and deserts. An estimated 220 species of freshwater turtle alone occupy the waters of all vegetated continents, from the tropics to just outside the Arctic Circle. Centres of biodiversity occur in eastern North America and in southern Asia.

Turtles first appear in the fossil record 210 million years ago (late Triassic), as a very early side-branch of reptilian evolution. No transitional forms exist. Turtles appear abruptly in the fossil record as *Proganochelys quenstedti* (Jaeckel, 1914, 1918) (Figure 1). This earliest known turtle has distinctive and well-developed chelonian features of the carapace and plastron (Figure 2), and the shoulder girdle is located within the rib cage (Gaffney, 1990).

The search for turtle ancestry has relied heavily on osteological data, usually taken from the skull, to compare *bona fide* turtles with groups of reptiles at or near the base of the amniote stock. Gaffney and Meylan (1988) link turtles with the Captorhinidae (anapsids with a generalized tetrapod body plan), but this would require the turtle lineage to have diverged in the early Permian or even the late Carboniferous, some 100 million years before *Proganochelys* appears in the fossil record. Reisz and Laurin (1991) argued that the procolophonids, a group of small tetrapod reptiles (or 'parareptiles') from the Permian of South Africa, are the ancestors of turtles. They found one postcranial and nine cranial characters unique to the two groups. Their hypothesis implies an origin for turtles in the late Permian, closer to the appearance of *Proganochelys* in the late Triassic. Unfortunately, neither of these hypotheses address the transition from a generalized tetrapod body plan to that of a turtle.

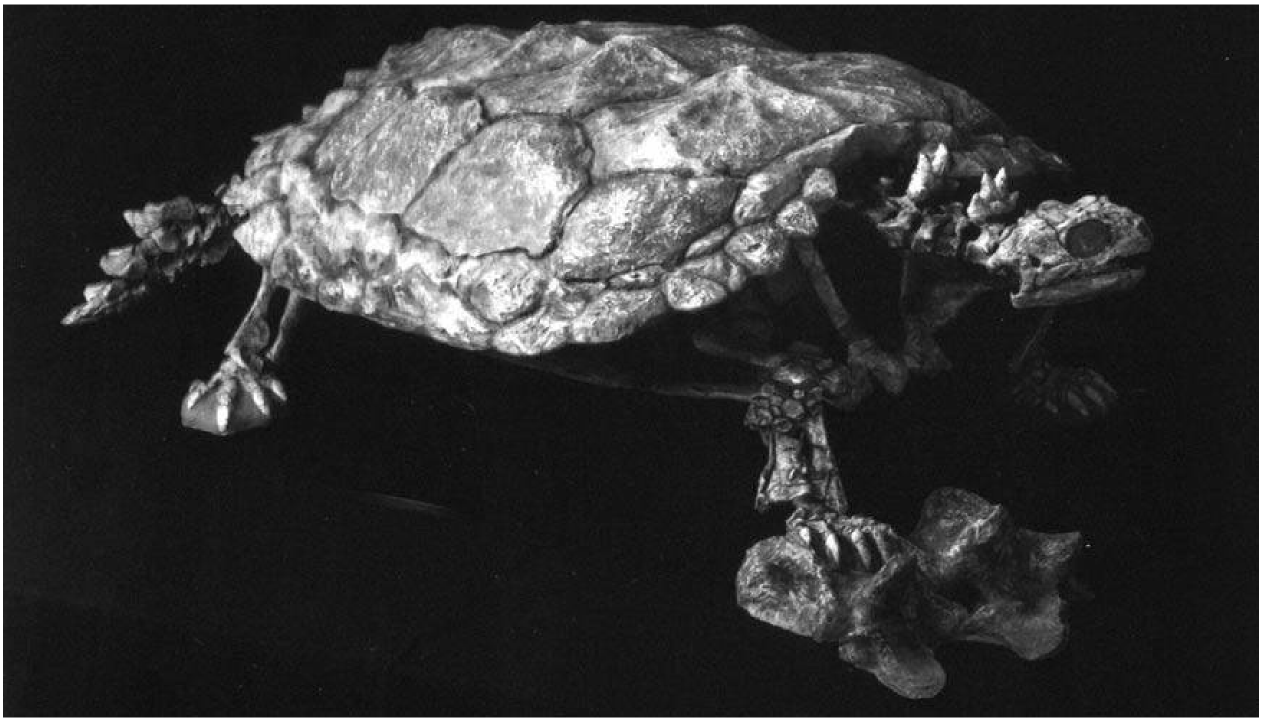


Figure 1. A cast of a reconstructed skeleton of the first known turtle, *Proganochelys quenstedti,* from the late Triassic Norian of Germany (with permission from the American Museum of Natural History).

Reprinted from *Evolution and Biogeography of Australasian Vertebrates* (Merrick *et al.*, Eds. 2006)

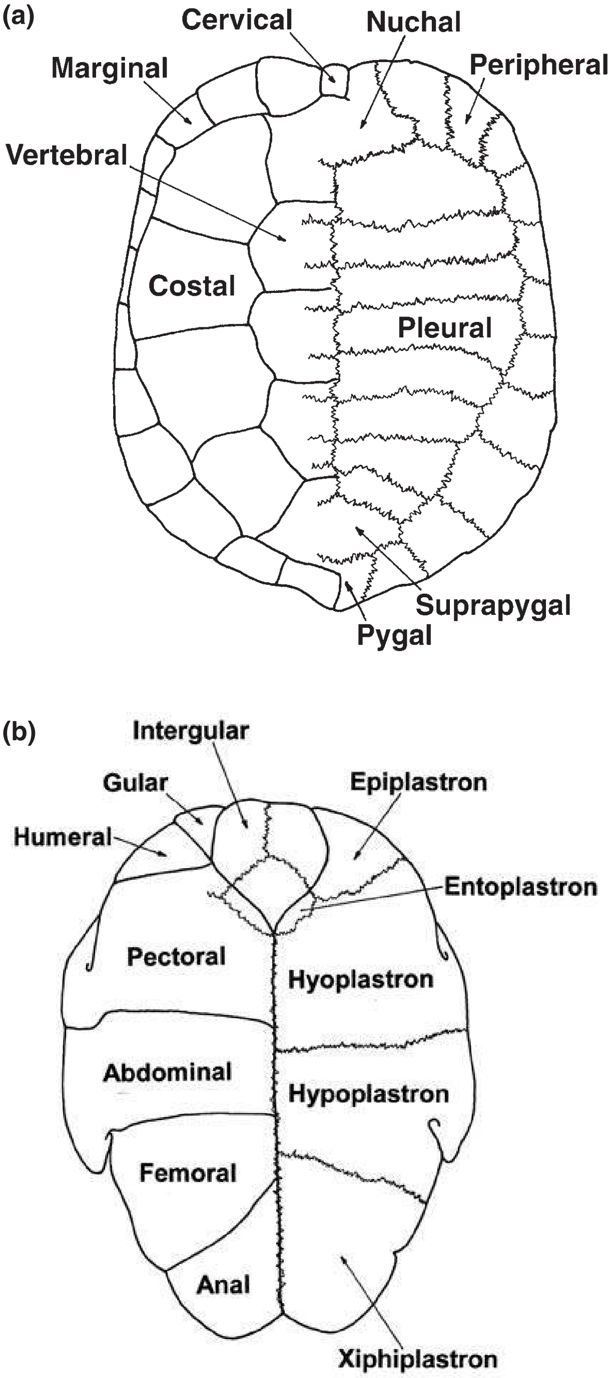


Figure 2. Shell of the chelid turtle *Pseudemydura umbrina* showing: **(a)** dorsal view of the carapace; and **(b)** ventral view of the plastron (after Burbidge, 1967). The sutures between dermal bony plates are shown as jagged lines; boundaries between the overlying epidermal keratinous scutes are shown as solid lines. Bony plates are labelled on the right of each view; scutes are labelled on the left. Neural plates are present only as subsurface elements in most Australian chelid turtles (Thomson and Georges, 1996) and so are not shown. Nomenclature follows that of Zangerl (1969).

Lee (1993) suggests that turtles have evolved from pareiasaurs (strictly, the Pareiasauridae). Pareiasaurs are large and clumsy herbivorous reptiles prominent in the late Permian (Araujo, 1984). Having established this relationship with an impressive array of shared derived characters, Lee speculates on the origins of the turtle shell. The dorsal surface, flanks and sometimes the belly of pareiasaurs were covered in longitudinal rows of bony plates. Lee argues that the extensive dermal ossifications in these animals and the dermal elements of the armour of turtles are homologous—'the precursors of the chelonian carapace and plastron can now be seen in the osteoderms of pareiasaurs' (Lee, 1993, p.1719). Fusion of these dermal osteoderms with the unmodified neural arches of the vertebrae and the ribs resulted in what we know as the turtle carapace. The migration of the pectoral girdle within the shell was possible because the long ribs of pareiasaurs extend laterally from the vertebral column with only slight curvature.

RELATIONSHIPS AND DISTRIBUTION

Proganochelys had unspecialized cervical vertebrae (Gaffney, 1990) and presumably was unable to retract its head beneath the shell. Head retraction was later achieved in two ways. Turtles of the Suborder Cryptodira flex their necks in the vertical plane when the head is retracted beneath the protection of the shell (Plate 62). The Cryptodira comprises nine extant families, and most of the living species of turtles (Pritchard, 1979). Most occur in temperate regions of the Northern Hemisphere—in Europe, Asia and North America, and in the tropics. Notable radiations include the soft-shelled turtles of Asia, Africa and North America (Trionychidae), the terrestrial tortoises of Asia, Europe, Africa and the Americas (Testudinidae), the pond and river turtles of all vegetated continents except Australia (Emydidae), and the marine turtles (Cheloniidae) (Ernst and Barbour, 1989). Marine turtles of the families Cheloniidae and Dermochelyidae, and the freshwater pig-nosed turtle, *Carettochelys insculpta* (Carettochelydidae) are the only living Australian cryptodires.

Turtles of the Suborder Pleurodira flex their neck in the horizontal plane when it is withdrawn into the shell (Plate 63). These are the so-called side-necked turtles. The suborder comprises two families. The Pelomedusidae includes five genera: *Erymnochelys* of Madagascar, *Pelomedusa* and *Pelusios* of Africa, and *Peltocephalus* and *Podocnemis* of South America. Pelomedusids were once much more widespread, with fossils known from deposits in Europe, North and South America, Africa, India and Asia. Their fossil record dates back to the Cretaceous (Pritchard, 1979). *Stupendemys geographicus*, from the Miocene of Venezuela, is the largest turtle known to have existed—with a carapace length of 2.3 m (Wood, 1976).

The second family, Chelidae, is represented by 13 genera—*Acanthochelys, Batrachemys, Chelus,* *Hydromedusa, Mesoclemmys, Phrynops* and *Platemys* of South America and *Chelodina, Emydura, Elseya, Elusor, Pseudemydura* and *Rheodytes* of the Australasian region. Their fossil record extends back to the late Cretaceous (de Broin, 1987) of South America and the Miocene of Australia (Gaffney *et al.*, 1989), but no fossil chelids are known from outside the present range of the family (Williams, 1953a, b; Gaffney, 1991). Their Gondwanan origins would appear beyond dispute. All but one living species of Australian freshwater turtle are chelids.

AUSTRALASIAN FAUNAS

FOSSIL RECORD

The fossil turtle fauna provides an essential backdrop to the interpretation of the living turtle fauna of Australia. Four of the six living genera of Australian freshwater turtles are monotypic (*Pseudemydura*, *Rheodytes*, *Elusor* and *Carettochelys*), represented by species that are distinct morphologically (Ramsay, 1886; Siebenrock, 1901; Legler and Cann, 1980; Cann and Legler, 1994) and biochemically (Georges and Adams, 1996). Each of these genera arises from lineages of considerable antiquity. Many distinctive species, including those in the genera above, are restricted to one or a few drainages. Many of these are threatened or endangered by virtue of their restricted natural distributions, coupled with the alterations to habitat brought about by human activities. Although today Australia is the driest vegetated continent on Earth, this was not always so. It is clear from the fossil record, that the extant freshwater fauna of Australia should be considered a relict of a much more diverse fauna of wetter times past (Table 1). There is no doubt that palaeontology provides a fertile field in which many more of our freshwater turtle ancestors await discovery.

The fossil record reveals that the land mass we now call Australia was once home to a number of families of turtle, both pleurodire and cryptodire (Table 1). Pleurodires were the dominant non-marine turtles in the Recent Australian fauna, and were the dominant turtles throughout the Tertiary (Gaffney, 1981), but only cryptodires have been found in the Australian Mesozoic (Gaffney, 1979, 1981; Gaffney *et al.*, 1998).

The oldest turtles from Australia with definitive stratographic data are marine, the chelonioids *Cratochelone* and *Notochelone* from the early Cretaceous Toolebuc Limestones of Julia Creek (Gaffney, 1981, 1991). The oldest freshwater turtle from Australia is *Otwayemys cunicularius*, a cryptodire from the early Cretaceous Eumeralla Formation of Cape Otway in Victoria. It has been assigned to the family Sinemydidae, found elsewhere in the Cretaceous of Mongolia (Brinkman and Peng, 1993).

Table 1. Fossil species of Chelonia from Australia and New Guinea. The list is restricted to fossils that have been assigned to specific species.

Current Name	Family	Original Reference	Horizon and Site
Carettochelys insculpta	Carettochelydidae	Glaessner (1942)	Late Miocene, Papua New Guinea.
Birlimarr gaffneyi	Chelidae	Megirian and Murray (1999)	Miocene Camfield Beds, N.T.
Chelodina insculpta	Chelidae	de Vis (1897)	Plio–Pleistocene, Darling Downs, Qld.
Chelodina longicollis	Chelidae	Thomson (2001, unpublished data)	Pleistocene, Naracoorte Caves, S.A.
Chelodina novaeguineae	Chelidae	Thomson and Mackness (1999)	Early Pliocene, Bluff Downs, Qld.
Elseya lavarackorum	Chelidae	White and Archer (1994)	Pleistocene, Riversleigh Station, Qld.
Elseya nadibajagu	Chelidae	Thomson and Mackness (1999)	Early Pliocene, Bluff Downs, Qld.
Elseya uberima	Chelidae	de Vis (1897)	Plio-Pleistocene, Darling Downs, Qld.
Emydura macquarii	Chelidae	Thomson and Mackness (1999)	Early Pliocene, Bluff Downs, Qld.
Rheodytes devisi	Chelidae	Thomson (2000b)	Plio-Pleistocene, Darling Downs, Qld.
Meiolania brevicollis	Meiolaniidae	Megirian (1992)	Middle Miocene, Bullock Creek, N.T.
Meiolania mackayi	Meiolaniidae	Anderson (1925)	Late Pleistocene, Walpole Island
Meiolania platyceps	Meiolaniidae	Owen (1886)	Late Pleistocene, Lord Howe Island, N.S.W.
Nynjemys oweni	Meiolaniidae	Woodward (1901)	Late Pleistocene, King's Creek, Qld.
Warkalania carinaminor	Meiolaniidae	Gaffney *et al.* (1992)	Miocene, Riversleigh Station, Qld.
Cratochelone berneyi	Chelonioidea	Longman (1915)	Early Cretaceous, Hughenden, Qld.
Notochelone costata	Chelonioidea	Owen (1882)	Early Cretaceous, Julia Creek, Qld.
Chelycharapookus arcuartus	Sinemydidae	Warren (1969)	Early Cretaceous, Merino Group, Vic.
Otwayemys cunicularius	Sinemydidae	Gaffney *et al.* (1998)	Early Cretaceous, Cape Otway, Vic.

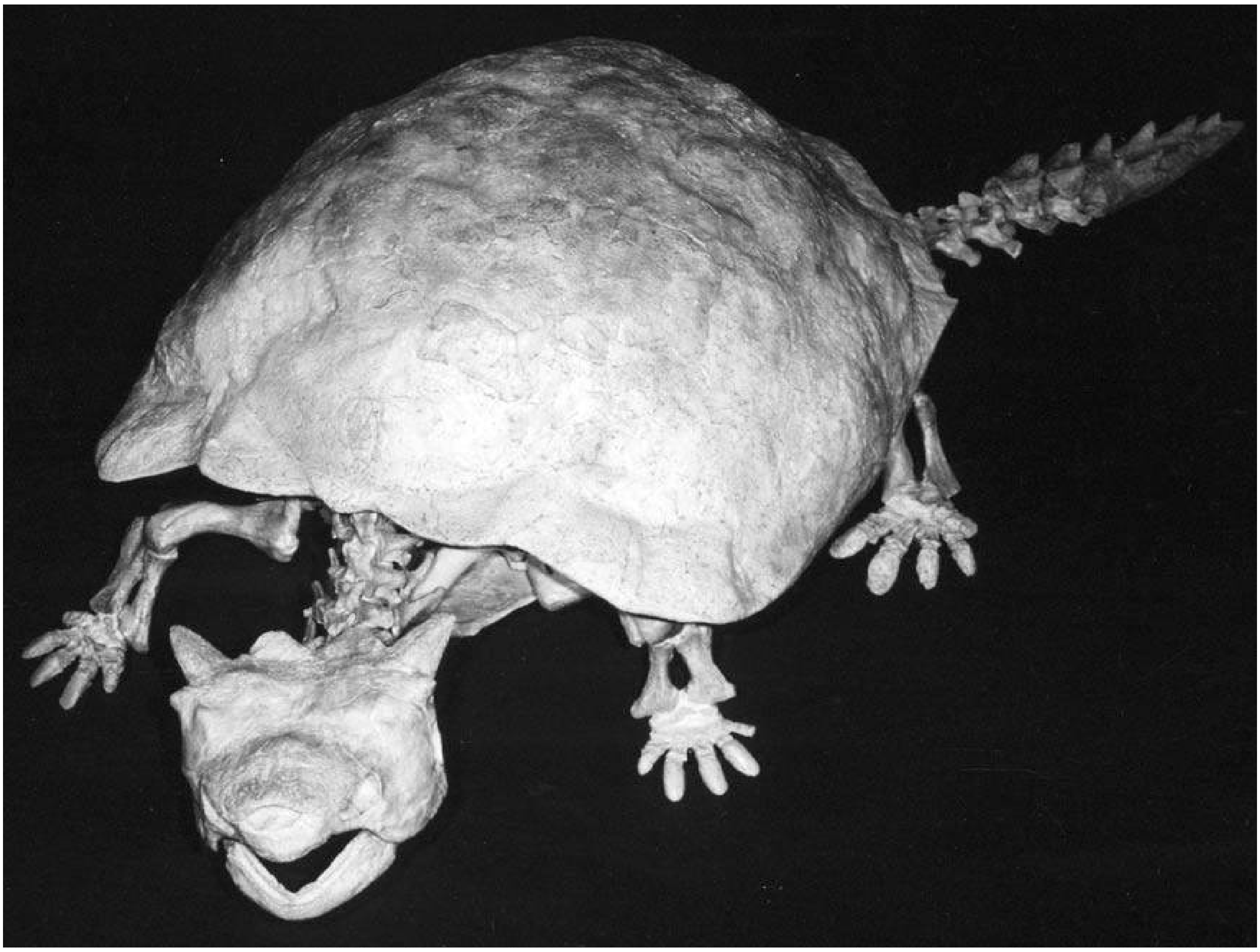


Figure 3. Reconstructed skeleton of *Meiolania platyceps*, from Pleistocene calcarenites of Lord Howe Island (with permission from the American Museum of Natural History).

Another Mesozoic cryptodire, *Chelycarapookus*, is known as an internal mold (Warren, 1969), and as fossil fragments from Lightning Ridge, New South Wales (Gaffney, 1981; Molnar, 1991). *Chelycarapookus* is of uncertain affinity, but it is similar in many features to the sinemydids (Gaffney *et al.*, 1998), to which it may one day be assigned.

The meiolaniids are the real novelties of our 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* from Lord Howe Island (Figure 3). 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, 1985). 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 (giant tortoises) of the Galapagos and Aldabra Islands (Gaffney, 1985). Phylogenetically, they form an unresolved trichotomy with the sinemydids and the modern cryptodires (Gaffney *et al.*, 1998).

Fossil trionychid 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 and Bartholomai, 1979). Trionychids were widespread through Queensland (White, 1994), distinct from the extant *Pelochelys* of New Guinea (White, 1990), and range from the Eocene of Murgon (White, 2000, personal communication) to the Pliocene of the Darling Downs and Chinchilla (de Vis, 1897, p.127; Mackness and Thomson, 2000, unpublished data). However, they are absent from the Oligo-Miocene deposits of Riversleigh (Gaffney *et al.*, 1989).

The chelid fossil fauna of Australia is poorly known. The fossil record for chelids dates to the Cretaceous, but the earliest Australian chelid is from the Eocene (White, 2000, personal communication). They dominate the fauna from the Miocene to the present. Good comparative morphological data on living forms are lacking, so *Emydura* and *Chelodina* have been used as broad receptacles for a range of fossil taxa in the Chelidae. Recent advances in our knowledge of the postcranial osteology of chelids (Thomson and Georges, 1996; Thomson *et al.*, 1997), and particularly the identification of characters that distinguish *Elseya* and *Emydura*, have permitted a re-examination of a number of fossil forms. They include *Elseya uberima* (de Vis, 1897) from Chinchilla in Queensland, *Rheodytes devisi* Thomson (2000b) from the Darling Downs, and *Elseya lavarackorum* (White and Archer, 1994) from Riversleigh in the Gulf country (Figure 4). The latter species was first described as a fossil (White and Archer, 1994) but is now known also from living populations in the rivers that flow into the Gulf of Carpentaria (Thomson *et al.*, 1997). Other recent work has uncovered a number of additional forms, such as *Birlimarr gaffneyi* (Megirian and Murray, 1999), from the Miocene Camfield Beds of the Northern Territory and *Elseya nadibajagu* Thomson and Mackness (1999) from Bluff Downs near Charters Towers in Queensland.

Riversleigh Station is a rich source of early to middle Miocene turtle fossils (Gaffney *et al.*, 1989). A specimen of *Chelodina* is the first Miocene record and oldest fossil of this living Australian genus. The discovery there of a fossil *Pseudemydura* is particularly notable as it dramatically extends the range of a genus now extremely rare and restricted to a single species, *Pseudemydura umbrina*, from the south-west corner of Western Australia. These discoveries, together with that of a third genus of freshwater turtle (*Emydura/Elseya*) and perhaps also a new genus at Riversleigh (White, 1993), extend the temporal and geographic range of living Australian turtle taxa and give a better glimpse of the Australian fauna during the Tertiary (Gaffney *et al.,* 1989).

DIVERSITY OF LIVING FORMS

The classification of Australasian chelid turtles is poorly founded, and in drastic need of review (Cogger, 2000). This has been a major impediment to conservation and has limited our understanding of how freshwater turtle biodiversity is distributed across the Australasian landscape. The situation has changed recently, with detailed surveys and analysis of species boundaries using allozyme electrophoresis (Georges and Adams, 1996; Georges *et al.*, 2002) and the subsequent formal description of a number of new species (Cann, 1997a, b, c, d; Thomson *et al.*, 1997; Thomson *et al.*, 2000). Further descriptions are imminent.

Emydura

Species of *Emydura* are widespread and abundant in eastern and northern Australia, where they occupy rivers and the larger, permanent waterholes and billabongs of their floodplains. They are omnivorous short-necked species and are general in their habitat requirements, pro-

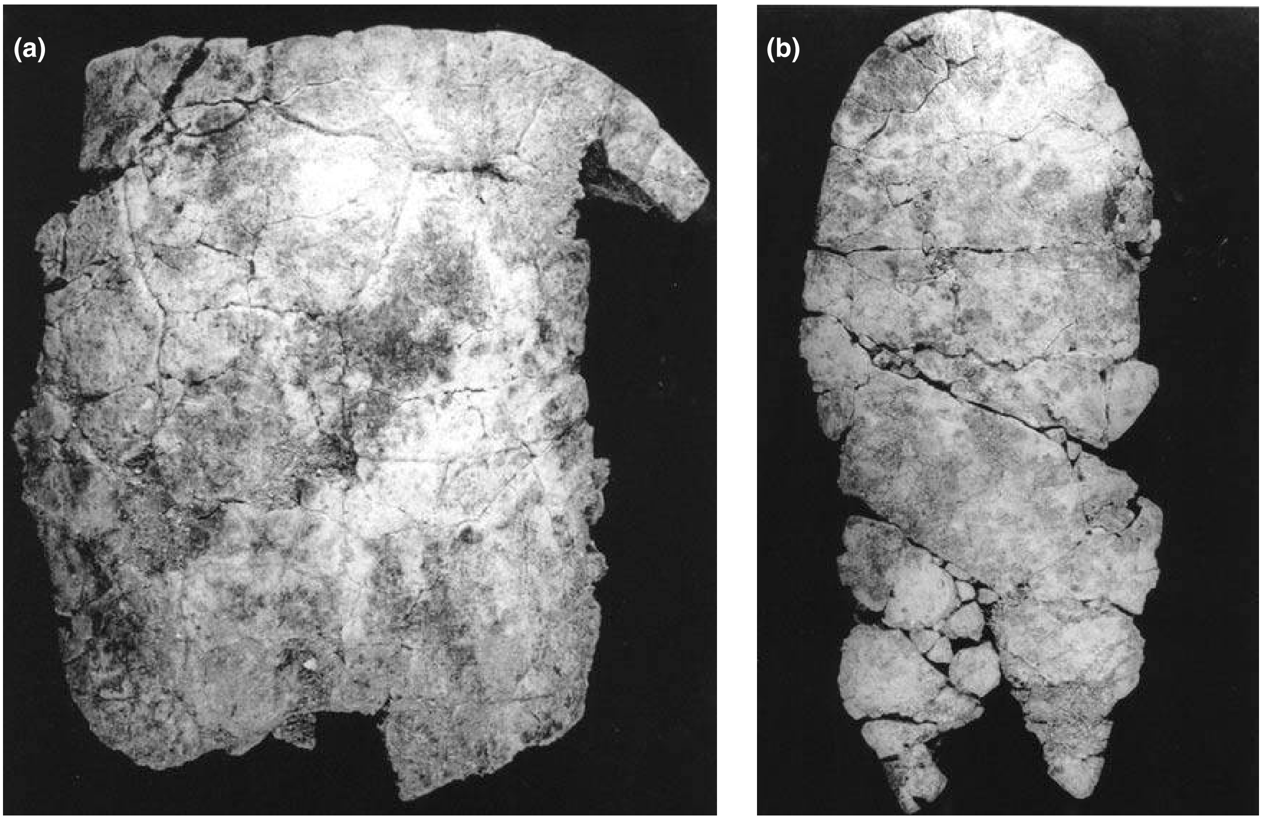


Figure 4. Shell features of a fossil of *Elseya lavarackorum* from the Pleistocene deposits at Riversleigh Station (Queensland). This species has since been found alive and well in the same region (Thomson *et al.*, 1997). **(a)** Dorsal view of the carapace; **(b)** ventral view of the plastron.

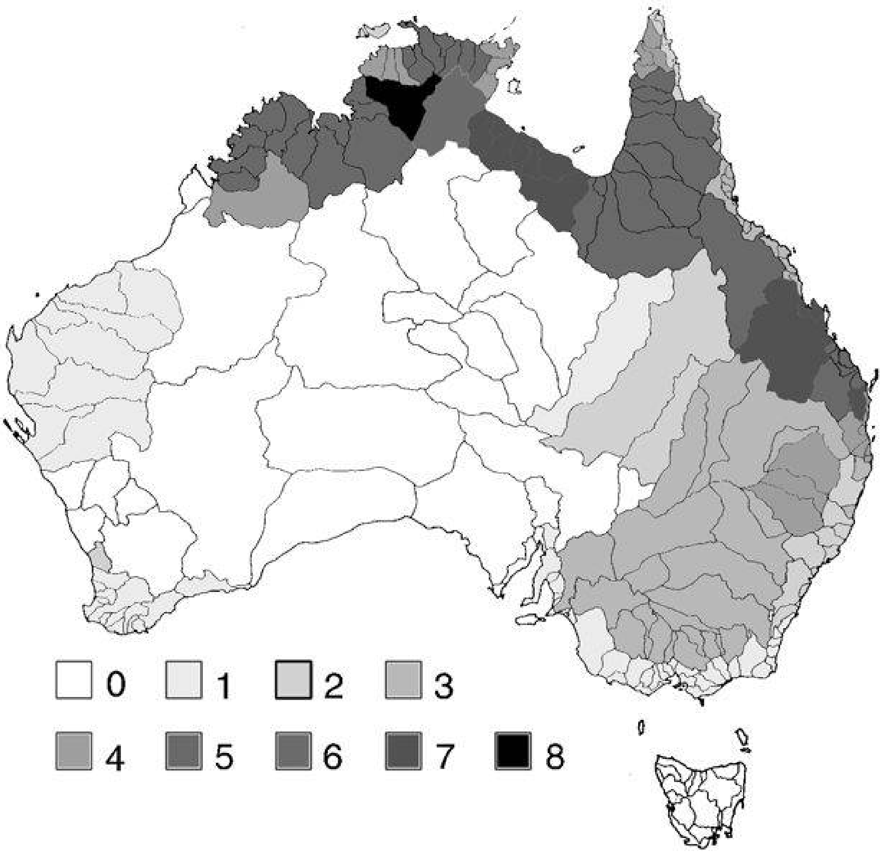


Figure 5. A map of drainage basins showing the distribution of turtle species richness across Australia. There are 'hot spots' in east coastal Australia, centred on the Fitzroy-Dawson drainage (6–7 species) and the 'Top End' centred on the Daly drainage (8 species). Lack of knowledge of the taxonomy prevents a similar map for New Guinea being presented.

vided the water is permanent. Electrophoretic surveys found no clear distinctions between *Emydura signata*, *E. krefftii* and *E. macquarii*. They are found nowhere in sympatry despite abutting distributions, which complicates assessment of species status for very closely related forms. In the absence of clear morphological characters to separate them, they should be regarded as a single biological species, *Emydura macquarii* (Georges and Adams, 1992, 1996). A case can be made for sub-specific distinctions using morphology, colouration and geographic range. Populations of the Murray-Darling drainage and coastal rivers from the Brisbane River south to the Hawkesbury-Nepean are recognized as *Emydura macquarii macquarii*, whereas populations from coastal Queensland north from the Mary River to the vicinity of Princess Charlotte Bay are *Emydura macquarii krefftii.* The population from Fraser Island, and from Cooper Creek in central Australia can each be regarded as subspecies, *Emydura macquarii nigra* McCord *et al.* (2003) and *E. macquarii emmotti* Cann *et al.* (2003) respectively. A number of other subspecies have been suggested for this widespread southern *Emydura* (Cann, 1998), and several workers still prefer to regard *Emydura krefftii* as a distinct species, though without clear diagnosis.

In the north, there are also a number of closely related species. The northern red-faced turtle, *Emydura victoriae*, ranges from the Fitzroy River of Western Australia east to the Daly River of the Northern Territory. The diamond-head or Worrell's turtle is found in the rivers from the Daly River in the west to the rivers flowing into the Gulf of Carpentaria along the west coast of Cape York. This form is electrophoretically indistinguishable from populations of *Emydura subglobosa* in New Guinea, but lacks the red suffusion of the New Guinean populations. It is best referred to as *Emydura subglobosa worrelli*. *Emydura subglobosa subglobosa* is found in the Jardine River at the tip of Cape York and is widespread in the southern flowing rivers of New Guinea. The northern yellow-faced turtle, *Emydura tanybaraga*, is widespread across northern Australia. All three species of *Emydura* are found in the Daly River.

These species of *Emydura* are all very closely related, differing at most by a few fixed allozyme differences, and are presumably a recent radiation. This is not the case for the genus *Elseya*.

Elseya

What was until recently regarded as a single widespread species, the northern snapping turtle (*Elseya den-*

Table 2. Described species of living freshwater turtle from Australia and New Guinea. Several other species that await description include *Chelodina* sp. (aff. *expansa*) from the Cadell River of the Northern Territory and undescribed species identified by Georges and Adams (1996).

Current Name	Original Name	Original Reference	Geographic Range
Carettochelys insculpta	*Carettochelys insculptus*	Ramsay (1886)	N.T. and southern New Guinea
Pelochelys bibroni	*Trionyx (Gymnopus) bibroni*	Owen (1853)	New Guinea, north of the central highlands
Pelochelys cantori	*Trionyx cantori*	Gray (1864)	New Guinea, south of the central highlands
Chelodina burrungandjii	*Chelodina burrungandjii*	Thomson *et al.* (2000)	Arnhem Land plateau and escarpment, N.T.
Chelodina canni	*Chelodina canni*	McCord and Thompson (2002)	North of Rockhampton, Qld, westwards to the Roper River, N.T.
Chelodina oblonga	*Chelodina colliei*	Gray (1856)	South-west W.A.
Chelodina expansa	*Chelodina expansa*	Gray (1857)	Murray-Darling and south coastal Qld.
*Chelodina kuchlingi**	*Chelodina kuchlingi*	Cann (1997c)	Kimberley, W.A.
Chelodina longicollis	*Testudo longicollis*	Shaw (1794)	Eastern Australia north to the Burdekin, Cooper Creek in central Australia
Chelodina mccordi	*Chelodina mccordi*	Rhodin (1994b)	Roti Island, Indonesia; East Timor
Chelodina novaeguineae	*Chelodina novae-guineae*	Boulenger (1888)	Southern New Guinea
Chelodina parkeri	*Chelodina parkeri*	Rhodin and Mittermeier (1976)	Fly/Strickland Rivers of New Guinea
Chelodina pritchardi	*Chelodina pritchardi*	Rhodin (1994a)	Kemp/Welch Rivers of New Guinea
Chelodina reimanni	*Chelodina reimanni*	Philippen and Grossman (1990)	Merauke region of west New Guinea
Chelodina rugosa	*Chelodina rugosa*	Ogilby (1890)	Northern Australia; Kimberley to Cape York
Chelodina steindachneri	*Chelodina steindachneri*	Siebenrock (1914)	Middle west of W.A.
Elseya belli	*Phrynops belli*	Gray (1841)	Namoi/Gwydir and Border Rivers (N.S.W.)
Elseya branderhorstii	*Emydura branderhorstii*	Ouwens (1914)	South-west New Guinea to Fly River
Elseya dentata	*Chelymys dentata*	Gray (1863)	North-west N.T. to Kimberley of W.A.
Elseya georgesi	*Elseya georgesi*	Cann (1997a)	Bellinger River, N.S.W.
Elseya irwini	*Elseya irwini*	Cann (1997b)	Burdekin River, Qld.
Elseya latisternum	*Elseya latisternum*	Gray (1867)	Richmond River N.S.W., coastal area to South Alligator River, N.T.
Elseya lavarackorum	*Emydura lavarackorum*	White and Archer (1994)	Nicholson River, Qld., to Roper River, N.T.
Elseya novaeguineae	*Platemys Novae Guineae*	Meyer (1874)	Vogelkopf Region of west New Guinea
Elseya purvisi	*Elseya purvisi*	Wells and Wellington (1985)	Manning River, N.S.W.
Elseya schultzei	*Emydura schultzei*	Vogt (1911)	Sepik River region of New Guinea
Elusor macrurus	*Elusor macrurus*	Cann and Legler (1994)	Mary River, Qld.
Emydura macquarii	*Chelys (Hydraspis) macquarii*	Gray (1830)	Murray-Darling system, eastern Qld. to Cooktown, coastal N.S.W. south to Sydney
Emydura subglobosa	*Euchelymys subglobosa*	Krefft (1876)	New Guinea and onshore islands, Cape York to Daly River, N.T.
Emydura tanybaraga	*Emydura tanybaraga*	Cann (1997d)	Cape York, Qld. to Kimberley region W.A.
Emydura victoriae	*Hydraspis victoriae*	Gray (1841)	Daly River, N.T. to Kimberley region W.A.
Pseudemydura umbrina	*Pseudemydura umbrina*	Seibenrock (1901)	Perth region of W.A.
Rheodytes leukops	*Rheodytes leukops*	Legler and Cann (1980)	Fitzroy River of Qld.

**Chelodina kuchlingi* was described from a single specimen of uncertain origin. It was held for a substantial period in captivity and its distinction from *C. rugosa* may be questioned.

Reprinted from *Evolution and Biogeography of Australasian Vertebrates* (Merrick *et al.*, Eds. 2006)

tata) is now known to be a series of highly divergent allopatric species (Georges and Adams, 1996). They are river turtles and largely herbivorous. *Elseya dentata* is restricted to the northern rivers west of, but not including, the Mary River of the Northern Territory. A distinct undescribed species occurs in the Mary River, the Alligator Rivers region and the rivers flowing north from the Arnhem Land plateau (*Elseya* sp. [Sth Alligator] of Georges and Adams, 1996). The Gulf snapping turtle, *Elseya lavarackorum*, is poorly known, but its distribution is thought to extend from the Roper River of the Northern Territory in the west to at least as far east as the Gregory-Nicholson systems in Queensland. There is an undescribed species in the Johnstone Rivers region near Cairns, *Elseya irwini* is restricted to the Burdekin and there is a third undescribed species in the Mary, Burnett and Fitzroy Rivers of south-eastern Queensland (Georges and Adams, 1996). A related form, the New Guinea snapping turtle *Elseya novaeguineae*, is widespread in New Guinea; however, *E. branderhorsti* is found only in southern rivers. It is likely that many more species will be discovered in New Guinea and adjacent islands (Rhodin and Genorupa, 2000; Sademi and Iskandar, 2000).

A second lineage of carnivorous and omnivorous species is currently grouped within *Elseya*. They tend to be most abundant in the upper reaches of rivers and their tributaries. The common sawshell, *Elseya latisternum,* is the most widespread. It occurs in coastal rivers from the Richmond River of northern New South Wales, to the Jardine River on the tip of Cape York, as well as rivers discharging into the Gulf of Carpentaria, and the headwaters of Arnhem Land plateau rivers. By contrast, other species in this group are very restricted. The Bellinger River turtle, *Elseya georgesi*, and Manning River turtle, *Elseya purvisi*, are each restricted to the respective coastal river systems (New South Wales) for which they are named. They are of particular interest because they are a cryptic species pair, morphologically difficult to distinguish on external examination, but deeply divergent genetically (Georges and Adams, 1996). Once thought to be a single species, the genetic examination prompted a closer look at their morphology and revealed that *Elseya purvisi* has a well-developed series of exposed neural bones, consistently lacking in *Elseya georgesi* (Thomson and Georges, 1996). Neural bones in most chelid turtles are reduced subsurface bony elements of the carapace lying immediately above the vertebral column (Thomson and Georges, 1996). A fourth species in this group, *Elseya belli*, is found in the granitic headwaters of the Namoi, Gwydir and Severn tributaries of the Darling River in inland New South Wales.

Other Short-necked Genera

The remaining short-necked chelid genera are monotypic. *Rheodytes leukops* is restricted to the Fitzroy-Dawson drainage, *Elusor macrurus* is found only in the Mary River of coastal Queensland, and *Pseudemydura umbrina* is restricted to coastal swamps near Perth.

Chelodina

Australia is well known for its snake-necked chelid turtles (genus *Chelodina*) because their necks can be spectacularly long in relation to their bodies, an innova-

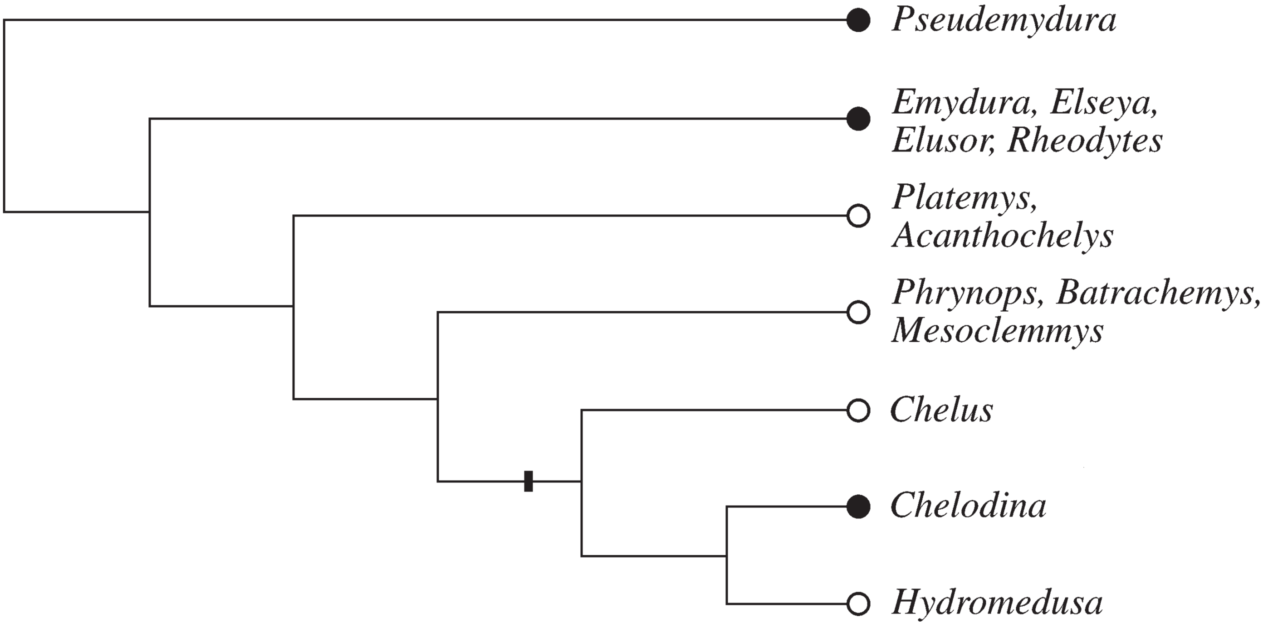


Figure 6. The most widely accepted hypothesis of the relationships among chelid turtles (Gaffney, 1977). Note that the three long-necked genera (*Chelus*, *Hydromedusa*, *Chelodina*) form a monophyletic group. This phylogeny, based on morphological characters, is at odds with the best molecular hypothesis (Georges *et al.*, 1998). Key to symbols: ▮ = long-necked; ● = Australian genera; ❍ = South American genera.

tion rare among the cryptodiran turtles that dominate the turtle fauna of the Northern Hemisphere. The evolution of long necks confers benefits of attenuated strike and gape feeding that enables these animals to secure fast-moving prey not available to their short-necked cousins. When feeding, the head and neck are thrust out against the inertia of the body. At the same time, the floor of the mouth is lowered causing an in-rushing of water to suck in the prey (Parmenter, 1976).

Species of *Chelodina* fall into three sub-generic groups (Burbidge *et al.*, 1974). *Chelodina longicollis* and *C. steindachneri* of Australia, *C. pritchardi, C. novaeguineae* and *C. reimanni* of New Guinea, *C. mccordi* of Roti and *C. canni* of Australia and New Guinea belong to Group A. They are carnivorous foragers with relatively narrow heads, shorter thinner necks and broader plastrons (Goode, 1967; Rhodin, 1994a, b). *Chelodina expansa, C. burrungandjii*, *C. rugosa, C. kuchlingi* and an undescribed species (*Chelodina* sp. aff. *expansa* [Cadell]) of Australia, and *C. siebenrocki* and *C. parkeri* of New Guinea belong to Group B. They are ambush predators with relatively broad heads, longer thicker necks and narrower plastrons (Goode, 1967; Rhodin and Mittermeier, 1976; Thomson *et al.*, 2000). *C. rugosa* and *C. siebenrocki* have been variously regarded as distinct species (Wermuth and Mertens, 1961; Burbridge *et al.*, 1974; Cogger, 1983) or the same (Siebenrock, 1909, 1915; Goode, 1967). Morphological evidence in support of their separation is scant. Burbidge *et al.* (1974) cite only ‘consistent, if minor, differences’ between the two as their basis for recognizing them as separate species. Rhodin and Mittermeier (1976) failed to reliably distinguish *C. rugosa* and *C. siebenrocki* following a morphological analysis, and chose to refer to them collectively as the *C. rugosa* complex. In the absence of any substantive diagnostic morphological differences or any substantive allozyme differences (Georges *et al.*, 2002), we synonymize *C. siebenrocki* with *C. rugosa* (the latter name has precedence). *Chelodina kuchlingi* was described from a single specimen of uncertain origin. It was held for a substantial period in captivity and, following a preliminary morphological analysis, we also have doubts about its separate identity from *C. rugosa*.

Chelodina oblonga of south-western Australia (= *C. colliei*, of Thomson, 2000a) is superficially similar to species of the Group B, and has often been placed in that group (Goode, 1967; Legler, 1981). However we follow Burbidge *et al.* (1974) and place it in a third subgeneric group, Group C. It is distinguished from other described *Chelodina* by a consistent set of well developed neural bones (Burbidge *et al.*, 1974; Thomson and Georges, 1996).

Carettochelys

Finally, the cryptodire, *Carettochelys insculpta*, is found in the Victoria, Fitzmaurice, Daly, South Alligator, East Alligator and Goomadeer Rivers of the Northern Territory.

In all there are 24 species of freshwater turtle currently described in Australia and 12 in New Guinea

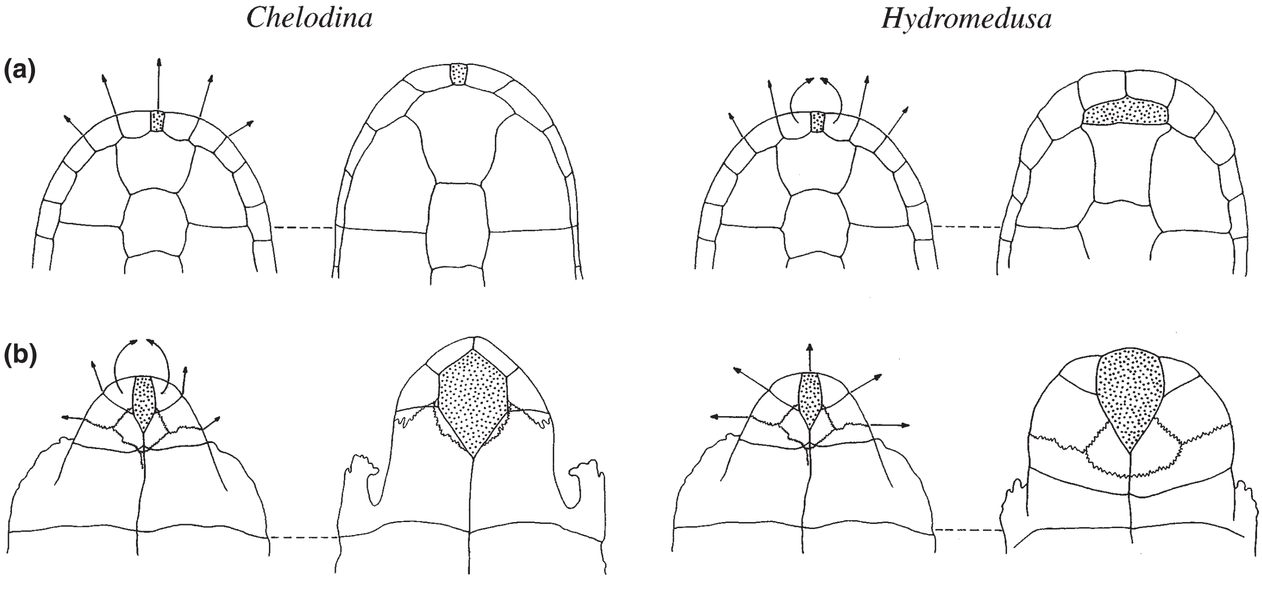


Figure 7. Shell and scute expansion in the evolution of *Chelodina* and *Hydromedusa* to accommodate the head and long neck within the shell. **(a)** Carapace. In *Chelodina*, expansion is achieved by elongation of the anterior vertebral and costal scutes, and the cervical scute (stippled) remains largely unaltered. In *Hydromedusa*, the cervical scute is expanded laterally and recedes behind the marginals. **(b)** Plastron. In *Chelodina*, the pectorals have elongated, and the gulars and humerals have migrated around the intergular scute (stippled). In *Hydromedusa*, the entoplastron and intergular scute are enlarged. Pritchard (1984) believes this argues against a close relationship between the two long-necked genera. Dashed line: common reference line. For scute names, refer to Figure 2. (After Pritchard, 1984).

(Table 2). As a result of recent molecular and morphological work we are, for the first time, able to map the distribution of freshwater turtle biodiversity across the Australian landscape (Figure 5). This map shows a hot spot of biodiversity in the Northern Territory. The Daly River alone has eight species and the broader region supports four endemics (*Carettochelys insculpta*, *Chelodina burrungandjii*, *Chelodina* sp. [Cadell], *Elseya* sp. [Sth Alligator] of Georges and Adams, 1996). There is a second hot spot in southern coastal Queensland, in the Mary, Burnett and Fitzroy drainages (Figure 5). The Fitzroy drainage basin alone supports six species and the broader region supports three endemics (*Rheodytes leukops*, *Elusor macrurus*, *Elseya* sp. [Burnett] of Georges and Adams, 1996). A seventh species, *Chelodina canni*, may also occur in the Fitzroy, as it is present in the small adjacent coastal drainage, the Styx. A third hot spot occurs in the south-western corner of Western Australia, based not on species richness, but on its two species, both endemic (*Chelodina oblonga, Pseudemydura umbrina*).

PHYLOGENY AND ZOOGEOGRAPHIC HYPOTHESES

Living and fossil chelid turtles are restricted to South America and Australasia, which raises the question of how the two faunas relate to each other.

SUGGESTED RELATIONSHIPS

The very early literature splits the Chelidae into two groups that do not recognize continental boundaries—those with a neck shorter than the shell (*Phrynops*, *Platemys*, *Elseya* and *Emydura*) and those with longer necks (*Chelus*, *Hydromedusa* and *Chelodina*) (Boulenger, 1888). This arrangement is reflected in the most widely accepted phylogeny for the chelids (Gaffney, 1977) based on a numerical cladistic analysis of a wide range of cranial and postcranial characters (Figure 6). It is also supported by the more recent work on fossil material from Argentina by de Broin and Fruente (1993), and the morphological analysis

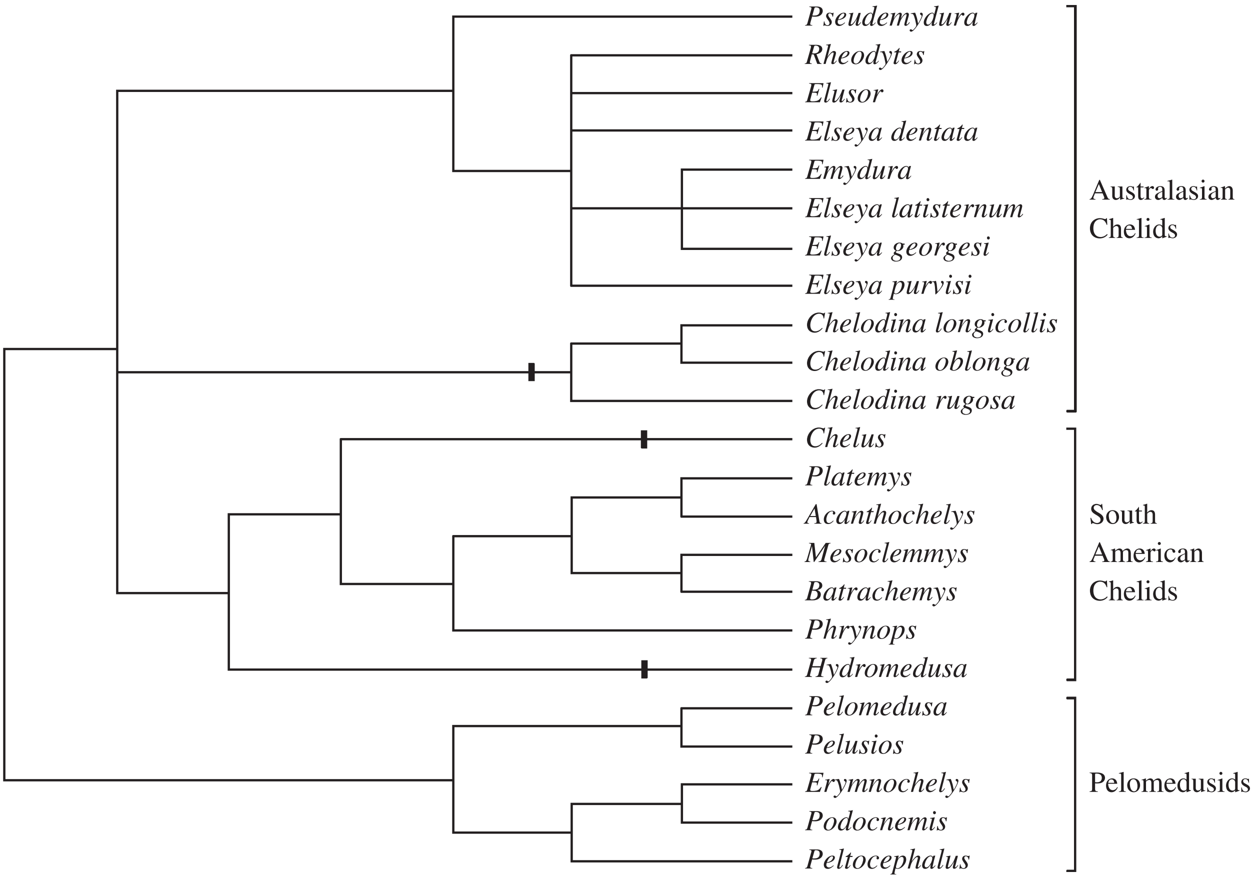


Figure 8. A consensus phylogeny for the Pleurodira, based on analysis of sequence data from three mitochondrial genes and one nuclear gene (Georges *et al.*, 1998). Bootstrap support for all resolved nodes exceeded 70%. The pelomedusids were used as an outgroup for the chelids. Note that the South American chelids are monophyletic, and that none of the long-necked genera (*Chelus*, *Hydromedusa*, *Chelodina*) are particularly closely related. Most of the molecular analyses had the Australian and South American chelids as reciprocally monophyletic, and the Australasian clade consisting of short-necked and long-necked lineages. Key: ▮ = long-necked.

of Shaffer *et al.* (1997) which consistently grouped *Chelodina* with *Chelus*. These analyses support a common derived origin of the long neck and associated habits of the South American *Hydromedusa*, *Chelus* and the Australian *Chelodina*, that pre-dated the separation of Australia and Antarctica from South America.

Although the above scheme summarized the prevalent view, it was not universally accepted. Pritchard (1984) took a more functional approach to his interpretation of characters than did Gaffney (1977). He argues that the development of a long neck requires expansion of the anterior plastral lobe and the anterior carapace to accommodate and protect the neck when withdrawn. Pritchard shows that turtles in the three genera have achieved this in fundamentally different ways (Figure 7), suggesting independent origins of the long neck, with supporting evidence from a range of other characters. Pritchard does not regard any of the long-necked genera as being particularly closely related, but regards *Hydromedusa* as more closely related to *Chelus* than to *Chelodina.*

The tensions that developed as a result of these conflicting views erupted in an interesting, if unproductive, debate between those who adhered to a numerical cladistic approach to phylogenetic reconstruction and Pritchard, who would admit functional interpretations of characters as evidence of close relationship or convergence (Pritchard, 1994; De Queiroz, 1995; Frost, 1995; Kluge, 1995; Meylan, 1995).

Pritchard's conclusion of independent origins of the long necks of *Chelodina* and the South American forms receives strong support from recent molecular studies (Seddon *et al.*, 1997; Shaffer *et al.*, 1997; Georges, 1997). The molecular phylogeny, based on DNA sequences from four mitochondrial genes (*12S rRNA*, *16S rRNA*, *CO1* and *cytochrome b*) and a nuclear gene (c-*mos*), has all South American chelids as a monophyletic assemblage to the exclusion of *Chelodina* and the other Australian chelids (Figure 8). Bootstrap values were in the range 76–82% (Georges *et al.*, 1998). Our reasons for preferring the molecular phylogeny over that generated by applying numerical cladistics to morphological data are presented by Georges *et al.* (1998). It would seem from the molecular analyses that the living Australian chelid turtles represent radiations that no longer have representatives in South America, though a strict analysis has the South American chelids, *Chelodina* and the remaining Australasian chelids in an unresolved trichotomy (Georges *et al.*, 1998). This caveat aside, much of the current freshwater turtle diversity in Australia most likely arose through radiations that occurred after the separation of Australia and Antarctica from South America, perhaps from a very limited surviving stock.

Carettochelydids are not of Gondwanan origin, as the fossil record for the family shows that it was a diverse group covering much of Laurasia by the Eocene (Meylan, 1987). *Carettochelys* is thought to have entered the Australasian region via South-east Asia.

Detailed molecular phylogenies are available for each of the short-necked and long-necked chelid turtles of Australasia (Georges and Adams, 1992; Georges *et al.*, 1998; Georges *et al.*, 2002), an essential prerequisite for generating zoogeographic hypotheses. The short-necked phylogeny is interesting in many respects (Figure 9). First, the genus *Elseya* is paraphyletic, as the closest common ancestor to the species of *Elseya* has *Emydura* among its descendants. This is an unacceptable arrangement for a genus, and is soon to be resolved by erecting a new genus for *Elseya latisternum*, *E. georgesi*, *E. purvisi* and *E. belli* (Thomson *et al.,* 2000, unpublished data).

A second interesting feature of the short-neck phylogeny is that the cryptic species pair, *Elseya georgesi* and *E. purvisi*, are not sister taxa (Georges and Adams, 1992; Georges *et al.*, 1998). *Elseya latisternum* and *E. belli* have arisen from a common ancestor with *E. georgesi* after the divergence of *E. georgesi* from *E. purvisi*. The rivers that they occupy are similar—clear, continuously flowing, over a stony bed—and in an area of long-term geological stability. There are two evolutionary scenarios to explain this aspect of the phylogeny. Either *Elseya georgesi* and *Elseya purvisi* have evolved independently but in parallel to maintain their striking similarity since they diverged, or they have jointly retained the primitive features of their common ancestor. The latter interpretation is much more likely, and if true, we have a rare window in time to view the ancestral form of *Elseya latisternum* and *E. belli*.

The *Chelodina* phylogeny is not contentious in most respects (Figure 10). One trend evident in the phylogeny is toward progressively greater robustness in the jaws of turtles most closely related to *Chelodina longicollis* (Group A species), culminating in the robust jaws of the molluscivorous *Chelodina reimanni*. Long robust necks and other modifications associated with an attenuated strike and suction mode of feeding, in response to a piscivorous diet (Pritchard, 1984), have evolved in species related to *Chelodina expansa* (Group B species). Traditionally, *Chelodina oblonga* was placed in this latter group, their similarity of form taken to indicate close phylogenetic relationship (Goode, 1967; Legler, 1981); however, recent molecular phylogenies (Georges and Adams, 1992; Georges *et al.*, 1998; Georges *et al.*, 2002) indicate that the adaptations associated with piscivory in this group have arisen twice independently. *Chelodina oblonga* has its closest relatives among the *Chelodina longicollis* group (Figure 10). Indeed, it would now appear that the exceptionally long necks and attenuated strike and suction mode of feeding have arisen four times in the Chelidae, in response to adopting a piscivorous diet (Pritchard, 1984), and perhaps because side-necked turtles are pre-disposed to do so. It has arisen in *Chelus* (sister to *Phyrnops*), *Hydromedusa* (sister to the remaining South American turtles), the *Chelodina expansa* group (sister to the remaining *Chelodina*), and *Chelodina oblonga* (sister to the *Chelodina longicollis* group) (Figures 8 and 10).

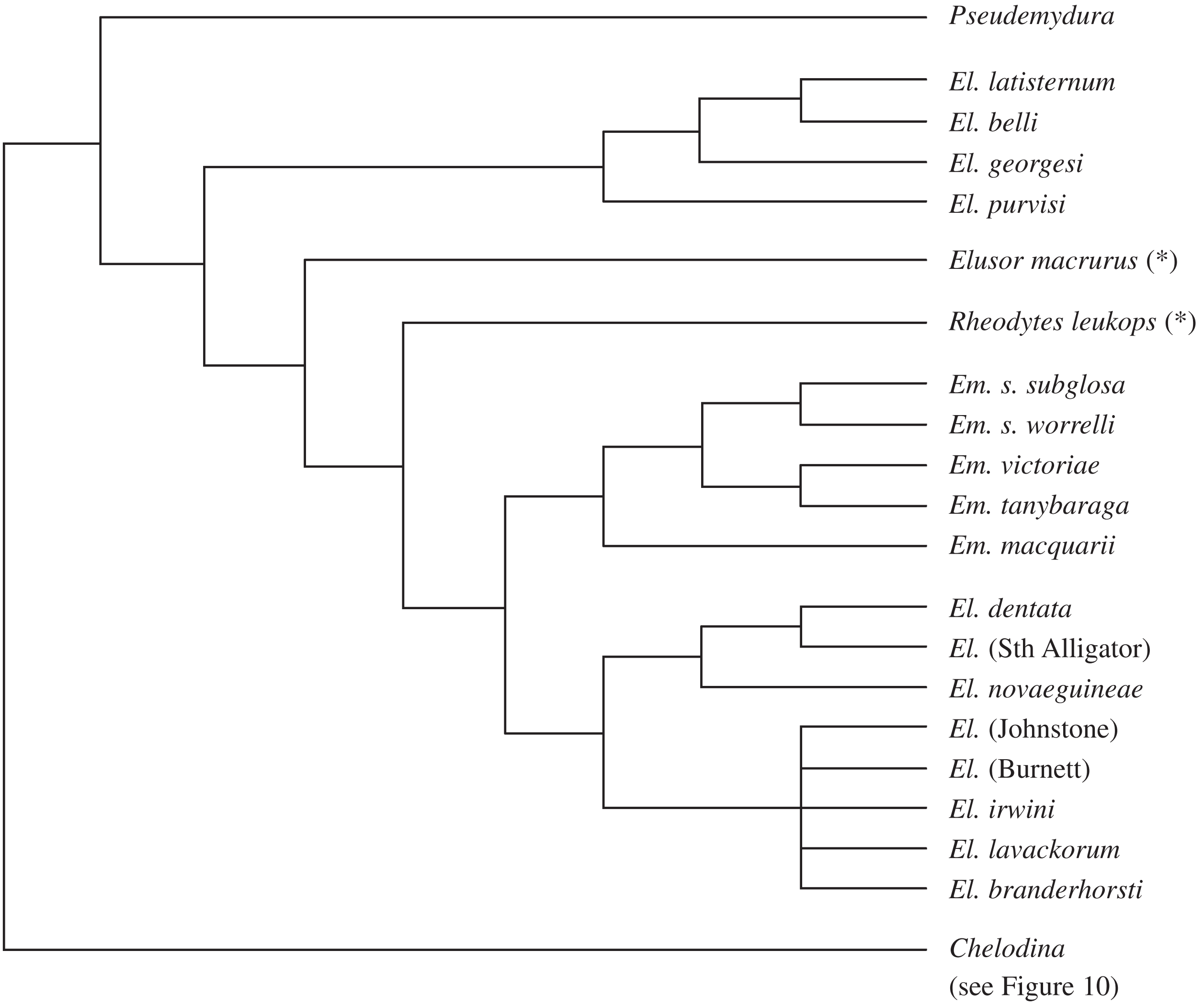


Figure 9. A phylogeny for the extant Australian chelids (outgroup = *Chelodina*), combining molecular (Georges and Adams, 1992; Georges *et al.*, 1998) and morphological results (Megirian and Murray, 1999). *Pseudemydura* was placed as sister to the remaining short-necks, to the exclusion of *Chelodina*, by the DNA sequence data (Georges *et al.*, 1998). The relationships of *Rheodytes leukops* and *Elusor macrurus* (*) are based entirely on the morphological data of Megirian and Murray (1999). Note that the genus *Elseya* is paraphyletic. Key to name abbreviations: *El.* = *Elseya*; *Em.* = *Emydura.*

DISTRIBUTION PATTERNS AND INFLUENCES

With the species boundaries well established and well supported phylogenies available for these species, it is possible to speculate on zoogeography within Australia. A number of climatic and geomorphological factors are thought to have influenced freshwater turtle distribution in Australia and Burbidge *et al.* (1974) first presented detailed arguments on the subject. They interpreted high endemism in the turtle fauna of south-west Western Australia to be a consequence of the sea that divided Australia from the Gulf of Carpentaria to the south coast in the Cretaceous and to the progressively increasing aridity and fragmentation of suitable habitat in the Tertiary. Discovery of a species of *Pseudemydura* from the Miocene of north-eastern Australia weakens the link to a sea barrier, but there is no doubt that increasing aridity in the Tertiary fragmented the landscape and limited dispersal opportunities. Turtles are absent from much of Australia's interior, and the western species *Chelodina steindachneri*, *Chelodina oblonga*, and *Pseudemydura* are isolated by aridity that extends to the coast.

Sea level change too has had an important influence. There have been 17 distinct glacial-interglacial cycles of at least 100,000 years duration during the last 1.8 million years of the Quaternary (Williams, 1984). These cycles have affected global eustatic sea levels (discounting local and regional tectonic and isostatic effects). Glacial episodes have resulted in low global sea levels, while

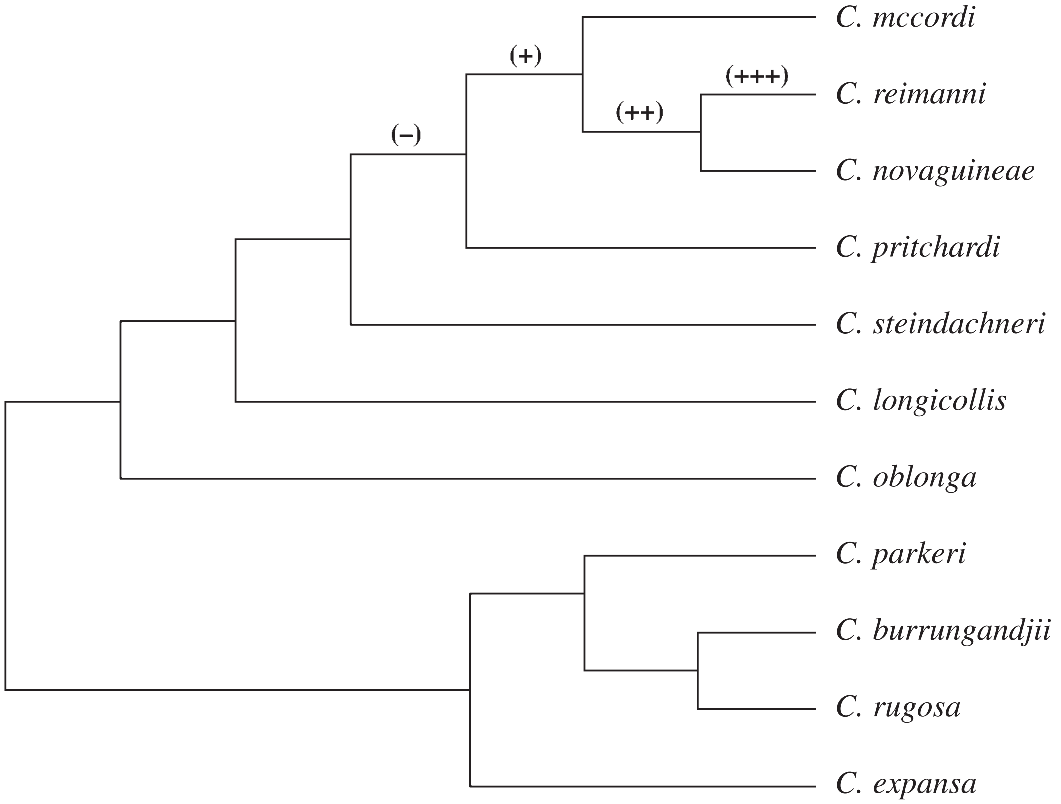


Figure 10. A phylogeny for the extant long-necked Australasian chelids (genus *Chelodina*) based on allozyme electrophoresis (Georges and Adams, 1992). No instances of paraphyly arise. Note that *Chelodina oblonga*, superficially similar to turtles in the *Chelodina expansa* group, has its strongest affinities with the *Chelodina longicollis* group. This arrangement is supported by the DNA sequence data (Georges *et al.*, 1998). Note that *C. reimanni* and *C. novaeguineae* (including *C. canni*) could not be separated electrophoretically, but we retain them as separate on the basis of morphological evidence (Philippen and Grossman, 1990; Rhodin, 1994a). Key to symbols: + = the progressive development of robusticity in both the skull and triturating surfaces; – = not robust.

glacial melting (interglacials) has resulted in high eustatic levels. Interglacial episodes with high global shorelines, such as those being experienced at present, have only accounted for about 10% of each cycle (Williams, 1984). Global sea levels are currently higher than at anytime during the last 120,000 years, separating Australia and New Guinea; however, Torres Strait has acted consistently as a land-bridge since the last interglacial about 118,000 years ago up until about 6,000 years ago, when marine transgression closed it (Chapell, 1983, 1994). This land-bridge is almost certainly the avenue by which *Emydura subglobosa subglobosa* entered Australia; the role of the exposed Sahul continental shelf and its implications for other New Guinean vertebrates has been discussed by Heinsohn and Hope (2006)—see pp.71–93.

About 12,000 years ago, sea levels were low enough that the Arafura Sill (53 m below current sea level) was exposed, and 20,000 years ago sea levels were 120 m below present levels (Chapell, 1994). The Arafura Sill is a broad feature nearly 100 km wide, with a total relief of less that 2 m (Torgerson *et al.*, 1983) that extends from the north-eastern extent of Arnhem Land to New Guinea east of Pulau Dolak and west of the mouth of the Fly. Between 12,000 and 55,000 years ago, the Gulf of Carpentaria was a large inland lake (Chapell, 1994) (Figure 11). The mighty Fly River flowed into the lake before being diverted to the east (Blake and Ollier, 1971; Torgersen *et al.*, 1988; McCulloch *et al.,* 1989). Pollen studies have shown that the vegetation surrounding the lake was very much as it is today in the open savanna country. The lake would have been fresh or brackish for much of its existence. If it connected to the sea, and no channel is evident from bathometry, then it would have done so to the west.

Evidence from deep core drilling reveals a pattern of establishment and marine inundation of Lake Carpentaria that appears to have been repeated. It was a freshwater lake in the Jurassic then inundated by a marine transgression (in limestone deposits), and there was a further freshwater episode in the Miocene, followed by another marine transgression (McConneckie, 1996, personal communication).

The current distribution of a number of northern turtle species can be explained by the opportunities the lake and the exposed Arafura Sill provided. *Chelodina rugosa* of Australia and *Chelodina siebenrocki* of New Guinea

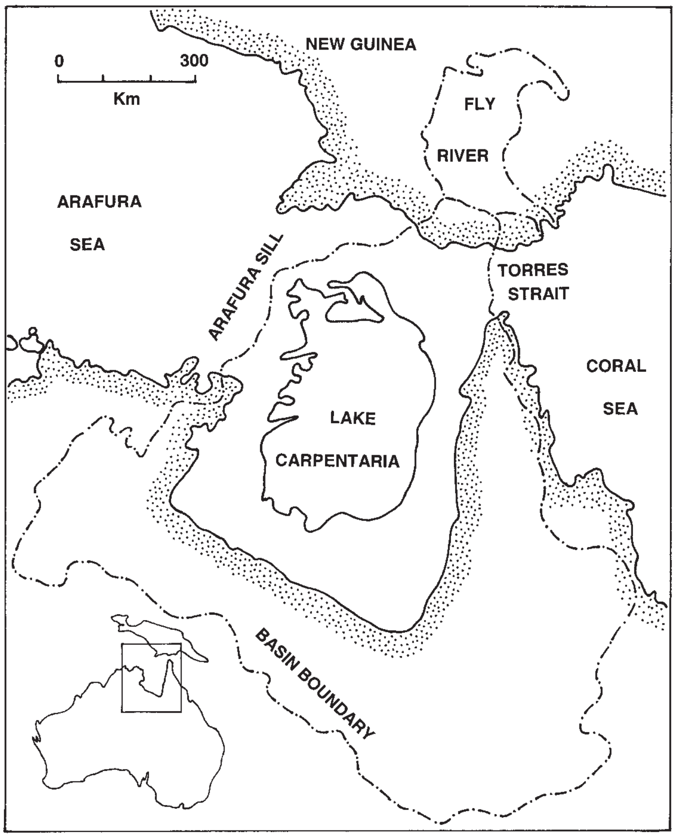


Figure 11. A map showing the relationship between Australia and New Guinea in the late Quaternary (55,000–12,000 years ago). The Gulf of Carpentaria was then a large inland freshwater or brackish lake. The Arafura Sill is 53 m below current sea levels, and Torres Strait is 12 m below current sea levels. The lake boundary corresponds to the –53 m contour, which corresponds to the maximum extent of Lake Carpentaria (Torgersen *et al.*, 1983; Torgersen *et al.*, 1985; Torgersen *et al.*, 1988). The Fly River flowed into the lake prior to its diversion into the Coral Sea in the late Quaternary. At the glacial maximum, most of what is shown as the Arafura Sea would have been terrestrial (after McCulloch *et al.*, 1989).

are indistinguishable electrophoretically (Georges *et al.*, 2002) and poorly differentiated morphologically (Rhodin and Mittermeier, 1976), and we regard them as a single taxon once forming a contiguous series of populations that circled Lake Carpentaria. Lack of variation shown by *Emydura subglobosa subglobosa* from southern Papua New Guinea and *Emydura subglobosa worrelli* from the Australian rivers discharging into the Gulf of Carpentaria (Georges and Adams, 1996) can be similarly interpreted. So too can the distribution of *Chelodina novaeguineae* and the closely related *C. canni*, and preliminary morphological analyses indicate that *Elseya lavarackorum* from the Gulf country and *Elseya branderhorsti* from southern New Guinea are very closely related. It seems that a number of contiguous turtle distributions have been disrupted in the last few tens of thousands of years by the inundation of Lake Carpentaria.

The Arafura Sill that defined the western boundary of Lake Carpentaria would also have provided a land-bridge to New Guinea presumably with drainages flowing west to the Timor Sea. This would have allowed potential interchange of forms between West Papua, Arnhem Land and the Kimberley via coastal rivers and associated habitat quite different from that provided by Lake Carpentaria. It would also have isolated the turtle fauna of these western and west-central rivers from those flowing into the eastern seaboard of Australia and south eastern New Guinea. This may explain the high level of endemism for the region from the Kimberley and western Arnhem Land—*Emydura victoriae*, *Carettochelys insculpta*, *Elseya dentata*, *Elseya* sp. [Sth Alligator], *Chelodina* sp. [Cadell] and *Chelodina burrungandjii*. *Carettochelys* presumably entered Australia from New Guinea via the opportunities that arose from the Arafura Sill land-bridge. These zoogeographic hypotheses, and others to do with Lake Carpentaria, could be tested by molecular comparisons between the Australian and New Guinean fauna.

In south-eastern Australia, the primary driving force behind current turtle distributions appears to be climatic. Australia's Pleistocene and Holocene climatic history is reasonably well documented (Frakes *et al.*, 1987). The last glacial build-up started about 30,000 years ago with the glacial maximum achieved about 18,000 years ago (Augustinus and Macphail, 1997). Ice sheets and glaciers were nowhere near as extensive as in the Northern Hemisphere. In Tasmania, where natural populations of freshwater turtles no longer exist, the ice cap was 700 m thick and covered an area of at least 6,000 km^2 (Kiernan 1990), whereas on mainland Australia, the glacial area was small, perhaps no more than 25 km^2. The area affected by frost and winter snowfalls was far more extensive however. Snowlines dropped as much as 1,000 m below current levels, and air temperatures were at least 6.5°C lower at the glacial maximum. Maximal aridity occurred about 12,000 years ago over south coastal and central Australia—81% of sampled lakes were low or dry (Harrison, 1993). Between 18,000 and 12,000 years ago in the Murray–Darling catchment the situation was similarly arid (Fried, 1993).

During these dry cold times, many of the more southerly distributed plant and animal species, including turtles, would have shifted their ranges north, suffering local extinction in the south, only to recolonize these areas after the retreat of glaciers around 10,000 years ago (Frakes *et al.*, 1987). *Emydura macquarii* currently ranges and breeds only as far into the colder regions of Australia as Burrinjuck Dam, near the border of the Australian Capital Territory. Its distribution in the Murray-Darling at the time of the glacial maximum would have contracted substantially, perhaps as far north as Brisbane, though to a lesser degree on the coast. *Chelodina expansa* would have been more severely affected, as it breeds in the autumn and winter, and its range extends less into colder regions than *Emydura macquarii*. Breeding populations of *Chelodina longicollis* occur near Cooma, which regularly receives winter snowfalls, so it would have been least affected. Accidental introductions of *Chelodina longicollis* in the north-west of Tasmania have shown that the climate is suitable for their establishment much further south than its current natural distribution.

Zoogeographic hypotheses relating to Pleistocene contractions of freshwater turtle populations, followed by rapid reinvasion during the current interglacial, are currently being tested using fine-scale molecular techniques of mtDNA and nuclear microsatellites (Shaffer *et al.*, 1999).

CONCLUSIONS

In summary, the zoogeography of the Australasian freshwater turtles can be understood on a number of temporal scales. Cryptodires dominated the Mesozoic turtle fauna of what we now call Australia, shifting to a chelid dominated fauna in the Tertiary. The Gondwanan origins of the Chelidae are not in doubt, as chelids are not known outside their present range, even as fossils. The Australian fauna was separated from that of South America in the Cretaceous, and the two chelid faunas now are probably reciprocally monophyletic (Georges *et al.*, 1998).

Progressively increasing aridity during the Tertiary reduced opportunities for freshwater turtles (now absent from much of central Australia) and fragmented the coastal regions, isolating in particular the fauna of the extreme south west (*Chelodina oblonga*, *Pseudemydura umbrina*). Recent rises and falls in sea level resulted in intermittent interconnection of Australia and New Guinea, providing opportunities for interchange between the two via a Torres Strait land-bridge, Lake Carpentaria and the rivers flowing west from the land-bridge formed by the exposure of the Arafura Sill. The terrestrial components of the land-bridges between New Guinea and Australia would have formed a barrier between the north-western fauna and the east coast fauna.

In the south, Pleistocene climate changes have resulted in the contraction and reinvasion of south-eastern Australia, particularly in the Murray-Darling drainage, and have resulted in isolated pockets of endemism in coastal New South Wales. These, coupled with Recent sea level rises, have prevented the reinvasion of Tasmania, although accidental introductions of *Chelodina longicollis* in the north-west of the island have shown that the climate is suitable for their establishment there. The Asian influence on our freshwater turtle fauna is represented by the cryptodires *Pelochelys bibroni* and *P. cantori* which have reached New Guinea but not yet Australia, and *Carettochelys insculpta*, which is found in both regions.

ACKNOWLEDGEMENTS

The authors wish to express their appreciation to Gene Gaffney for his interest and efforts in providing figures; the assistance of the American Museum of Natural History (New York) in providing illustrations is acknowledged. Arthur White (Sydney) is also thanked for permission to use unpublished information, and Jan Martin kindly reviewed the literature on Lake Carpentaria.

REFERENCES

Anderson, C. 1925. Notes on the extinct chelonian *Meiolania*, with a record of a new occurrence. *Records of the Australian Museum*, Vol. 14, pp.223–242.

Araujo, D.C.F. 1984. Sistematica e taxonomia dos pareiasaurios: historico prespectivas atuais. *Pesquisas, Porto Alegre,* Vol. 16, pp.227–249.

Augustinus, P.C. and Macphail, M.K. 1997. Early Pleistocene stratigraphy and timing of the Bulgobac Glaciation, western Tasmania, Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, Vol. 128, pp.153–167.

Blake, D.H. and Ollier, C.D. 1971. Alluvial plains of the Fly River, Papua. *Zeitschrift für Geomorphologie*, *Supplement* 12, pp.1–17.

Boulenger, G.A. 1888. On the chelydoid chelonians of New Guinea. *Annali del Museo Civico di Storia Naturale di Genova*, Vol. 6, No. 2, pp.449–452.

Brinkman, D.B. and Peng, J.H. 1993. Ordosemys leios, n.gen., n.sp., a new turtle from the early Cretaceous of the Ordos Basin, Inner Mongolia. *Canadian Journal of Earth Sciences,* Vol. 30, pp.2128–2138.

Broin, F. de 1987. The late Cretaceous fauna of Los Alamitos, Patagonia, Argentina. Part IV. Chelonia. Revista del Museo Argentino de Ciencias Naturales, Bernardino Rivadavia. *Paleontologia,* Vol. 3, No. 3, pp.131–139.

Broin, F. de and Fuente, M. 1993. Les tortues fossiles d'Argentine: synthese. *Annales de Paleontologie,* Vol. 79, pp.169–232.

Burbidge, A.A. 1967. *The biology of south-western Australian tortoises*. PhD Thesis (unpublished). University of Western Australia, Perth, W.A.

Burbidge, A.A., Kirsch, J.A.W. and Main, A.R. 1974. Relationships within the Chelidae (Testudines: Pleurodira) of Australia and New Guinea. *Copeia*, 1974, pp.392–409.

Cann, J. 1997a. Georges short-necked turtle. *Monitor (Victorian Herpetological Society, Melbourne),* Vol. 9, pp.18–23, 31, 32.

Cann, J. 1997b. Irwin's turtle. *Monitor (Victorian Herpetological Society, Melbourne),* Vol. 9, No. 1, pp.36–40, 31–32.

Cann, J. 1997c. Kuchling's long-neck turtle. *Monitor (Victorian Herpetological Society, Melbourne),* Vol. 9, No. 1, pp.41–44, 31–32.

Cann, J. 1997d. The northern yellow-faced turtle. *Monitor (Victorian Herpetological Society, Melbourne),* Vol. 9, No. 1, pp.24–29, 31–32, 34–35.

Cann, J. 1998. *Australian Freshwater Turtles*. Beaumont Publishing, Singapore. 292pp.

Cann, J. and Legler, J. 1994. The Mary River tortoise: a new genus and species of short-necked chelid from Queensland, Australia (Testudines: Pleurodira). *Chelonian Conservation and Biology,* Vol. 1, pp.81–96.

Cann, J., McCord, W.P. and Joseph-Ouni, N. 2003. Emmett's short-necked turtle, *Emydura macquarii emotti* spp. nov. *Reptilia*, Vol. 27, pp.60–61.

Chapell, J. 1983. A revised sea-level record for the last 300,000 years from Papua New Guinea. *Search*, Vol. 14, pp.99–100.

Chapell, J. 1994. Upper quaternary sea levels, coral terraces, oxygen isotopes and deep sea temperatures. *Journal of Geography,* Vol. 103, pp.828–840.

Cogger, H.G. 1983. *Reptiles and Amphibians of Australia*. A.H. and A.W. Reed, Sydney. 640pp.

Cogger, H.G. 2000. *Reptiles and Amphibians of Australia*. Reed New Holland, Sydney. 808pp.

De Queiroz K. 1995. Phylogenetic approaches to classification and nomenclature, and the history of taxonomy (an alternative interpretation). *Herpetological Review,* Vol. 26, pp.79–81.

Ernst, C.H. and Barbour, R.W. 1989. *Turtles of the World*. Smithsonian Institution Press, London.

Frakes, L.A., McGowran, B. and Bowler, J.M. 1987. Evolution of Australian environments. Pp.1–16. In Dyne, G.R. and Walton, D.W. (eds). *Fauna of Australia. Volume 1A. General Articles.* Australian Government Publishing Service, Canberra. 338pp.

Fried, A.W. 1993. Late Pleistocene river morphological change, south-eastern Australia: the conundrum of sinuous channels during the Last Glacial Maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology,* Vol. 101, pp.305–316.

Frost, D. 1995. Response to Peter Pritchard. *Herpetological Review,* Vol. 26, pp.81–83.

Gaffney, E.S. 1977. The side-necked turtle family Chelidae: a theory of relationships using shared derived characters. *American Museum Novitates*, No. 2620, pp.1–28.

Gaffney, E.S. 1979. Fossil chelid turtles of Australia. *American Museum Novitates*, No. 2681, pp.1–23.

Gaffney, E.S. 1981. A review of the fossil turtles of Australia. *American Museum Novitates*, No. 2720, pp.1–38.

Gaffney, E.S. 1983. The cranial morphology of the extinct horned turtle, *Meiolania platyceps*, from the Pleistocene of Lord Howe Island, Australia. *Bulletin of the American Museum of Natural History*, Vol. 175, pp.361–480.

Gaffney, E.S. 1985. *Meiolania platyceps* Owen 1886. The Lord Howe Island horned turtle. Pp.132–136. In Rich, P.V. and van Tets, G.F. (eds). *Kadimakara. Extinct Vertebrates of Australia*. Pioneer Design Studio, Melbourne. 284pp.

Gaffney, E.S. 1990. The comparative osteology of the Triassic turtle *Proganochelys*. *Bulletin of the American Museum of Natural History*, Vol. 194, pp.1–263.

Gaffney, E.S. 1991. The fossil turtles of Australia. Pp.704–720. In Vickers-Rich, P., Monaghan, J.M., Baird, R.F. and Rich, T.H. (eds). *Vertebrate Palaeontology of Australasia.* Pioneer Design Studio and Monash University Publications Committee, Melbourne. 1437pp.

Gaffney, E.S., Archer, M. and White, A. 1989. Chelid turtles from the Miocene freshwater limestones of Riversleigh Station, Northwestern Queensland, Australia. *American Museum Novitates*, No. 2959, pp.1–10.

Gaffney, E.S., Archer, M. and White, A. 1992. *Warkalania*, a new meiolaniid turtle from the Tertiary Riversleigh deposits of Queensland, Australia. *The Beagle (Records of the Museums and Art Galleries of the Northern Territory),* Vol. 9, No. 1, pp.35–48.

Gaffney, E.S. and Bartholomai, A. 1979. Fossil trionychids of Australia. *Journal of Paleontology*, Vol. 53, pp.1354–1360.

Gaffney, E.S., Kool, L., Rich, T., Vickers-Rich, P., Pledge, N., Archer, M. and White, A. 1998. *Otwayemys*, a new cryptodiran turtle from the early Cretaceous of Australia. *American Museum Novitates*, No. 3233, pp.1–28.

Gaffney, E.S. and Meylan, P.A. 1988. A phylogeny of turtles. Pp.157–219. In Brenton, M.J. (ed). *The Phylogeny and Classification of the Tetrapods*. (Systematics Association Special Volume 35A). Clarendon Press, Oxford.

Georges, A. and Adams, M. 1992. A phylogeny for Australian chelid turtles based on allozyme electrophoresis. *Australian Journal of Zoology*, Vol. 40, pp.453–476.

Georges, A. and Adams, M. 1996. Electrophoretic delineation of species boundaries within the short-necked chelid turtles of Australia. *Zoological Journal of the Linnean Society*, Vol. 118, pp.241–260.

Georges, A., Adams, M. and McCord, W. 2002. Delineation of species boundaries and a phylogeny for the snake-necked freshwater turtles of Australasia (Testudines: Chelidae: Chelodina). *Zoological Journal of the Linnean Society,* Vol. 134, pp.401–421.

Georges, A., Birrell, J., Saint, K., McCord, W.P. and Donnellan, S. 1998. A phylogeny for side-necked turtles (Chelonia: Pleurodira) based on mitochondrial and nuclear gene sequences. *Biological Journal of the Linnean Society*, Vol. 67, pp.213–246.

Glaessner, M.F. 1942. The occurrence of the New Guinea turtle (*Carettochelys*) in the Miocene of Papua. *Records of the Australian Museum*, Vol. 21, pp.106–109.

Goode, J. 1967. *Freshwater Tortoises of Australia and New Guinea (in the Family Chelidae).* Lansdowne Press, Melbourne. 154pp.

Gray, J.E. 1830. A synopsis of the species of the class Reptilia. Pp.1–110. In Griffith, E. (ed). *The Animal Kingdom. Arranged in Conformity with its Organization by the Baron Cuvier*. Whittaker, Treacher, London.

Gray, J.E. 1841. A catalogue of the species of reptiles and amphibia hitherto described as inhabiting Australia, with a description of some new species from Western Australia. Pp.422–449. In Grey, G. (ed). *Journals of Two Expeditions of Discovery in North-west and Western Australia, during the years 1837, 38 and 39, under the Authority of Her Majesty's Government.* T. and W. Boone, London.

Gray, J.E. 1856. On some new freshwater tortoises from North America, Ceylon and Australia, in the collection of the British Museum. *Proceedings of the Zoological Society of London*, 1856, pp.197–202.

Gray, J.E. 1857. Description of a new species of *Chelodina* from Australia. *Proceedings of the Zoological Society of London,* 1856, pp.369–371.

Gray, J.E. 1863. On the species of *Chelymys* from Australia, with the description of a new species. *Annals and Magazine of Natural History*, Vol. 12, pp.98–99, 246.

Gray, J.E. 1864. Revision of the species of Trionychidae found in Asia and Africa, with the descriptions of some new species. *Proceedings of the Zoological Society of London,* 1864, No. 6, pp.76–98.

Gray, J.E. 1867. Description of a new Australian tortoise (*Elseya latisternum*). *Annals and Magazine of Natural History*, Vol. 20, pp.43–45.

Harrison, S.P. 1993. Late quaternary lake-level changes and climates in Australia. *Quaternary Science Reviews*, Vol. 12, pp.211–231.

Heinsohn, T. and Hope, G. 2006. The Torresian connections: zoogeography of New Guinea. Pp.71–93. In Merrick, J.R., Archer, M., Hickey, G.M. and Lee, M.S.Y (eds). *Evolution and Biogeography of Australasian Vertebrates*. Auscipub Pty. Ltd., Sydney. 942pp.

Jaekel, O. 1914. Ueber die Wirbeltierfunde in der oberen Trias von Halberstadt. *Palaeontologica Zhurnal,* Vol. 1, pp.155–215.

Jaekel, O. 1918. Die Wirbeltierfunde aus dem Keuper von Halberstadt. Series II. Testudinata. Teil 1. *Stegochelys dux*, n.g., n.sp. *Palaeontologica Zhurnal*, Vol. 2, pp.88–214.

Kiernan, K. 1990. The extent of late Cainozoic glaciation in the central highlands of Tasmania, Australia. *Arctic and Alpine Research*, Vol. 22, pp.341–358.

Kluge, A.G. 1995. Parsimony. *Herpetological Review*, Vol. 26, pp.77–78.

Krefft, G. 1876. Notes on Australian animals in New Guinea with description of a new species of fresh water tortoise belonging to the genus *Euchelymys* (Gray). *Annali di Museo Civico di Storia Naturale di Giacomo Doria*, Vol. 1, pp.390–394.

Lee, M.S.Y. 1993. The origin of the turtle body plan: bridging a famous morphological gap. *Science*, Vol. 261, pp.1716–1720.

Legler, J.M. 1981. The taxonomy, distribution, and ecology of Australian freshwater turtles (Testudines: Pleurodira: Chelidae). *National Geographic Society Research Reports*, Vol. 13, pp.391–404.

Legler, J.M. and Cann, J. 1980. A new genus and species of chelid turtle from Queensland, Australia. *Contributions to Science (Natural History Museum of Los Angeles County)*, Vol. 324, pp.1–18.

Longman, H.A. 1915. On a giant turtle from the Queensland lower Cretaceous. *Memoirs of the Queensland Museum*, Vol. 3, pp.24–29.

McCord, W.P., Cann, J. and Joseph-Ouni, N. 2003. Fraser Island short-neck turtle, *Emydura macquarii nigra* spp. nov. *Reptilia*, Vol. 27, pp.62–63.

McCord, W.P. and Thompson, S.A. 2002. A new species of *Chelodina* (Testudinata: Pleurodira: Chelidae) from northern Australia. *Journal of Herpetology*. Vol. 36, pp.255–267.

McCulloch, M.T., DeDeckker, P. and Chivas, A.R. 1989. Strontium isotope variations in single ostracod valves from the Gulf of Carpentaria, Australia. A paleoenvironmental indicator. *Geochimica et Cosmochemica Acta*, Vol. 53, No. 7, pp.1703–1710.

Megirian, D. 1992. *Meiolania brevicollis* sp. nov. (Testudines: Meiolaniidae): a new horned turtle from the Australian Miocene. *Alcheringa*, Vol. 16, pp.93–106.

Megirian, D. and Murray, P. 1999. Chelid turtles (Pleurodira, Chelidae) from the Miocene Camfield Beds, Northern Territory of Australia, with a description of a new genus and species. *The Beagle (Records of the Museums and Art Galleries of the Northern Territory)*, Vol. 15, pp.75–130.

Meyer, A.B. 1874. *Platemys novae-guineae* sp. nov. Eine Mittheilung von Hrn. Adolf Bernhard Meyer uber die von ihm auf Neu-Guinea und den Inseln Jobi, Mysore und Mafoor im Jahre 1873 gesammelten Amphibien. *Monatsberichte der Koniglich Preussischen Akademie der Wissenschaften zu Berlin*, Vol. 39, pp.128–140.

Meylan, P.A. 1987. The phylogenetic relationships of soft-shelled turtles (Family Trionychidae). *Bulletin of the American Museum of Natural History*, Vol. 186, pp.1–101.

Meylan, P. 1995. Cladistics: a response to Pritchard. *Herpetological Review*, Vol. 26, pp.83–85.

Molnar, R.E. 1991. Fossil reptiles in Australia. Pp.605–702. In Vickers-Rich, P., Monaghan, J.M., Baird, R.F. and Rich, T.H. (eds). *Vertebrate Palaeontology of Australasia*. Pioneer Design Studio and Monash University Publications Committee, Melbourne. 1437pp.

Ogilby, J.D. 1890. Description of a new Australian tortoise. *Records of the Australian Museum*, Vol. 1, pp.56–59.

Ouwens, P.A. 1914. List of Dutch East Indian Chelonians in the Buitenzong Zoological Museum. *Contributions a la Faune des Indes Neelandaises*, Vol. 1, pp.29–32.

Owen, R. 1853. *Descriptive Catalogue of the Osteological Series contained in the Museum of the Royal College of Surgeons of England. Volume 1. Pisces, Reptilia, Aves, Marsupalia*. Taylor and Frances, London.

Owen, R. 1882. On an extinct chelonian reptile (*Notochelone costata*, Owen) from Australia. *Journal of the Geological Society of London*, Vol. 38, pp.178–183.

Owen, R. 1886. Description of fossil remains of two species of a Megalanian genus (*Meiolania*) from "Lord Howe Island". *Transactions of the Royal Society of London*, Vol. 177, pp.471–480.

Parmenter, C.J. 1976. *The natural history of the Australian freshwater turtle* Chelodina longicollis *Shaw (Testudinata, Chelidae).* PhD Thesis (unpublished), University of New England, Armidale, N.S.W.

Philippen, H.D. and Grossman, P. 1990. Eine neue Schlangenhalsschildkrote von Neuguinea: *Chelodina reimanni* sp. n. (Reptilia, Testudines, Pleurodira, Chelidae). *Zoologische Abhandlungen, Staatliches Museum für Tierkunde, Dresden*, Vol. 46, No. 5, pp.95–102.

Pritchard, P.C.H. 1979. Taxonomy, evolution, and zoogeography. Pp.1–42. In Harless, M. and Morlock, H. (eds). *Turtles: Perspectives and Research.* John Wiley, New York. 695pp.

Pritchard, P.C.H. 1984. Piscivory in turtles, and evolution of the long-necked Chelidae. *Symposia of the Zoological Society of London*, Vol. 52, pp.87–110.

Pritchard, P.C.H. 1994. Cladism: the great delusion. *Herpetological Review*, Vol. 25, pp.103–110.

Ramsay, E.P. 1886. On a new genus and species of fresh water turtle from the Fly River, New Guinea. *Proceedings of the Linnean Society of New South Wales*, Vol. 1, pp.158–162.

Reisz, R.R. and Laurin, M. 1991. *Owenetta* and the origin of turtles. *Nature*, Vol. 349, pp.324–326.

Rhodin, A.G.J. 1994a. Chelid turtles of the Australasian Archipelago: I. A new species of *Chelodina* from south-eastern Papua New Guinea. *Breviora (Museum of Comparative Zoology),* No. 497, pp.1–36.

Rhodin, A.G.J. 1994b. Chelid turtles of the Australasian Archipelago: II. A new species of *Chelodina* from Roti Island, Indonesia. *Breviora (Museum of Comparative Zoology)*, No. 498, pp.1–31.

Rhodin, A.G.J. and Genorupa, V.R. 2000. Conservation status of freshwater turtles in Papua New Guinea. *Chelonian Research Monographs*, Vol. 2, pp.129–136.

Rhodin, A.G.J. and Mittermeier, R.A. 1976. *Chelodina parkeri*, a new species of chelid turtle from New Guinea, with a discussion of *Chelodina siebenrocki* Werner, 1901. *Bulletin of the Museum of Comparative Zoology*, Vol. 147, No. 11, pp.465–488.

Sademi and Iskandar, D.T. 2000. Freshwater turtle and tortoise conservation and utilization in Indonesia. *Chelonian Research Monographs*, Vol. 2, pp.106–111.

Seddon, J.M., Georges, A., Baverstock, P.R. and McCord, W. 1997. Phylogenetic relationships of chelid turtles (Pleurodira: Chelidae) based on mitochondrial 12S rRNA gene sequence variation. *Molecular Phylogenetics and Evolution*, Vol. 7, pp.55–61.

Shaffer, H.B., Meylan, P. and McKnight, M.L. 1997. Tests of turtle phylogeny: molecular, morphological, and paleontological approaches. *Systematic Biology*, Vol. 46, pp.235–268.

Shaffer, H.B., Storz, B.L., Georges, A. and Starkey, D. 1999. Pleistocene glaciation, population substructure, and genetic differentiation in long-generation time vertebrates: a case study in eastern Australian turtles. *Evolution*, Vol. 99.

Shaw, G. 1794. *Zoology of New Holland*. J. Davis, London.

Siebenrock, F. 1901. Beschreibung einer neuen Schildkrotengattung aus der Familie Chelydidae aus Australien: Pseudemydura. *Anzeiger der Akademischen Wissenschaften Wien,* Vol. 38, pp.248–251.

Siebenrock, F. 1909. Synopsis der rezenten Schilderkroten. *Zoologische Jahrbucher*, *Supplement* No. 10, pp.427–618.

Siebenrock, F. 1914. Eine neue Chelodina Art aus Westaustralien. *Anzeiger der Akademischen Wissenschaften Wien*, Vol. 17, pp.386–387.

Siebenrock, F. 1915. Die Schildkrotensammlung *Chelodina* Fitz. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathmatisch-Naturwissenschaftliche Classe, Wien,* Vol. 124, pp.13–35.

Thomson, S.A. 2000a. On the identification of the holotype of *Chelodina oblonga* (Testudinata: Chelidae) with a discussion of the taxonomic implications. *Chelonian Conservation and Biology,* Vol. 3, No. 4, pp.745–749.

Thomson, S.A. 2000b. A revision of the fossil chelid turtles (Pleurodira) described by C.W. DeVis (1897). *Memoirs of the Queensland Museum*, Vol. 43, pp.593–598.

Thomson, S.A. and Georges, A. 1996. Neural bones in chelid turtles. *Chelonian Conservation and Biology*, Vol. 2, pp.82–86.

Thomson, S.A., Kennett, R. and Georges, A. 2000. A new species of long necked turtle (Chelidae:Chelodina) from the Arnhem Land plateau, Northern Territory, Australia. *Chelonian Conservation and Biology*, Vol. 3, No. 4, pp.675–685.

Thomson, S.A. and Mackness, B. 1999. Fossil turtles from the early Pliocene Bluff Downs Local Fauna, with a description of a new species of *Elseya. Transactions of the Royal Society of South Australia*, Vol. 123, pp.101–105.

Thomson, S.A., White, A. and Georges, A. 1997. Re-evaluation of *Emydura lavarackorum*: identification of a living fossil. *Memoirs of the Queensland Museum*, Vol. 42, pp.327–336.

Torgersen, T., Hutchinson, M.F., Searle, D.E. and Nix, H.A. 1983. General bathymetry of the Gulf of Carpentaria and the Quaternary physiography of Lake Carpentaria. *Palaeogeography, Palaeoclimatology, Palaeoecology*, Vol. 41, pp.207–225.

Torgersen, T., Jones, M.R., Stephens, D.E. and Ullman, W.J. 1985. Late Quaternary hydrological changes in the Gulf of Carpentaria. *Nature*, Vol. 313, pp.785–787.

Torgersen, T., Luly, J., De Decker, P., Jones, M.R., Searle, D.E., Chivas, A.R. and Ullman, W.J. 1988. Late Quaternary environments of the Gulf of Carpentaria, Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, Vol. 67, pp.245–261.

Vis C.W. de 1897. The extinct fresh-water turtles of Queensland. *Annals of the Queensland Museum,* Vol. 3, pp.1–7.

Vogt, T. 1911. *Emydura schultzei*, sp. nov. Reptilien und Amphibien aus Neu Guinea. *Sitzgunsberichte der Gesellschaft der naturforschenden Freunde, Berlin*, Vol. 9, pp.410–412.

Warren, J.W. 1969. A fossil chelonian of probable lower Cretaceous age from Victoria. *Memoirs of the National Museum, Victoria*, Vol. 29, pp.23–28.

Wells, R. and Wellington, R. 1985. A classification of the Amphibia and Reptilia of Australia. *Australian Journal of Herpetology, Supplementary Series*, No. 1, pp.1–61.

Wermuth, H. and Mertens, R. 1961. *Schildkroten, Krokodile, Bruckenechsen.* Gustav Fischer Velag, Jena.

White, A. 1990. 'Murgon's Salad Bowl'. The only thing missing is the dressing. *Riversleigh Notes,* Vol. 10, pp.6–7.

White, A. 1994. The fossil history of soft-shelled turtles. *Riversleigh Notes*, Vol. 14, pp.2–4.

White, A.W. 1993. Riversleigh researchers. Part 3—Arthur White reveals much about aspects of his "Turtlemania". *Riversleigh Notes*, Vol. 17, pp.4–6.

White, A.W. and Archer, M. 1994. *Emydura lavarackorum*, a new Pleistocene turtle (Pleurodira: Chelidae) from fluvatile deposits at Riversleigh, northwestern Queensland. *Records of the South Australian Museum*, Vol. 27, pp.159–167.

Williams, E.E. 1953a. Fossils and the distribution of Chelyid turtles (1). *Breviora (Museum of Comparative Zoology)*, No. 13, pp.1–8.

Williams, E.E. 1953b. Fossils and the distribution of Chelyid turtles (2). *Breviora (Museum of Comparative Zoology)*, No. 32, pp.1–6.

Williams, M.A.J. 1984. Paleoclimates and paleoenvironments. Pp.42–47. In Veevers, J.J. (ed). *Phanerozoic Earth history of Australia*. Clarendon Press, Oxford. 418pp.

Wood, R.C. 1976. *Stupendemys geographicus*, the world's largest turtle. *Breviora (Museum of Comparative Zoology)*, No. 436, pp.1–31.

Woodward, A.S. 1901. On some extinct reptiles from Patagonia, of the genera *Meiolania, Dinilysia*, and *Genyodectes*. *Proceedings of the Zoological Society of London* 1901, pp.169–184.

Zangerl, R. 1969. The turtle shell. Pp.311–339. In Gans, C., Bellairs, A.d'A. and Parsons, T.S. (eds). *Biology of the Reptilia.* Academic Press, New York.

Plate 62. The mode of withdrawal of the head and neck in an Australian hidden-necked turtle (Cryptodira: Carettochelyidae), the pig-nosed turtle *Carettochelys insculpta*. Photograph J. Cann.

Plate 63. The mode of withdrawal of the head and neck in an Australian side-necked turtle (Pleurodira: Chelidae), the Gulf snapper *Elseya lavarackorum*. Photograph A. Georges.

Plate 64. This broad-shelled turtle (*Chelodina expansa*) has a broad range in the Murray–Darling and southern North-east Coast drainage divisions. This secretive species can be found in both rivers and still impoundments, such as farm dams. Photograph J. Cann.

Plate 65. Another freshwater turtle from the Namoi River, New South Wales. This is one of the *Elseya latisternum* group from mid-eastern Australia. Photograph J. Cann.

Reprinted from *Evolution and Biogeography of Australasian Vertebrates* (Merrick *et al.*, Eds. 2006)