ELSEVIER

Cretaceous Research 24 (2003) 277–303

CRETACEOUS RESEARCH

Cretaceous marine reptiles of Australia: a review of taxonomy and distribution

Benjamin P. Kear[a,b]

[a] South Australian Museum, North Terrace, Adelaide 5000, South Australia (current address)
[b] Vertebrate Palaeontology Laboratory, School of Biological, Earth and Environmental Sciences, University of New South Wales, New South Wales, Sydney 2052, Australia

Accepted 8 April 2003

Abstract

Marine reptile fossils are common in the Cretaceous epicontinental and continental-margin marine deposits of Australia but much of the material is sparsely documented. A review of current localities indicates that the majority of remains are known from the Aptian–Albian epicontinental marine units of the Eromanga Basin in Queensland, New South Wales and South Australia. Fragmentary specimens have also been recovered from Berriasian, Hauterivian–Barremian, Albian–Cenomanian, Cenomanian–Turonian and Maastrichtian marine deposits of Western Australia, Aptian or Albian continental margin rocks of the Northern Territory and Aptian–Albian freshwater sediments of New South Wales and Victoria. Interestingly, many of these deposits represent Cretaceous high latitude-polar environments and some include palaeoclimatic indicators suggesting very cold to near freezing conditions. As currently known, the Australian Cretaceous marine reptile fauna comprises one family of ichthyosaurs (Ophthalmosauridae), as many as five families of plesiosaur (Rhomaleosauridae, Pliosauridae, Polycotylidae, Elasmosauridae and possibly Cryptoclididae or Cimoliasauridae sensu Acta Zool. Fenn. 213 (2001)), one family of chelonioid sea turtle (Protostegidae) and indeterminate mosasaurids. Although few named Australian species may be regarded as valid, the stratigraphic distribution of taxa correlates well with that from elsewhere. Plesiosaurs and ichthyosaurs dominate Lower Cretaceous deposits with plesiosaurs showing a high taxonomic diversity (including the earliest known polycotylids), particularly in the Aptian. Albian faunas see the advent of chelonioid turtles with a corresponding reduction in plesiosaur diversity (through the loss of rhomaleosaurids) and a marked increase in the numbers of ichthyosaur remains. Upper Cretaceous units have produced only fragmentary specimens of primarily plesiosaurs and mosasaurs with ichthyosaurs limited to rocks of Cenomanian age.

Keywords: Marine reptiles; Cretaceous; Australia; Current deposits; Taxonomy; Distribution

1. Introduction

Marine reptile remains have long been known from the extensive Cretaceous epicontinental and continental margin marine deposits of Australia, and in particular, those of the Eromanga Basin in northern and central Queensland. The fossils include relatively common ichthyosaurs, plesiosaurs and turtles, with rare mosasaurs also recorded from the Carnarvon Basin and Perth Basin in Western Australia. Of the currently productive units, the Rolling Downs Group (Queensland and New South Wales) has been most prolific, containing large exposures of Aptian–Cenomanian marine sediments, that have proved readily accessible to both Australian and international researchers over the years. Unfortunately, there have been few published studies, although some key historical works (e.g. Etheridge, 1897 Etheridge, 1904; Longman, 1915, 1922, 1924, 1943; White, 1935; Persson, 1960), and various recent analyses based mainly on discrete finds (e.g. Gaffney, 1981; Persson, 1982; Murray, 1985, 1987; Wade, 1984, 1990; Molnar, 1982a,b, 1991; Thulborn and Turner, 1993; Cruickshank and Long, 1997; Long and Cruickshank, 1998; Cruickshank et al., 1999; Choo, 1999; Kear, 2001; Kear 2002a,b,c), have been undertaken. It is, therefore, the purpose of this article to review the current state of

E-mail address: kear.ben@saugov.sa.gov.au (B.P. Kear).

0195-6671/03/$ - see front matter
doi:10.1016/S0195-6671(03)00046-6

existing knowledge on Australian Cretaceous marine reptile fossils and provide a basis for informed future study.

2. Abbreviations and terminology

Repository abbreviations: AM, Australian Museum, Sydney; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; NMV, Melbourne Museum, Melbourne; NTM, Museum and Art Gallery of the Northern Territory, Darwin; QM, Queensland Museum, Brisbane; SAM, South Australian Museum, Adelaide; WAM, Western Australian Museum, Perth. Lithostratigraphic nomenclature for Australian Lower Cretaceous deposits follows Vine et al. (1967) for Queensland localities, Wopfner et al. (1970) for South Australian, Rich and Rich (1989) for Victorian, Burton and Mason (1998) for White Cliffs, Mory (1988) for the Darwin area, Shafik (1990) for the Perth Basin and Hocking et al. (1987) for the Carnarvon Basin units. Systematic terminology follows Motani (1999) and McGowan and Motani for Ichthyosauria Hirayama (1994, 1997, 1998) for Chelonioidea. High-level classification of the Plesiosauria follows O'Keefe (2001) except in the ranking of Sauropterygia and Plesiosauria, both which follow the more conventional system of Carroll (1988), Benton (1997) and Rieppel (2000).

3. Current localities and horizons

The quality of most Australian marine reptile holotypes is poor, although surprisingly, a large number of often exceptionally preserved undescribed specimens (representing a wide variety of major clades) do exist in current collections. The majority of these remains have been recovered as chance occurrences in the Wallumbilla Formation, Toolebuc Formation, Allaru Mudstone, Mackunda Formation (Eromanga Basin) and Bungil Formation (Surat Basin) of Queensland, Bulldog Shale and Oodnadatta Formation (Eromanga Basin) of South Australia, Darwin Formation (Money Shoals Platform) of the Northern Territory, Barrow Group, Birdrong Sandstone, Alinga Formation, Miria Formation (Carnarvon Basin) and Molecap Greensand (Perth Basin) of Western Australia and the freshwater deposits of the Wonthaggi Formation (Gippsland Basin) and Eumeralla Formation (Otway Basin) in Victoria and Griman Creek Formation (Surat Basin) of the New South Wales/Queensland border area (see Fig. 1, Table 1).

The Wallumbilla Formation, Toolebuc Formation and Allaru Mudstone (Rolling Downs Group) are best represented in the Hughenden–Richmond region of central northern Queensland (Fig. 1), where they currently include some the most productive Australian localities for ichthyosaurs, plesiosaurs and chelonioid turtles. The deposits comprise shallow marine, laminated, clayey mudstones that produce excellently preserved (although often incomplete) fossil skeletons encased within carbonate limestone nodules. Assignment of most existing specimens to a specific stratigraphic horizon is problematic (owing largely to poor locality information), although broad age ranges (derived primarily from palynological data; see Table 1) can be established based upon the unit of origin. The majority of remains are derived from the Toolebuc Formation, which has been placed within the latest mid to Upper Albian *Pseudoceratium ludbrookiae* dinoflagellate Zone, and upper *Coptospora paradoxa* spore-pollen Zone in the southern Eromanga Basin (Moore et al., 1986; Alexander and Sansome, 1996), and diachronously in the Upper Albian *Phimopollenites pannosus* spore-pollen Zone further north (McMinn and Burger, 1986). The overlying Allaru Mudstone (which corresponds to the Oodnadatta Formation of South Australia; Moore and Pitt, 1985; Moore et al., 1986) correlates with the upper *C. paradoxa* Zone, and the *P. pannosus*, *C. denticulata*, and *P. ludbrookiae* zones, indicating a mid–Upper Albian age (Krieg and Rodgers, 1995). The underlying Wallumbilla Formation, which also crops out in northern New South Wales and equates to the Bulldog Shale in South Australia (Krieg and Rodgers, 1995), preserves a somewhat different marine reptile fauna (including ichthyosaurs and a diverse range of plesiosaurs but no chelonioids; see Table 2), and spans the Lower Aptian–mid Albian *Cyclosporites hughesii* and *Crybelosporites striatus* spore-pollen zones, and the *Odontochitina operculata*, *Diconodinium davidii* and *Muderongia tetracantha* dinoflagellate zones (Helby et al., 1987). Unlike the southern Bulldog Shale deposits, however, the Wallumbilla Formation also continues into the *C. paradoxa*, *C. denticulata* and lower part of the *P. ludbrookiae* zones, indicating an age extension into the Late Albian (Helby et al., 1987; Alexander and Sansome, 1996).

Fragmentary plesiosaur remains have been recorded from the Lower Aptian (lower *C. hughesii*–lower *O. operculata* zones; Burger, 1980; Morgan, 1980) Bungil Formation (Minmi Member), Roma district (Fig. 1), and Upper Albian–Lower Cenomanian (*P. ludbrookiae*/*P. pannosus*–*Appendiscisporites distocarinatus* zones, Rodgers, 1995) Mackunda Formation, of Hampden Downs and Wetherby near Richmond in Queensland (Fig. 1). Both of these units comprise fine-grained sediments with abundant calcareous and carbonaceous material representing paralic to brackish/non-marine depositional environments.

The subsurface opal-bearing deposits of the Bulldog Shale at Coober Pedy and Andamooka in South Australia, and the Doncaster Member of the Wallumbilla Formation at White Cliffs in New South

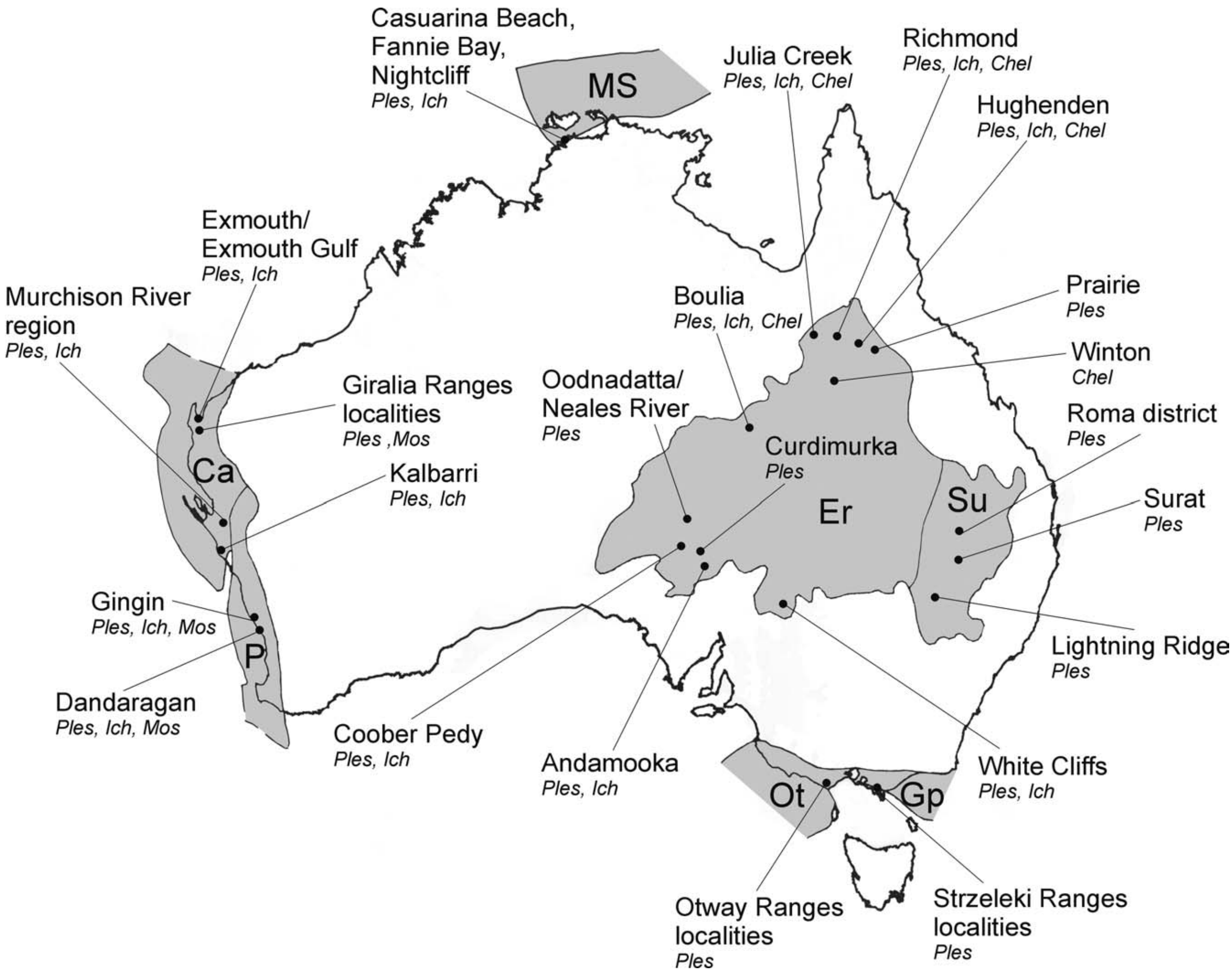


Fig. 1. Map showing Australian sedimentary basins with major Australian localities that have produced Cretaceous marine reptile fossils. Abbreviations: Ca, Carnarvon Basin; *Chel*, Chelonioidea; Er, Eromanga Basin; Gp, Gippsland Basin; *Ich*, Ichthyosauria; *Mos*, Mosasauridae; MS, Money Shoals Platform; Ot, Otway Basin; P, Perth Basin; *Ples*, Plesiosauria; Su, Surat Basin.

Wales (Fig. 1) represent localities of some significance, producing ichthyosaurs and a high diversity of plesiosaur taxa (Table 2). The sediments comprise predominantly finely laminated shaly mudstones and claystones representing deposition under transgressive shallow marine conditions, and in an Early Cretaceous high latitude zone (60°–70°S; Embleton and McElhinny 1982; Embleton, 1984; Idnurm 1985). Because of severe weathering and often-poor locality data (a result of specimens being discovered serendipitously and extracted during opal mining), assignment of most marine reptile fossils to exact stratigraphic horizons is again problematic. However, a predominantly Aptian age can be suggested on the basis of macroinvertebrate assemblages (Ludbrook, 1966; Johns, 1968; Day, 1969; Henderson et al., 2000), and the presence of potentially ice-rafted quartzite/porphyritic boulders and glendonite (pseudomorphs of the calcium carbonate hexahydrate mineral ikaite) nodules (Robertson and Scott, 1990; Sheard, 1990; Krieg and Rodgers, 1995; Burton and Mason, 1998). These conspicuous sedimentary structures characterise the early depositional stages of the Bulldog Shale and Wallumbilla Formation in the southern Eromanga Basin and have been correlated with a period of very cold to near-freezing climatic conditions during the Late Neocomian–Early Albian (Frakes and Francis, 1988, 1990; Frakes et al., 1995; De Lurio and Frakes, 1999).

A similar cool temperate to very cold environmental setting has been suggested (Stevens and Clayton, 1971; Gregory et al., 1989; Rich and Rich, 1989; Dettmann et al., 1992; Vickers-Rich, 1996; Constantine et al., 1998) for the Lower-mid Albian (*C. paradoxa* Zone; Burger, 1980) estuarine–coastal plain facies of the Griman Creek Formation at Lightning Ridge, New South Wales/Surat region, Queensland (Fig. 1), and the Aptian–Lower

Table 1
Spore-pollen and dinoflagellate zonation for the Australian Cretaceous (follows Helby et al., 1987) with correlations to Australian marine-reptile producing units. Abbreviations: SUB-GP, sub-group; FMN, formation.

Period	Epoch	Age	Spore-pollen zones	Microplankton zones	North-central Eromanga Basin QLD/NSW units	Southwestern Eromanga Basin SA units	Southern Surat Basin QLD/NSW units	Otway Basin/ Gippsland Basin VIC units	Money Shoals Platform NT Units	Carnarvon Basin/ Perth Basin WA units
CRETACEOUS	LATE	MAASTRICHTIAN	*Forcipites longus*; *Tubulifloriditès lilliei*	*Mannumiella drugii*; *Isabelidinium korojonense*						MIRIA FORMATION
CRETACEOUS	LATE	CAMPANIAN	*Nothofagidites senectus*	*Xenikoon australis*; *Nelsoniella aceras*						
CRETACEOUS	LATE	SANTONIAN	*Tricolporites apoxyexinus*	*Isabelidinium cretaceum*; *Ondontochitina porifera*						
CRETACEOUS	LATE	CONIACIAN	*Phyllocladites mawsonii*	*Conosphaeridium striatoconus*						
CRETACEOUS	LATE	TURONIAN	*Phyllocladites mawsonii*	*Conosphaeridium striatoconus*						
CRETACEOUS	LATE	CENOMANIAN	*Appendicisporites distocarinatus*	*Palaehystricophora infusorioides*; *Diconodinium multispinum*	ROLLING DOWNS GROUP: WINTON FORMATION					GEARLE SILTSTONE; ALINGA FORMATION; MOLECAP GREENSAND
CRETACEOUS	EARLY	ALBIAN	*Phimopollenites pannosus*; *Coptospora paradoxa*	*Xenascus asperatus*; *Pseudoceratium ludbrookiae*; *Canninginopsis denticulata*; *Muderongia tetracantha*	ROLLING DOWNS GROUP: MACKUNDA FORMATION; ALLARU MUDSTONE; TOOLEBUC FMN; WALLUMBILLA FORMATION	MARREE SUB-GP: OODNADATTA FMN; BULLDOG SHALE	GRIMAN CREEK FORMATION	EUMERALLA FORMATION		GEARLE SILTSTONE; ALINGA FORMATION
CRETACEOUS	EARLY	APTIAN	*Crybelosporites striatus*; *Cyclosporites hughesii*	*Diconodinium davidii*; *Odontochitina operculata*	WALLUMBILLA FORMATION	BULLDOG SHALE	BUNGIL FORMATION	EUMERALLA FORMATION; WONTHAGGI FORMATION	DARWIN FORMATION	
CRETACEOUS	EARLY	BARREMIAN	*Foraminisporis wonthaggiensis*	*Muderongia australis*; *Muderongia testudinaria*				WONTHAGGI FORMATION		BIRDRONG SANDSTONE
CRETACEOUS	EARLY, NEOCOMIAN	HAUTERIVIAN	*Foraminisporis wonthaggiensis*	*Phoberocysta burgeri*; *Senoniasphaera tabulata*				WONTHAGGI FORMATION		
CRETACEOUS	EARLY, NEOCOMIAN	VALANGINIAN	*Foraminisporis wonthaggiensis*	*Systematophora areolata*				WONTHAGGI FORMATION		
CRETACEOUS	EARLY, NEOCOMIAN	BERRIASIAN	*Cicatricosisporites australiensis*	*Egmontodinium torynum* to *Cribroperidinium perforans* zones						BARROW GROUP
JURASSIC		TITHONIAN	*Retitriletes watherooensis*	*Egmontodinium torynum* to *Cribroperidinium perforans* zones						
JURASSIC		KIMMERIDGIAN	*Murospora florida*	*Dingodinium swanense*; *Wanaea spectabilis*						

Table 2
Distribution of Cretaceous marine reptile families and superfamilies in the marine and freshwater deposits of Australia. Stages listed represent specific ages of marine reptile specimen localities rather than age of the unit as a whole. See footnotes for source texts included.[10,21,28]

Wallumbilla Formation	Toolebuc Formation	Allaru Mudstone	Mackunda Formation	Bulldog Shale	Oodnadatta Formation	Bungil Formation	Griman Creek Formation
(Eromanga Basin)	(Eromanga Basin)	(Eromanga Basin)	(Eromanga Basin)	(Eromanga Basin)	(Eromanga Basin)	(Surat Basin)	(Surat Basin)
Aptian-Albian	Albian	Albian	Albian-Cenomanian	Aptian–Albian	Albian	Aptian	Albian
Ophthalmosauridae[15,16,17,18,24] Elasmosauridae[5,6,15,16,33,35,41] Pliosauridae[1,2,5,6,15,16,33,35,41] ?Polycotylidae[5,6,16,38]	Ophthalmosauride[15,16,17,18,32,39,40] Elasmosauridae[5,6,7,15,16,26,33,35,39] Pliosauridae[25,6,15,16,33,35,40] Polycotylidae[26,33,35,40] Chelonioidea[13,15,16,33]	Ophthalmosauridae[15,16,17,18,33,40] Elasmosauridae[5,6,15,16,33,40] Chelonioidea?[16,33]	Polycotylidae[5,6,16]	Ophthalmosauridae[11,16,37,40] Elasmosauridae[5,6,9,11,33,37,40] Rhomaleosauridae[30,33,37,40] Pliosauridae[11,37,40] Cryptoclididae/ Cimoliasuaurida?[34,40]	Elasmosauridae[8,37,40]	Pliosauroidea[15,16,40]	Pliosauroidea[16,33]
Coastal-offshore shallow marine[12,23]	Restricted shallow marine[12,19,31]/offshore[19]	Shallow marine[19]/paralic[12,31]	Marginal marine[19]/paralic[12,19]	Coastal-offshore[9]/shallow marine[19,27]	Low energy shallow marine[19,27]	Paralic/freshwater-brackish marine[14]	Fluviatile coastal plain[25]

Darwin Formation	Barrow Group	Birdrong Sandstone	Alinga Formation	Gearle Siltstone	Miria Formation	Molecap Greensand	Wonthaggi Formation	Eumarella Formation
(Money Shoals Platform)	(Carnarvon Basin)	(Carnarvon Basin)	(Carnarvon Basin)	(Carnarvon Basin)	(Carnarvon Basin)	(Perth Basin)	(Strzeleki Ranges)	(Otway Ranges)
Aptian/Albian	Berriasian	Hauterivian-Barremian	Albian-Cenomanian	Cenomanian	Maastrichtian	Cenomanian-Turonian	Aptian	Albian
Ophthalmosauridae[3,16,17,18,20,40] Elasmosauridae [15,21,35,40] Rhomaleosauridae[35,40]	Rhomaleosauridae[34,40]	Ophthalmosauridae[16,33,36] Rhomaleosauridae[30,33,34,35,40]	Ophthalmosauridae[36]	Pliosauroidea[34]	Mosasauridae[33,34]	Ophthalmosauridae[3,16,32,36] Elasmosauridae[33,34] Pliosauroidea? [34] Mosasauridae [4,16,33]	Pliosauroidea[29]	Pliosauroidea[16,29,35]
Shallow near-shore marine[32]/paralic[12]/possibly tidal[20]	Fluviatile-delataic[22]	Coastal near-shore shallow marine[22]/paralic[10]	Near-shore shallow marine[22]	Offshore marine [22]	Low energy marine shelf[22]	Shallow marine[34]	Fluviatile, braided meandering rivers[29]	Fluviatile, braided rivers[29]

[1] Etheridge (1904). [2] Longman (1924). [3] Teichert and Matheson (1944). [4] Lundelius and Warne (1960). [5] Persson (1960. [6] Pearson 1963. [7] Pearson 1982). [8] Freytag (1964). [9] Ludbrook (1966).. [10] Condon (1968). [11] Pledge (1980). [12] Smart and Senior (1980). [13] Gaffney (1981). [14] Day et al. (1983). [15] Molnar (1982b. [16] Molnar 1991). [17] Wade (1984. [18] Wade 1990). [19] Moore and Pitt (1985). [20] Murray (1985,. [21] Murray 1987). [22] Hocking et al. (1987). [23] Burger (1988). [24] Bardet (1992). [25] Dettmann et al. (1992). [26] Thulborn and Turner (1993). [27] Krieg and Rodgers (1995). [28] McLoughlin et al. (1995). [29] Vickers-Rich (1996). [30] Cruickshank and Long (1997). [31] McConachie et al. (1997). [32] Henderson (1998). [33] Long (1998). [34] Long and Cruickshank (1998). [35] Cruickshank et al. (1999). [36] Choo (1999). [37] Alley and Pledge (2000). [38] Sato and Storrs (2000). [39] Kear (2001. [40] 2002a. [41] Kear 2002c).

Albian (*C. hughsii* Subzone–*C. striatus* Subzone sensu Dettmann and Playford, 1969; Wagstaff and McEwen Mason, 1989) braided stream and overbank floodplain deposits of the Wonthaggi and Eumeralla formations in Victoria (Fig. 1). These units have produced a handful of plesiosaur remains (mainly isolated teeth) that represent animals living near to or within the Cretaceous southern polar circle and evidently adapted to at least seasonal occupation of inland freshwater environments (Rich and Rich, 1989; Rich, 1996; Vickers-Rich, 1996).

Largely isolated ichthyosaur and plesiosaur elements have been recovered from the shallow marine, continental margin deposits of the Darwin Formation at Casuarina Beach, Fannie Bay and Nightcliff near Darwin in the Northern Territory (Fig. 1). This unit is typically characterised by glauconitic sandstones and radiolarian mudstones with localised nodular phosphorite horizons (Henderson, 1998). The Darwin Formation has historically been considered Albian in age on the basis of its macroinvertebrate (Day, 1969; Skwarko, 1966, 1968; Henderson, 1990) fauna; however, palynological (Burger, 1978) and recent stratigraphic analyses (Henderson, 1998) suggest an alternative Late Aptian (*D. davidii* Zone) age.

Western Australian Cretaceous deposits producing marine reptile remains (Fig. 1) include the predominantly Neocomian (Long and Cruickshank, 1998 gave a Berriasian age for their specimen locality, which corresponds to the lower *Biretisporites eneabbensis* Zone/ *Cicatricosporites australiensis* Zone of Helby et al., 1987) fluviatile-deltaic sediments of the Barrow Group near Exmouth, various Upper Hauterivian–Barremian (*M. australis* Zone, Helby et al., 1987; McLoughlin et al., 1995) outcrops of the marine Birdrong Sandstone, shallow marine sediments of the upper Alinga Formation and upper Gearle Siltstone in the Murchison River area (regarded as Upper Albian–Cenomanian in age on the basis of selachian faunas; Siverson, 1999), exposures of the Molecap Greensand near the townships of Dandaragan and Gingin (originally considered Upper Coniacian–Lower Santonian in age sensu McWae et al., 1958, and Belford, 1958, but now regarded as predominantly Cenomanian–Lower Turonian; Shafik, 1990), and Upper Maastrichtian (suggested primarily on the basis of ammonite assemblages' Henderson and McNamara, 1985) shallow marine deposits of the Miria Formation in the Giralia Range. The Lower Cretaceous units have yielded mainly isolated elements of plesiosaurs and ichthyosaurs; however, several fragmentary skeletons have been recovered from the shallow marine–paralic, predominantly glauconitic Birdrong Sandstone near Exmouth. The Upper Cretaceous shallow marine, shelf calcarenite deposits of the Miria Formation and glauconitic sandstones of the upper Molecap Greensand are significant because they have produced Australia's only known mosasaur remains.

4. Systematic survey of Australian marine reptile taxa

Subclass: Diapsida Osborn, 1903
Superorder: Ichthyopterygia Owen, 1840
Order: Ichthyosauria Blainville de, 1835

Remarks. Ichthyosaur fossils are regularly encountered in the Lower Cretaceous, largely Aptian–Albian, rocks of the Eromanga Basin, with rare occurrences also known from the Carnarvon Basin and Money Shoals Platform. Their remains are particularly common in the Upper Albian deposits of the Toolebuc Formation (Eromanga Basin) where they far outnumber those of plesiosaurs and chelonioids. In the predominantly Aptian strata (Bulldog Shale/Wallumbilla Formation) of the southwestern Eromanga Basin, however, ichthyosaurs form a less significant component of the fauna, which is otherwise dominated by a diverse range of plesiosaur taxa.

Few remains of Australian ichthyosaurs are known from the Upper Cretaceous and these are all of poor quality. Teichert and Matheson (1944) reported several fragmentary vertebrae and other elements from the lower Molecap Greensand of Dandaragan in Western Australia, suggesting that the material may be of Low Santonian age. Choo (1999), however, noted that the specimens were recovered from an exploratory sample for a commercial mining operation and thus their original stratigraphic disposition is unclear. In addition, recent biostratigraphic revision of the Molecap Greensand has suggested a much older, probably Cenomanian–Low Turonian (Shafik, 1990) age for the deposit. The youngest undisputed occurrence of ichthyosaurs from Australia (and only other Upper Cretaceous occurrence for the group) therefore is based on a single phalanx and centrum from the Upper Albian–Cenomanian upper Alinga Formation of the Murchison River area, Western Australia (Choo, 1999).

Several Australian Cretaceous ichthyosaur species have been named although most have proved to be indeterminate. These problematic taxa are included with potentially valid species in Table 3. A chronostratigraphically organised list of Australian ichthyosaur (and other Mesozoic reptile) occurrences was presented by Molnar (1991), and Cretaceous finds have been reviewed by McGowan (1972), Wade (1990), Bardet (1992), Choo (1999) and Kear (2002a).

Family: Ophthalmosauridae Baur, 1887 (sensu McGowan and Motani, 2003)
Genus *Platypterygius* von Huene, 1922

Type species. *Platypterygius platydactylus* (Broili, 1907), p. 160, pls. 12, 13, by subsequent designation of Huene von, 1922, p. 99.

Diagnosis. Characters follow Maisch and Matzke (2000) unless cited otherwise. Large-bodied ichthyosaur

Table 3
A list of Australian Cretaceous ichthyosaur taxa, their synonyms and current status (bold).

Taxon	Holotype	Material	Locality	Horizon	Synonyms and status
Ichthyosaurus australis (McCoy, 1867) (nomen dubium)	lost (numbered 48)	several vertebral centra	Flinders River region, Queensland	Aptian or Albian	*Myopterygius australis* (Teichert and Matheson, 1944), *Platypterygius australis* (McGowan, 1972; McGowan and Motani, 2003), ***P. longmani* (Wade, 1990)**
Ichthyosaurus marathonensis (Etheridge, 1888) (nomen dubium)	QM F1448	snout fragment	Walker's Table Mountain, near the Flinders River, Queensland	Upper Albian	*I. australis* (Jack and Etheridge, 1892), *Myopterygius marathonensis* (Huene von, 1922), *Platypterygius australis* (McGowan, 1972), ***P. longmani* (Wade, 1990)**
Platypterygius longmani Wade, 1990	QM F2453	partial skeleton	Telemon Lease, Dunluce Station near Hughenden, Queensland	Upper Albian	**currently valid**, *Platypterygius australis* (McGowan and Motani, 2003)

up to 9 m in length. Skull low-crowned with long snout, small orbit and long postorbital region. Maxilla extremely long anteriorly. Dentition robust with roots of teeth quadrangular in cross-section. External naris subdivided; septomaxilla well ossified. Squamosal lost. Condylus occipitalis semi-hemispherical with area extracondylaris extremely reduced. Stapes large with rounded head (Motani, 1999). Atlas-axis co-ossified with third cervical vertebra; intercentra not differentiated. Humerus with very strong trochanter dorsalis and two or three distal facets. Anterior and posterior accessory digits of forefin well developed (two or three preaxial accessory digits, at least two postaxial accessory digits; Motani, 1999) with all podial elements very thick, forming a close-fitting polygonal mosaic pattern. Pelvic girdle and hind limb poorly known but apparently reduced. Caudal peduncle short.

Remarks. *Platypterygius* is currently regarded as the most widespread valid genus of Cretaceous ichthyosaur (McGowan, 1972; Bardet, 1992; Arkhangelsky, 1998; Maisch and Matzke, 2000; Storrs et al., 2000; McGowan and Motani, 2003) and the taxon to which most if not all of the Australian Cretaceous ichthyosaur material can be assigned. Specimens definitively attributable to *Platypterygius* have been recorded from the Upper Hauterivian–Barremian Birdrong Sandstone of Western Australia (McLoughlin et al., 1995; Choo, 1999), Aptian–Lower Albian Bulldog Shale of South Australia (Pledge, 1980; Alley and Pledge, 2000), Aptian or Albian deposits of the Darwin Formation, Northern Territory (Murray, 1987; Wade, 1990; Kear, 2002a) and mid–Upper Albian Toolebuc Formation and Allaru Mudstone of Queensland (McGowan, 1972; Wade, 1984, 1990; Kear, 2002b). Non-diagnostic fragmentary or isolated ichthyosaur remains also probably attributable to *Platypterygius* have been described from the Aptian–Albian Wallumbilla Formation, New South Wales (Etheridge, 1904), Albian–Cenomanian Alinga Formation (Choo, 1999) and Cenomanian–Turonian Molecap Greensand (Teichert and Matheson, 1944; McGowan, 1972; Wade, 1990; Long, 1998) both of Western Australia.

Platypterygius longmani Wade, 1990, figs. 2, 3A–C.

1867 *Ichthyosaurus australis* McCoy, p. 355 (nomen dubium).

1888 *Ichthyosaurus marathonensis* Etheridge, p. 408, pl. 7, figs 1–3 (nomen dubium).

1922 *Myopterygius marathonensis* von Huene, p. 98 (nomen dubium).

1944 *Myopterygius australis* Teichert and Matheson, p. 169 (nomen dubium).

1972 *Platypterygius australis* McGowan, p. 17, pl. 4A–E (nomen dubium?).

Holotype. QM F2453, a partial skeleton comprising the skull (Fig. 2 A), proximal forefin elements, pectoral girdle and most of the vertebral column.

Type locality. Telemon Lease, Dunluce Station, near Hughenden in central northern Queensland, Australia (see Wade, 1990).

Stratigraphic horizon. Toolebuc Formation (Rolling Downs Group), Eromanga Basin, latest mid to Upper Albian *P. ludbrookiae* Zone/upper *C. paradoxa*–*P. pannosus* Zone (Moore et al., 1986; McMinn and Burger, 1986). Remains assigned to *P. longmani* have also been recovered from the overlying Allaru Mudstone, mid–Upper Albian *P. ludbrookiae* Zone/upper *C. paradoxa*–*P. pannosus*/*C. denticulata* zones (Krieg and Rodgers, 1995).

Diagnosis. The following diagnosis is modified from Wade (1990). With the features of the genus. External naris subdivided with well-developed anterior foramen and one or more foramina present (in nasal) posterodorsal to external bony nasal opening. Humerus (Fig. 2B, C) bearing tapering crest-like dorsal trochanter (Choo, 1999) and three distinct distal facets for articulation with the ulna, radius and an anterior zeugopodial element. Three preaxial accessory digits and three postaxial accessory digits present in forefin with digital bifurcation occurring in the primary axis (digit IV, Fig. 2D). Neural spines of at least neck and anterior trunk vertebra divided into anterior and posterior peaks by an asymmetric V-shaped apical notch. Caudal centra from tail stock region may bear weakly developed haemal arch facets (Kear, 2002a).

Remarks. *Platypterygius longmani* was originally established by Wade (1990) with the intent of stabilising the nomenclature for ichthyosaur taxa from the Aptian–Albian deposits of the Eromanga Basin. Initially, McCoy (1867) had attributed material from this region to *Ichthyosaurus australis*, a species described on the basis of several vertebral centra from an unspecified unit of the Rolling Downs Group in the Flinders River area of northern Queensland. Etheridge (1888) established a second taxon, *I. marathonensis*, based on a snout fragment from Walker's Table Mountain near the head of the Flinders River (Rolling Downs Group). von Huene (1922) suggested reassignment of *I. marathonensis* to the genus *Myopterygius*, a conclusion also followed by Teichert and Matheson (1944) for *I. australis*. McGowan (1972) regarded *I. marathonensis* as a junior synonym of *I. australis*, and consequently placed all Australian Cretaceous ichthyosaur remains within the single taxon, *Platypterygius australis*. Wade (1990), however, noted that the type of *P. australis* (McCoy's 'specimen 48', probably associated with MV P12989, MV P12992, MV P22653–P22654, and MV P22656–P22661 collected from the type locality) was both

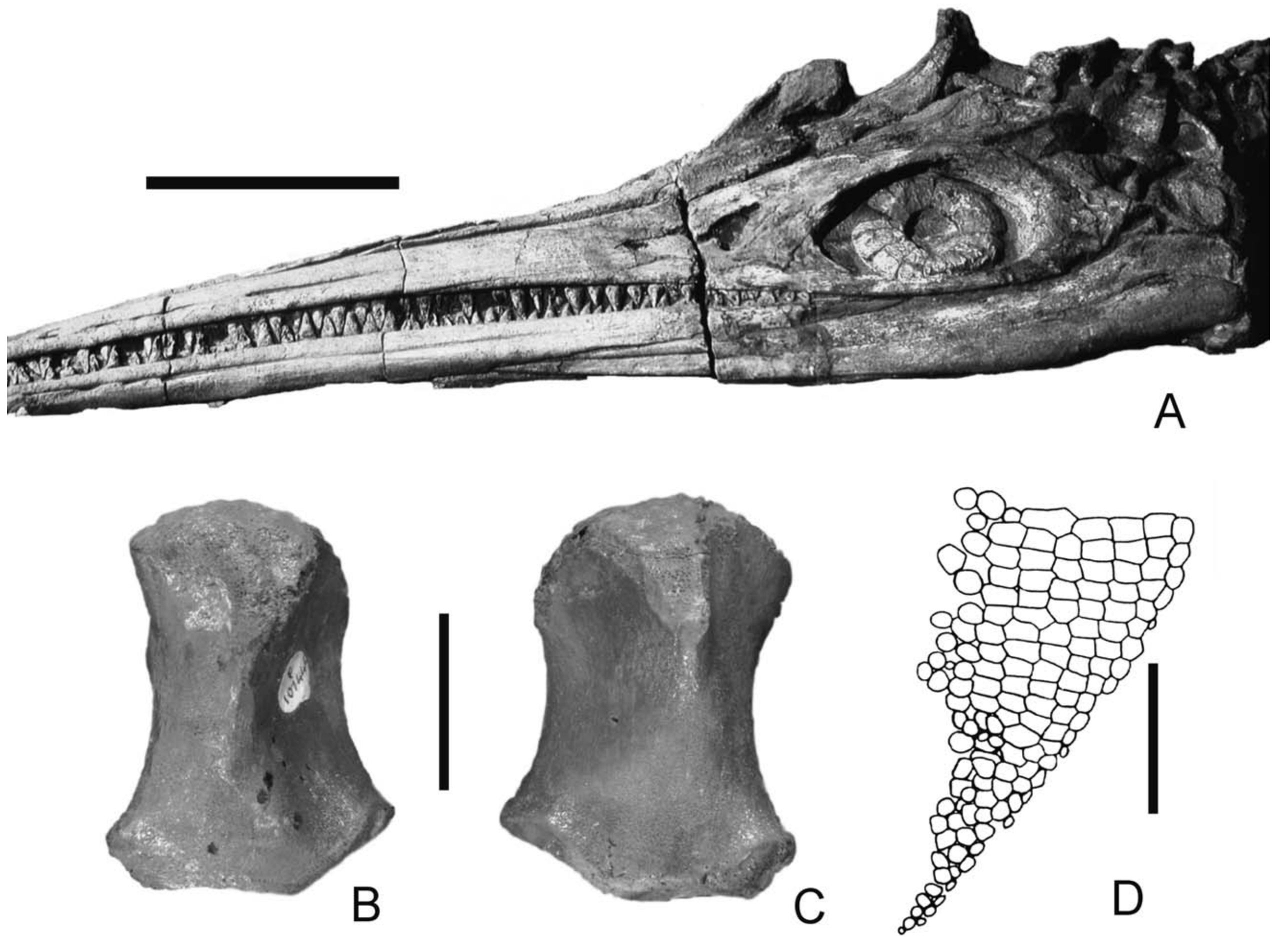


Fig. 2. *Platypterygius longmani* Wade, 1990 from the Lower Cretaceous (Aptian–Albian) deposits of Australia. A, skull and mandible of holotype specimen QM F2453 (after Wade, 1990); scale bar represents 300 mm. B, dorsal and C, ventral views of humerus AM F107444; scale bar represents 50 mm. D, articulated distal forefin (QM F10686) showing digital bifurcation in the primary, axis digit IV (after Molnar, 1991); scale bar represents 300 mm.

non-diagnostic and currently lost, and therefore proposed the creation of *P. longmani* (holotype QM F2453). Interestingly, McGowan and Motani (2003) have recently suggested that the description by McCoy (1867) satisfied Articles 11 and 12 of the ICZN, and therefore his name *I. australis* could not be invalidated in the manner employed by Wade (1990). Consequently, they reinstated *Platypterygius australis* (sensu McGowan, 1972) as a valid taxon and relegated *P. longmani* to a junior synonym.

Other remains attributable to *P. longmani* have been recorded from Aptian–Lower Albian deposits of the Bulldog Shale in South Australia (Pledge, 1980; Molnar, 1982a, 1991; Wade, 1990; Bardet, 1992) and Aptian or Albian Darwin Formation sediments in the Northern Territory (Murray, 1985, 1987; Wade, 1990; Kear, 2002a). Choo (1999) suggested that ichthyosaur material from the Upper Hauterivian–Barremian Birdrong Sandstone of Western Australia may constitute a separate taxon; however, the remains are too fragmentary for definitive diagnosis.

Superorder: Sauropterygia Owen, 1860
Order: Plesiosauria Blainville de, 1835

Remarks. Plesiosaur remains are widespread in the Cretaceous deposits of Australia, with finds occurring in sediments of Berriasian to Cenomanian–Turonian age. The most diverse assemblages are encountered in the Lower Cretaceous, predominantly Aptian rocks of the Bulldog Shale (Eromanga Basin) in South Australia, where as many as four families (Rhomaleosauridae, Pliosauridae, Elasmosauridae and possibly Cryptoclididae or Cimoliasauridae sensu O'Keefe, 2001) may be present. A wide variety of taxa have also been recorded from the Lower Aptian–Upper Albian Wallumbilla Formation and Upper Albian Toolebuc Formation of the Eromanga Basin in Queensland. Interestingly, these units appear to preserve quite different faunas with plesiosaurs dominating the older Wallumbilla Formation sediments, but giving way to chelonioid turtles and a marked increase in the number of ichthyosaur fossils in the younger Toolebuc Formation.

Largely fragmentary plesiosaur specimens have been recovered from other Lower Cretaceous units in the Eromanga Basin as well as the Carnarvon Basin, Money Shoals Platform and freshwater facies of the Surat Basin, Gippsland Basin and Otway Basin. In contrast Upper Cretaceous plesiosaur fossils are limited to the deposits of the Carnarvon and Perth basins in Western Australia, with isolated occurrences in the northern Eromanga Basin of Queensland. Of these, the Perth Basin's Molecap Greensand has been most productive, yielding a number of fragmentary vertebrae and other skeletal elements (Long and Cruickshank, 1998).

Several Australian Cretaceous plesiosaur genera and species have been named, although often on the basis of very poor holotype material. Consequently, most of these taxa are now regarded as indeterminate with only two being potentially valid (Table 4). Diagnostic specimens representing new taxa have been recovered from the Bulldog Shale, South Australia (Cruickshank et al., 1999; Alley and Pledge, 2000) and Toolebuc Formation of Queensland (Thulborn and Turner, 1993; Cruickshank et al., 1999), but as yet these remains have not been formally described. Reviews of Australian plesiosaur discoveries have been presented by Persson (1960, 1963), Molnar (1982a, 1991), Thulborn and Turner (1993), Long (1998), Long and Cruickshank (1998), Cruickshank et al. (1999) and Kear (2002a).

Superfamily: Plesiosauroidea Welles, 1943
Family: Elasmosauridae Cope, 1869a

Elasmosauridae gen. et sp. indet.

1867 *Plesiosaurus sutherlandi* McCoy, p. 356 (nomen dubium).

1904 *Cimoliasaurus sutherlandi*, p. 312 (nomen dubium).

1914 *Pliosaurus sutherlandi* Chapman, p. 278 (nomen dubium).

Referred material. NMV P22572, single cervical vertebra.

Referred material locality. Unknown locality (possibly Marathon Station; see Persson, 1960), upper Flinders River region, northern Queensland, Australia.

Stratigraphic horizon. Exact stratigraphic horizon is uncertain due to absence of detailed locality data.

Remarks. *Plesiosaurus sutherlandi* has the distinction (along with *P. macrospondylus*) of being Australia's earliest described plesiosaur taxon. Established by McCoy (1867) on the basis of an isolated vertebra, the species has undergone numerous revisions over the years. Initially evaluated by Jack and Etheridge (1892) and later by Etheridge (1904), *P. sutherlandi* was re-assigned to the genus *Cimoliasaurus* Leidy, 1851 by Etheridge (1904) on the basis of its platycoelous centrum with strongly ellipsoidal articular surfaces. A subsequent review by Chapman (1914) referred *P. sutherlandi* to the genus *Pliosaurus* Owen, 1841 a conclusion also followed by Howchin (1928). Persson (1960) briefly re-described the holotype specimen, concluding that it was inadequate for generic or specific determination, and thus attributable only to Cimoliasauridae? gen. et sp. indet. This classification has been widely accepted by many subsequent workers including Molnar (1982b) and Thulborn and Turner (1993). Welles (1962), however, noted that the holotype of *P. sutherlandi* showed some similarity to the posterior cervicals of elasmosaurids and therefore proposed a tentative referral of the specimen to Elasmosauridae gen. et sp. indet., a conclusion followed herein.

Elasmosauridae gen. et sp. indet.

1867 *Plesiosaurus macrospondylus* McCoy, p. 356 (nomen dubium).

1914 *Pliosaurus macrospondylus* Chapman, p. 278 (nomen dubium).

Referred material. NMV P22548, two associated cervical vertebra.

Referred material locality. Unknown locality (possibly Marathon Station; see Persson 1960), upper Flinders River region, northern Queensland, Australia.

Stratigraphic horizon. Exact stratigraphic horizon is uncertain due to absence of detailed locality data.

Remarks. McCoy (1867) established *Plesiosaurus macrospondylus*, along with *P. sutherlandi*, in a brief report on marine reptile fossils from Cretaceous strata of the Flinders River region, Queensland. Chapman (1914) referred the taxon to the genus *Pliosaurus* Owen, 1841, although Persson (1960) subsequently transferred it to Elasmosauridae gen. et sp. indet. on the basis of centrum proportions and the presence of lateral longitudinal ridges on the centrum body. This classification has been widely accepted by many recent workers (e.g. Molnar, 1982b; Thulborn and Turner, 1993) and is also followed herein.

Elasmosauridae gen. et sp. indet.

1904 *Cimoliasaurus maccoyi* Etheridge, p. 312, pls. 42–44 (nomen dubium).

Referred material. AM F9630–9928, partial vertebral column, parts of limb girdles, limb elements (Fig. 3 C, D).

Referred material locality. Unspecified mine locality, White Cliffs opal fields, near Wilcannia, northwestern New South Wales, Australia.

Stratigraphic horizon. Doncaster Member, Wallumbilla Formation (Rolling Downs Group), Eromanga Basin. This unit is represented by predominantly Aptian rocks in the White Cliffs area (see Burton and Mason, 1998) and corresponds to the *C. hughesii*–lowermost

Table 4
A list of Australian Cretaceous plesiosaur taxa, their synonyms and current status (bold).

Taxon	Holotype	Material	Locality	Horizon	Synonyms and status
Plesiosaurus sutherlandi (McCoy, 1867) (nomen dubium)	NMV2572	anterior cervical centrum	?Marathon Station, Queensland	?Albian	*Cimoliasaurus sutherlandi* (Etheridge, 1904), *Pliosaurus sutherlandi* Chapman, 1914),**?Elasmosauridae indet. (**Welles, 1962**; this study),** Cimoliasauridae (sensu Persson, 1963) indet. (Molnar, 1982a)
Plesiosaurus macrospondylus (McCoy, 1867) (nomen dubium)	NMV P22548	2 cervical centra	?Marathon Station, Queensland	?Albian	*Pliosaurus macrospondylus* (Chapman, 1914), **Elasmosauridae indet. (**Persson, 1960**)**
Cimoliasaurus leucoscopelus Etheridge, 1897 (nomen dubium)	AM F6266-AM F6298	vertebrae, teeth, limb bones	White Cliffs, New South Wales	Aptian	?*Dolichorhynchops* sp. (Persson, 1960; Welles, 1962; Sato and Storrs, 2000), ?*Trinacromerum leucoscopelus* (Molnar, 1982a),?**Polycotylidae indet (this study)**
Cimoliasaurus maccoyi Etheridge, 1904 (nomen dubium)	AM F9630-AM F9928	vertebrae, tooth, limb elements	White Cliffs, New South Wales	Aptian	Plesiosauroidea indet. (Welles, 1962), **?Elasmosauridae indet. (**Kear, 2002c**)**
Kronosaurus queenslandicus Longman, 1924	QM F1609	symphyseal region of mandibles	Hughenden–Richmond region, Queensland	Aptian–Albian	**currently valid**
Woolungasaurus glendowerensis Persson, 1960 (nomen dubium)	QM F6890	vertebrae, limb girdles, limb elements	Glendower Station near Richmond, Queensland	Aptian	**Elasmosauridae indet. (**Welles, 1962**)**
Leptocleidus clemai Cruickshank and Long, 1997	WAM 92.8.1-1-68	fragmentary skeleton	near Kalbarri, Western Australia	Upper Hauterivian–Barremian	**currently valid**

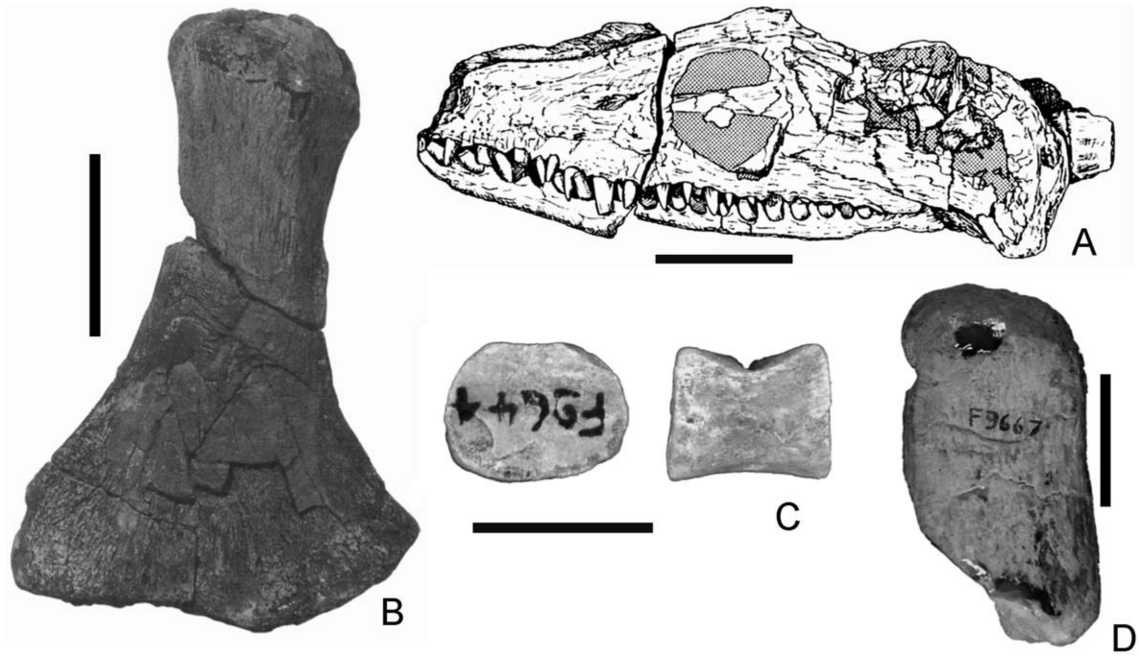


Fig. 3. Indeterminate elasmosaurid remains from Lower Cretaceous (Aptian–Albian) deposits of Australia. A, elasmosaurid skull and mandible (QM F11050) attributed to *Woolungasaurus glendowerensis* Persson, 1960 (nomen dubium) by Persson (1982) (after Thulborn and Turner, 1993); scale bar represents 100 mm. B, propodial of holotype specimen (QM F6890) of *Woolungasaurus glendowerensis* (nomen dubium) (after Molnar, 1991); scale bar represents 100 mm. C, anterior and lateral views of anterior cervical vertebra (AM F9644) of holotype specimen (AM F9630-9928) of *Cimoliasaurus maccoyi* Etheridge, 1904 (nomen dubium); scale bars represents 40 mm. D, incomplete propodial (AM F9667) of holotype specimen (AM F9630-9228) of *Cimoliasaurus maccoyi* Etheridge, 1904 (nomen dubium); scale bar represents 40 mm.

C. striatus Zone/*O. opercilata*-*D. davidii* Zone of Helby et al. (1987).

Remarks. *Cimoliasaurus maccoyi* was established by Etheridge (1904) and later revised by Persson (1960) who included it within the plesiosauroid family Cimoliasauridae Delair, 1959. Welles (1962), however, regarded *C. maccoyi* to be a nomen dubium based on non-diagnostic material. Consequently, he abandoned Cimoliasauridae and re-assigned all of its constituent taxa to other groups. Despite this, Persson (1963) retained both *C. maccoyi* and Cimoliasauridae (with an emended diagnosis) within a revised classification of the Plesiosauria, a scheme that has been followed in some later studies (e.g. Molnar, 1982a,b, 1991; Thulborn and Turner, 1993; Long, 1998). Recent re-assessment of the *C. maccoyi* holotype specimen by Kear (2002c) found the diagnostic characters of Persson (1960) to be either uninformative beyond higher taxonomic levels, ontogenetically related or misinterpreted and suggested an alternative provisional referral of the remains to Elasmosauridae gen. et sp. indet. (based on the derived elongation of the more anterior cervical centra relative to their height and the presence of platycoelous articular surfaces). This placement is more in accordance with recent analyses of plesiosaur in-group relationships (e.g. Brown, 1993; Brown and Cruickshank, 1994; Carpenter, 1996, 1997; Bardet et al., 1999; Storrs, 1999), which have largely excluded Cimoliasauridae (sensu Persson, 1960) leaving the group's taxonomic status in doubt (Storrs, 1999; Kear, 2002c). Indeed, the genus *Cimoliasaurus* has come to be regarded as a non-diagnosable 'waste-basket taxon' (Williston, 1903; Storrs et al., 2000). Despite this, the most current comprehensive cladistic analysis and taxonomic revision of the Plesiosauria (O'Keefe, 2001) has revived the family designation but modified it to include the enigmatic *Kimmerosaurus* Brown, 1981 and *Morturneria* Chatterjee and Small, 1989, taxa previously regarded as either derived cryptoclidids (see Brown, 1981, 1993; Chatterjee and Small, 1989; Cruickshank and Fordyce, 1998, 2002) or elasmosaurids (*morturneria* only see Bardet et al., 1991). The relationships of this clade to many of the more 'traditional' cimoliasaurids such as *C. maccoyi*, however, remains unclear and requires both further material and considerable additional study before any definitive taxonomic affinity can be established.

Elasmosauridae gen. et sp. indet.
1960 *Woolungasaurus glendowerensis* Persson, p. 11, pl. 1, figs. 3, 4, pls. 2, 3 (nomen dubium).

Referred material. QM F6890, partial vertebral column, fragmentary pectoral and pelvic girdles, partial fore and hind limbs (Fig. 3B).

Referred material locality. Glendower Station, near Prairie in central northern Queensland, Australia.

Stratigraphic horizon. Doncaster Member, Wallumbilla Formation (Rolling Downs Group), Eromanga Basin. This unit is represented by predominantly Aptian rocks in the northeastern Eromanga Basin (see Day, 1969) and corresponds to the *C. hughesii*–lowermost *C. striatus* Zone/*O. opercilata*-*D. davidii* Zone of Helby et al., (1987).

Remarks. *Woolungasaurus glendowerensis* is the only formally named Australian elasmosaurid that has been described in any detail. Persson (1960) distinguished the taxon primarily on the basis of its cervical vertebra morphology (including the presence of elongate anterior cervical centra with well-developed lateral longitudinal ridges on the centrum body), structure of the scapula, lack of separation between the posterior margins of the coracoids and the presence of a prominent mid-ventral keel along the inter-coracoid contact. Welles (1962), however, regarded these characters as non-diagnostic and suggested that the holotype specimen was too incomplete for accurate determination. Consequently he designated *W. glendowerensis* a nomen dubium and relegated all of its referred material to Elasmosauridae gen. et sp. indet. Despite this, *W. glendowerensis* has continued to be recognised in the literature (e.g. Persson, 1963, 1982; Molnar, 1982a,b, 1991; Murray, 1987; Long, 1998; Long and Cruickshank, 1998; Cruickshank et al., 1999) with additional specimens (mostly fragmentary and isolated remains) being attributed from deposits of the Upper Albian Toolebuc Formation (Persson, 1982), Queensland, the Aptian–Lower Albian Bulldog Shale (Pledge, 1980) and Upper Albian Oodnadatta Formation (Persson, 1960; Freytag, 1964; Ludbrook, 1966) of South Australia. Of these, probably the most significant is a near complete although badly crushed skull (QM F11050; see Fig. 3A) from the Toolebuc Formation deposits of Yamborra Creek, near Maxwelton (between Julia Creek and Richmond; see Fig. 1) in central Queensland. Persson (1982) tentatively assigned this specimen to *W. glendowerensis* on the basis of similarities in the associated cervical centra; however, a subsequent re-examination by Thulborn and Turner (1993) demonstrated that there was no sound taxonomic basis for this placement. Consequently they listed the specimen (pending a more thorough description and reappraisal) as a possible new unnamed genus and species of elasmosaurid closely resembling *Libonectes morgani* (Welles, 1949) from the Turonian (Upper Cretaceous) Britton Formation of Texas, USA (see Carpenter, 1997).

Other largely fragmentary Australian Cretaceous elasmosaurid remains have been recorded from the Aptian–Lower Albian Bulldog Shale of South Australia (Cruickshank et al., 1999), Aptian or Albian Darwin Formation of the Northern Territory (Murray, 1987; Kear, 2002a), Upper Albian Toolebuc Formation of Queensland (Kear, 2001) and Cenomanian–Turonian Molecap Greensand (Long and Cruickshank, 1998) of Western Australia. Most of this material lacks any clear affinities; however, Long and Cruickshank (1998) suggested that an isolated dorsal vertebra from the Molecap Greensand showed some resemblance to those of *Mauisaurus haasti* Hector, 1874, a Late Cretaceous elasmosaurid from New Zealand. Kear (2001) also noted similarities in the structure of the basioccipital between a fragmentary elasmosaurid from the Toolebuc Formation and the Late Cretaceous taxon *L. morgani*.

To date, elasmosaurids have been considered the only long-necked plesiosauroid family known from Australia. However, Cruickshank et al. (1999) and Kear (2002a) indicated the possible presence of cryptoclidids in the Aptian Bulldog Shale deposits of South Australia. This identification has recently been re-evaluated following observations of a partial skeleton from the opal-bearing sediments of Andamooka South Australia (Kear in prep.), a popular account of which was given by Rich and Rich (1985). This specimen bears highly derived tooth morphology similar to *Kimmerosaurus*, a Late Jurassic 'cryptoclidid' recently reassigned to a revised cimoliasaurid clade by O'Keefe (2001). Although it has yet to be fully described, the Andamooka skeleton is clearly distinguishable from elasmosaurids and indicates that a greater diversity of long-necked plesiosauroid taxa was present in the Australian Early Cretaceous than has been previously suspected.

Family: Polycotylidae Williston, 1908

Polycotylidae gen. et sp. indet.

1897 *Cimoliasaurus leucoscopelus* Etheridge, p. 24, pls. 5–7 (nomen dubium).
1960 *Dolichorhynchops*? sp. Persson, p. 4.
1982a *Trinacromerum*? *leucoscopelus* Molnar p. 186 (nomen dubium).

Referred material. AM F6266–6298, fragmentary skeleton comprising cranial elements, teeth, partial vertebral column, rib fragments, limb elements (Fig. 4 A–D).

Referred material locality. Unspecified mine locality, White Cliffs opal fields, near Wilcannia, northwestern New South Wales.

Stratigraphic horizon. Doncaster Member, Wallumbilla Formation (Rolling Downs Group), Eromanga Basin. In the White Cliffs area, this unit is represented by rocks of predominantly Aptian age (see Burton and Mason, 1998) and corresponds to the *C. hughesii*–lowermost *C. striatus* Zone/*O. opercilata*-*D. davidii* Zone of Helby et al. (1987).

Remarks. Originally described as *Cimoliasaurus leucoscopelus* by Etheridge (1897), AM F6266–6298 was

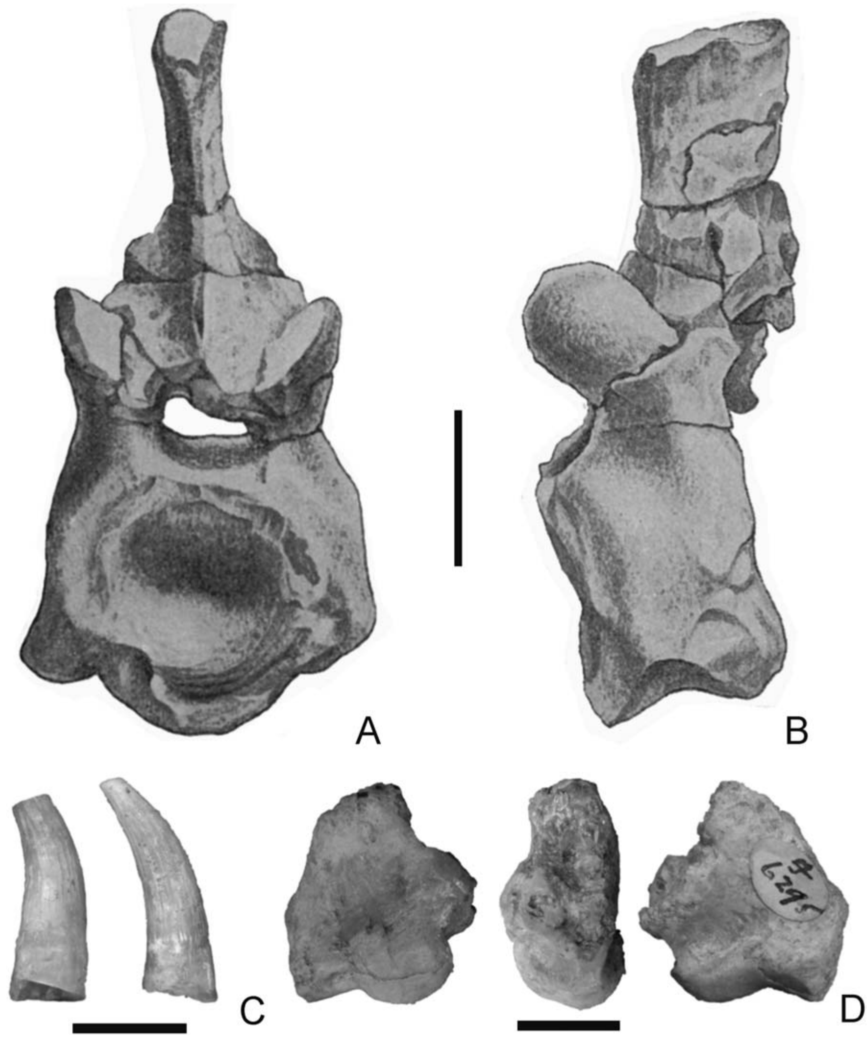


Fig. 4. Polycotylid remains attributed to *Dolichorhynchops* sp. (=*Cimoliasaurus leucoscopelus* Etheridge, 1897, nomen dubium) by Persson (1960) from the Lower Cretaceous (Aptian) deposits of White Cliffs, northwestern New South Wales, Australia. Cervical vertebra (AM F6269) in A, anterior and B, lateral views (after Etheridge, 1897); scale bars represents 20 mm. C, teeth (AM F6273); scale bar represents 10 mm. D, quadrate (AM F6295) in posterior, lateral and anterior views; scale bar represents 10 mm.

subsequently referred to *Dolichorhynchops*? sp. by Persson (1960) on the basis of similarities in tooth and vertebral morphology. This assignment was later modified by Molnar (1982a, 1991), who transferred *Dolichorhynchops*? sp. to the genus *Trinacromerum* Cragin, 1888 (as a junior synonym sensu Welles, 1962) and reinstated the species name *T. leucoscospelus* for convenience. More recent analyses (Sato and Storrs, 2000) have revived the use of *Dolichorhynchops*? sp. for the White Cliffs material (following recognition of *Dolichorhynchops* and *Trinacromerum* as separate taxa sensu Carpenter, 1989, 1996, 1997; Storrs, 1999; Sato and Storrs, 2000) and place it as the earliest known representative of the Polycotylidae. The specimen is, however, extremely fragmentary and cannot be clearly allied to any current polycotylid genus. For example, the teeth (Fig. 4C) are slender, similar to *Dolichorhynchops osborni* Williston, 1903, but exhibit prominent striae that extend to the tip of the crown as in *Polycotylus latipinnis* Cope, 1869a and species of *Trinacromerum* (see Carpenter, 1996; Storrs, 1999). The vertebral centra have a strongly constricted mid-section and bear amphicoelous articular surfaces whose rims are elevated and expanded anteriorly (Fig. 4A, B). This is a condition regarded as characteristic for all members of the family Polycotylidae (Sato and Storrs, 2000). Similarly, the vertebral centra are anteroposteriorly compressed with their length, being less than half the height. This is shared with *P. latipinnis* and species of *Trinacromerum* but differs from *D. osborni*, in which the centra are only slightly higher than long (see Carpenter, 1996; Storrs, 1999). Unusually, the quadrate (Fig. 4D) has a markedly reduced pterygoid process (resembling that of *D. osborni*; Storrs, 1999) and the neural spines on the cervical vertebrae exhibit transversely expanded dorsal apexes (Fig. 4A, B). This latter feature is unlike any other member of the group and appears to represent a unique characteristic of the White Cliffs remains. AM F6266–6298 is, therefore, provisionally assigned to Polycotylidae gen. et sp. indet. pending a more thorough re-examination and the discovery of more diagnostic material.

Recently, Long (1998, citing a pers. comm. from A. Cruickshank, 1996) noted some resemblance between the cervical vertebrae of AM F6266–6298 and those of the Cretaceous rhomaleosaurid *Leptocleidus* Andrews, 1922. While this is certainly true, the vertebrae of AM F6266–6298 differ in key features such as the transversely expanded dorsal apexes on the cervical neural spines. The morphology of the quadrate and dentition also distinguish AM F6266–6298 from all currently described species of *Leptocleidus* (for which cranial material is known). For example, the quadrate of AM F6266–6298 is short and stocky, with anteroposteriorly bulbous articular condyles (see Fig. 4D), unlike that of *Leptocleidus* spp., which is large and elongate with a very wide, anteroposteriorly narrow articular surface (best seen in an undescribed skull, AM F99374, from the Lower Cretaceous Bulldog Shale of South Australia and in the published description of the cranial elements in *L. superstes* Andrews, 1922). Similarly, the dentition of AM F6266–6298 lacks the mesodistal carinae present on the teeth of *Leptocleidus* spp. (Cruickshank, 1997), although the slightly recurved tooth shape and an absence of striations from the buccal surface of the crown are characteristics shared by both forms.

Other Australian specimens attributable to Polycotylidae have been recorded from the Upper Albian Toolebuc Formation and Upper Albian–Lower Cenomanian Mackunda Formation of Queensland with fragmentary polycotylid-like remains also reported from Aptian–Lower Albian Bulldog Shale deposits near Curdimurka in South Australia (Anonymous, 2001). Most of this material is very incomplete with only a single skeleton (currently under study by M. Wade of the Queensland Museum and R. A. Thulborn of the University of Queensland and figured by Long, 1998, p. 146) from the Toolebuc Formation being diagnostic beyond family level.

Superfamily: Pliosauroidea Welles, 1943 (sensu O'Keefe, 2001)
Family: Pliosauridae Seeley, 1874
Genus *Kronosaurus* Longman, 1924

Type species. *Kronosaurus queenslandicus* Longman, 1924, p. 26, pl. 4.

Diagnosis. The following diagnosis is preliminary pending a more thorough examination of all referred material. Characters follow Longman (1924), White (1935), Romer and Lewis (1959), Hampe (1992) and O'Keefe (2001). Large-bodied pliosaurid up to and probably in excess of 9 m. Snout and mandibular rostrum both long and narrow. Anterior interpterygoid vacuity absent; ectopterygoid and pterygoid form lateral flanges that meet in a short dished, mid-line contact ventrolateral to the posterior pterygoid vacuity. Premaxilla bears four large caniniform teeth. Mandibular symphysis elongate and extending back to sixth tooth position. Teeth conical and coarsely striated without distinct carinae. Twelve cervical vertebrae with single-headed cervical ribs.

Remarks. *Kronosaurus* is currently the only valid Australian Cretaceous pliosaurid genus and one of the largest known pliosaurids from anywhere in the world. Longman (1924) initially allied the taxon with the Pliosauridae on the basis of large size, elongate mandibular symphysis and robust, coarsely striated teeth. This assignment has been widely accepted by many subsequent workers (e.g. White, 1935, 1940; Romer and Lewis, 1959, Persson, 1960, 1963; Brown, 1981; O'Keefe, 2001); although, Welles (1962) suggested an alternative placement within the polyphyletic family Dolichorhynchopidae Welles, 1962, established to include various Cretaceous pliosauromorph taxa all exhibiting an elongate mandibular symphysis, single-headed cervical ribs, and short epipodials. In contrast, Hampe (1992) proposed an affinity with the Brachauchenidae Williston, 1925 (a family erected for the single taxon *Brachauchenius lucasi* Williston, 1903), and described a second species, *K. boyacensis*, Hampe, 1992 from Upper Aptian deposits of the Boyaca region in northern Colombia. Carpenter (1996) briefly reviewed the status of *Kronosaurus*, retaining it within the Brachauchenidae, but noting a distinctive orientation of the interpterygoid vacuity beneath the basicranium, a condition unlike that of *B. lucasi* in which the interpterygoid fenestra is situated more anteriorly. Recent cladistic analysis by O'Keefe (2001), however, has grouped both *Kronosaurus* and *Brachauchenius* within a revised pliosaurid clade (also containing the genera *Macroplata* Swinton, 1930, *Hauffiosaurus* O'Keefe, 2001, *Peloneustes* Lydekker 1889a, *Liopleurodon* Sauvage, 1873 and *Pliosaurus* Owen, 1841), and recognised similarities in the structure of the palate between *Kronosaurus* and the Late Jurassic taxon *Peloneustes*.

Australian specimens assigned to *Kronosaurus* have been recorded from the mid–Upper Albian Toolebuc Formation (Longman, 1924, 1930, 1932, 1935; Molnar, 1982a,b, 1991) and Aptian–Albian Wallumbilla Formation (White, 1935; Romer and Lewis, 1959) of Queensland. Fragmentary or isolated large pliosaurid remains also probably attributable to *Kronosaurus* have been described from the Wallumbilla Formation deposits of New South Wales (Woodward, 1895; Gürich, 1901; Seeley, 1898; Etheridge, 1904; Persson, 1960; Kear, 2002c) and Aptian–Lower Albian Bulldog

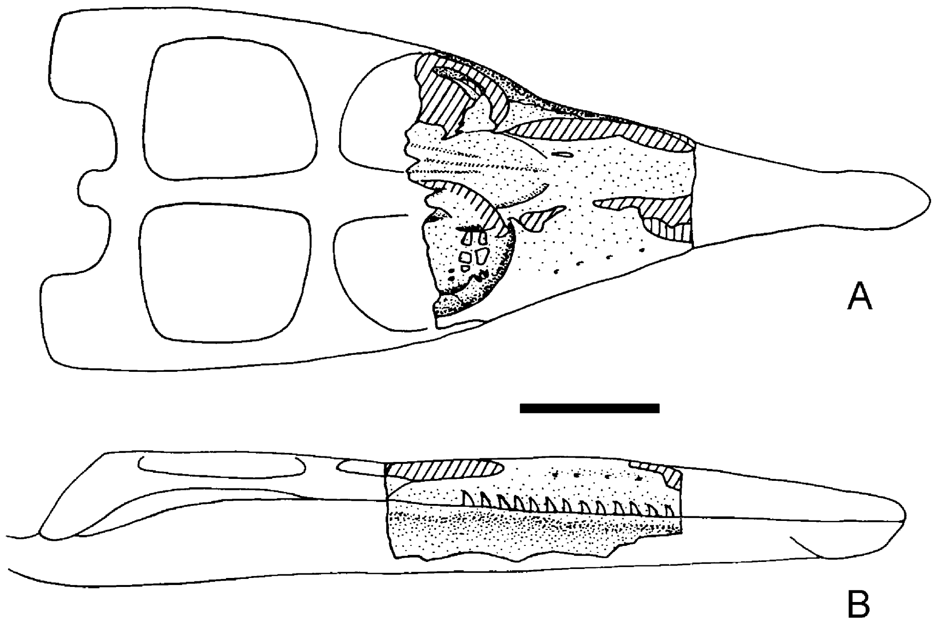


Fig. 5. Skull reconstruction of *Kronosaurus* Longman, 1934 from Molnar (1991) based on an incomplete specimen (QM F2446) from the Lower Cretaceous (Upper Albian) Toolebuc Formation of Queensland, Australia. Hatched areas indicate matrix; scale bar represents 300 mm.

Shale of South Australia (Pledge, 1980; Alley and Pledge, 2000; Kear, 2002a).

Kronosaurus queenslandicus Longman, 1924, p. 26, pl. 4.

Holotype. QM F1609, fragment of mandibular symphysis including remnants of six teeth.

Type locality. Unknown locality, Hughenden area, northern Queensland, Australia.

Stratigraphic horizon. Exact stratigraphic horizon is not known for the holotype specimen due to absence of detailed locality data. Molnar (1982a,b, 1991) and Thulborn and Turner (1991), however, suggested that the type horizon is most likely to be the Toolebuc Formation (Rolling Downs Group), Eromanga Basin, latest mid to Upper Albian *P. ludbrookiae* Zone/upper *C. paradoxa*-*P. pannosus* Zone (Moore et al., 1986; McMinn and Burger, 1986). Remains attributable to *K. queenslandicus* have also been recovered from the underlying Doncaster Member of the Wallumbilla Formation, which corresponds to the *C. hughesii*–lowermost *C. striatus* Zone/*O. opercilata*–*D. davidii* Zone of Helby et al. (1987).

Diagnosis. The following preliminary diagnosis includes characters identified by Longman (1924), White (1935), Romer and Lewis (1959), Molnar (1982a, 1991), Carpenter (1996) and O'Keefe (2001), with the features of the genus. Skull markedly broad and flat with large, dorsally directed orbits (condition reported as being less marked in specimens derived from Doncaster Member deposits, Molnar, 1982a, 1991); interorbital region bearing up to three distinct longitudinal grooves. Pterygoids extensively underlapping basicranium and with interpterygoid vacuity situated beneath rather than anterior to the basicranium (character state is unknown in *K. boyacensis*). Paroccipital process contacts quadrate flange of pterygoid at lateral articulation only. Hyoids robust. Posterior mandibular teeth apparently projecting lateral to the snout whilst maxillary teeth project medial to the lower jaw. Zygapophyses apparently absent from both posterior dorsal and caudal vertebrae. Coracoid and pubis both markedly anteroposteriorly elongate.

Remarks. *Kronosaurus queenslandicus* was established by Longman (1924) on the basis of a poorly preserved mandibular symphysis fragment probably derived from mid–Upper Albian Toolebuc Formation deposits near Hughenden in northern Queensland. Longman (1930, 1935) later described further material (also most likely from the Toolebuc Formation) including fragmentary postcranial elements and part of an unusually broad, flat skull (Fig. 5 A, B) from the Telemon Lease of Dunluce Station near Hughenden. White (1935) attributed cranial remains associated with a partial skeleton (MCZ 1285, collected by the Museum of Comparative Zoology, Harvard University in 1931 and later discussed by Romer and Lewis, 1959) to *K. queenslandicus* from the slightly older (Aptian–Lower Albian) Doncaster Member (Wallumbilla Formation) sediments near the town of Richmond, Queensland. Persson (1960, 1963) considered both the Toolebuc Formation and Doncaster Member specimens to represent a single valid taxon. In contrast, Welles (1962) suggested that because *K. queenslandicus* was based on a poorly preserved holotype, it should be regarded as a nomen dubium pending re-examination of the Harvard skeleton (MCZ 1285) and designation of a more complete holotype specimen. The inadequacy of the type material of Longman (1924) was also recognised by Molnar (1982a, 1991) who suggested that the Harvard example may not be conspecific with the younger Toolebuc Formation remains (described by Longman, 1924, 1930, 1935), but represent a second species (tentatively assigned to *Kronosaurus* sp. by Thulborn and Turner, 1993) characterised by a deeper, more robust skull. As indicated by White (1935), however, much of the skull roof of MCZ 1285 was not preserved in the original fossil specimen and is largely the product of plaster reconstruction. As a result, any attempt at resolving species-level relationships must await a thorough re-examination of the Harvard material (figured by Long, 1998, pp. 138–141) and assessment of the undescribed remains currently housed in the Queensland Museum, Brisbane.

Family: Rhomaleosauridae Kuhn, 1961
Genus *Leptocleidus* Andrews, 1922

Type species. *Leptocleidus superstes* Andrews, 1922, p. 296, pls. 14, 15.

Diagnosis. Characters follow Cruickshank (1997) and Cruickshank and Long (1997) unless cited otherwise. A small-bodied rhomaleosaurid characterised by the skull being triangular in outline with a prominent mid-nasal ridge that merges with the sagittal crest; sagittal crest flanked by deep depressions which delineate protruding orbital rims; forward-pointing expansion on the squamosal mid-line present at the rear of the sagittal crest. Dorsomedian foramen present on the mid-nasal ridge of the premaxillae. Pterygoids with expanded lateral rami. Strongly descending flange present on the postorbital bar. Snout bearing a rosette of procumbent teeth which are conical and circular in section with striae and weak carinae; tooth count reduced to 21 on each side of the upper jaw; estimated tooth count of 35 on each side of the mandible. Spatulate mandibular symphysis probably with five pairs of teeth. Dorsomedially directed trough on the articular. Weakly anteroposteriorly compressed (spool-shaped) cervical centra with centrum lengths consistently less than heights (O'Keefe, 2001); cervical neural arches with large prezygapophyses oriented approximately 45° to the horizontal axis; cervical vertebra count high consisting of as many as 20 centra not including the atlas-axis; cervical ribs single-headed. Interclavicle and clavicle large in comparison to the scapula.

Remarks. *Leptocleidus* is currently the most widely distributed plesiosaur genus known from Australia. Diagnostic material has been recovered from the Upper Hauterivian–Barremian Birdrong Sandstone (Cruickshank and Long, 1997; Long, 1998; Cruickshank et al., 1999) and Neocomian Barrow Group (Long and Cruickshank, 1998) of Western Australia, Aptian–Lower Albian Bulldog Shale of South Australia (Cruickshank et al., 1999; Alley and Pledge, 2000; Kear, 2002a) and Aptian or Albian Darwin Formation of the Northern Territory (Kear, 2002a). Isolated remains also possibly attributable to *Leptocleidus* have been described from Albian freshwater sediments of the Griman Creek Formation at Lightning Ridge in New South Wales and the Surat district of Queensland (Molnar, 1991). The bulk of these specimens consist of isolated teeth (Smith, 1999), although some skeletal elements, including a large propodial similar to that of *Leptocleidus clemai* Cruickshank and Long, 1998 (from the Hauterivian–Barremian Birdrong Sandstone of Western Australia), have been discovered (Long, 1998). Fragmentary pliosauroid teeth and ribs closely resembling those of *Leptocleidus* sp. have also been recorded from the freshwater braided stream and overbank floodplain deposits of the Wonthaggi and Eumeralla formations in Victoria (Rich and Rich, 1989; Rich, 1996; Vickers-Rich, 1996). Interestingly, these deposits were laid down in a very cold, high-latitude environment and provide evidence of plesiosaurs living within inland streams and rivers at the Cretaceous South Pole.

Leptocleidus clemai Cruickshank and Long, 1997, p. 268, figs 3–16.

Holotype. WAM 92.8.1-1-68, a partial skeleton comprising incomplete vertebral column, proximal forelimb/hindlimb elements and fragments of pelvic girdle (Fig. 6 A–E).

Type locality. Murchison House Station area, near Kalbarri on the central west coast of Western Australia (see Cruickshank and Long, 1997).

Stratigraphic horizon. Birdrong Sandstone (Barrow Group), Carnarvon Basin, Upper Hauterivian–Barremian *M. australis* Zone (Helby et al., 1987; McLoughlin et al., 1995).

Diagnosis. Species diagnosis from Cruickshank and Long (1998). With the features of the genus, vertebrae (Fig. 6E) at least 30% greater in linear dimensions and propodials 10–15% greater in size than other species of *Leptocleidus* (see measurements of Cruickshank and Long, 1997 and Fig. 6A–C). Epipodials (Fig. 6D) wider than long.

Remarks. *Leptocleidus clemai* Cruickshank and Long, 1997 is Australia's most recently described Cretaceous marine reptile taxon. It is based on two fragmentary postcranial skeletons, both recovered from the Upper Hauterivian–Barremian Birdrong Sandstone near Kalbarri on the central western coast of Western Australia. Cruickshank and Long (1997) distinguished

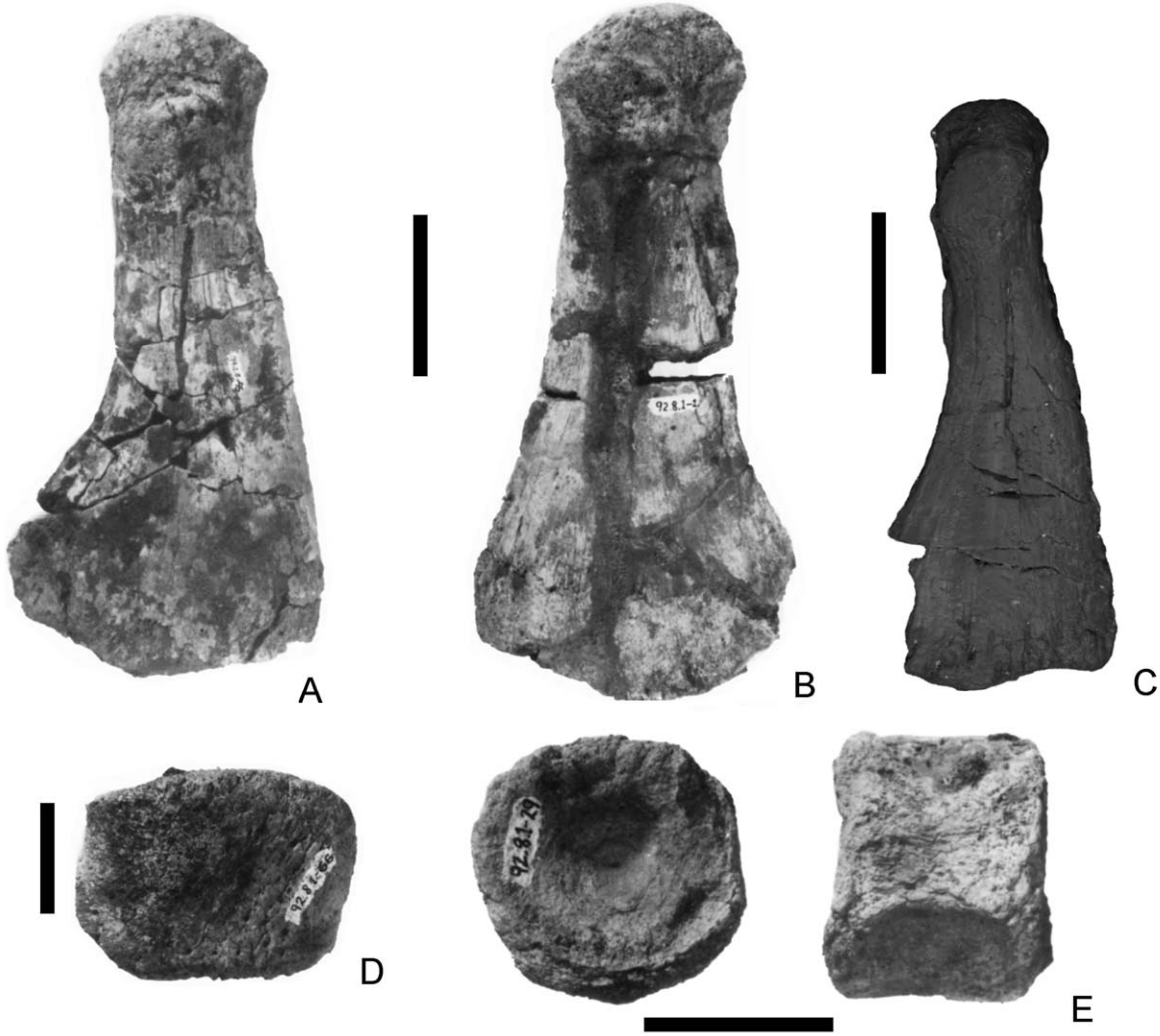


Fig. 6. Elements attributed to *Leptocleidus* Andrews, 1922 from Lower Cretaceous (Upper Hauterivian–Aptian) deposits of Australia. A, dorsal view of humerus (WAM 94.1.6-95) and B, femur (holotype specimen WAM 92.8.1-2) assigned to *Leptocleidus clemai* Cruickshank and Long, 1997 (after Cruickshank and Long, 1991); scale bar represents 40 mm. C, dorsal view of isolated femur (SAM P35053), cast of NTM P913-5) attributed to *Leptocleidus* sp. by Kear (2002a); scale bar represents 50 mm. D, dorsal view of tibia (holotype specimen WAM 92.8.1-66) assigned to *Leptocleidus clemai* Cruickshank and Long, 1997 (after Cruickshank and Long, 1991); scale bar represents 20 mm. E, cervical vertebrate (WAM 92.8.1-29) of *Leptocleidus clemai* Cruickshank, 1997, holotype specimen (WAM 92.8.1-1.-68) in anterior and lateral views (after Cruickshank and Long, 1991); scale bars represents 30 mm.

the species somewhat tenuously on the basis of its large size [around 3 m compared with *L. superstes* from the Upper Weald Clay of Sussex, England and *L. capensis* (Andrews, 1911) from the Sundays River Formation, South Africa, both of which are estimated to have reached around 2 m in length; see Cruickshank, 1997] and derived epipodial morphology. No other more diagnostic characters were provided. Recently, numerous remains, including a near-complete skeleton (AM F99374), of a second species of *Leptocleidus* have been identified from Aptian Bulldog Shale deposits of South Australia (Cruickshank and Long, 1997; Cruickshank et al., 1999; Alley and Pledge, 2000; Kear, 2002a). Most of this material is undescribed although Long (1998) and Kear (2002a) have provided preliminary evaluations of some specimens.

Order: Squamata Oppel, 1811
Infraorder: Anguimorpha Fürbringer, 1900
Family: Mosasauridae Gervais, 1853

Remarks. Mosasaurs are rare and very poorly known in Australia. To date their remains have been recovered only from the Upper Cretaceous deposits of the Perth and Carnarvon basins in Western Australia. Lundelius and Warne (1960) described an indeterminate forelimb, including an abraded ulna and other elements, from the Cenomanian–Lower Turonian upper Molecap Greensand (Perth Basin) near Gingin, noting similarities (primarily size and slender proportions of the ulna) to the North American/European taxa *Platecarpus* Cope, 1869b and *Clidastes* Cope, 1868. This represents one of the earliest records of the Mosasauridae. Long (1998)

Table 5
A list of Australian Cretaceous chelonioid taxa, their synonyms and current status (bold).

Taxon	Holotype	Material	Locality	Horizon	Synonyms and status
Cratochelone berneyi Longman, 1915	QM F550	shoulder girdle, limb and plastron fragments	Hughenden region, Queensland	Upper Albian	**currently valid**
Notochelone costata (Owen, 1882)	AM F67326	ant. carapace, plastron, parts of shoulder girdle	Flinders River region, Queensland	Upper Albian	*Notochelys costata* (Owen, 1882), **currently valid**

recorded three associated caudal vertebrae from the Upper Maastrichtian Miria Formation (Carnarvon Basin) in the Giralia Range, south of Exmouth Gulf. These were apparently well preserved and represented a large (around 6–8 m) mosasaurid of uncertain affinity. Recently, the Molecap Greensand has also yielded further mosasaur remains, including a series of articulated vertebrae from near the township of Dandaragan (Long 1999). All of this material is currently under study by J. Martin of the Dakota School of Mines and J. Long of the Western Australian Museum (J. Long, pers. comm. 2002).

Subclass: indet.
Order: Testudines Linnaeus, 1758
Megaorder: Cryptodira Gray, 1825
Superfamily: Chelonioidea Agassiz, 1857

Remarks. To date, Australian Cretaceous marine turtles have been recorded solely from deposits of the Rolling Downs Group of Queensland. Their remains are particularly common in the mid–Upper Albian Toolebuc Formation where they represent one of the most frequently preserved tetrapod fossils (Molnar, 1982a, 1991). Molnar (1982a, 1991) also reported marine turtle material from the overlying mid–Upper Albian Allaru Mudstone; however, this has yet to be confirmed. Kear (2002a) speculated that the restricted distribution of Australian Cretaceous chelonoids might be a product of environmental factors such as low average water temperatures. Indeed, studies of sedimentary sequences (Frakes and Francis, 1988; Frakes and Krassay, 1992; Frakes et al., 1995; Constantine et al., 1998), climatic modelling (Barron and Washington, 1982) and isotope data (Gregory et al., 1989; Pirrie et al., 1995) have suggested that strongly seasonal climates with winter freezing and at least seasonal sea ice characterised the high latitudes of Australia during the Early Cretaceous. Such conditions may have been unfavourable to chelonioids and provided an effective barrier to the group's dispersal into the Australian region prior to the Late Albian. As an interesting note, the distribution of sympatric ichthyosaur and plesiosaur taxa appears to have been unaffected, and may reflect adaptation (perhaps including elevated metabolic levels, annual migration or hibernation) by these groups to cope with highly seasonal, low-temperature environments.

Marine turtle remains are virtually unknown from the Upper Cretaceous of Australia. However, Molnar (1991) reported an unusually flattened carapace impression (QM F12413) resembling that of a marine turtle from the Cenomanian (*A. distocarinatus* Zone; Rodgers, 1995) fluviatile deposits of the Winton Formation, near Winton in Queensland. As yet no work has been undertaken on this specimen; thus, its identification has yet to be verified.

Currently, only two Australian Cretaceous chelonioid species have been named and both are regarded as valid (Table 5). Reviews of Australian fossil marine turtles have been presented by Gaffney (1981, 1991), Molnar (1982a, 1991) and Long (1998).

Family: Protostegidae Cope, 1872
Genus *Cratochelone* Longman, 1915

Type species. *Cratochelone berneyi* Longman, 1915, p. 24, pls. 12, 13, figs. 1, 2.

Diagnosis. Characters follow Longman (1915) and Long (1998). Large-bodied protostegid turtle with plastron length of around 2 m. Scapulo-precoracoid and coracoid short and robust. Humeral head greatly expanded transversely. Entoplastron laterally expanded (into distinct wings sensu Hirayama, 1998) but potentially lacking a posterior process.

Remarks. The monotypic genus *Cratochelone* was established by Longman (1915) and subsequently reviewed by Gaffney (1981, 1991), who suggested an affinity with the Protostegidae. This is supported by the presence of a laterally expanded entoplastron (forming distinct wings sensu Hirayama, 1998), which is considered a derived feature within the group (Gaffney and Meylan, 1988; Elliott et al., 1997; Hooks, 1998). Hirayama (1998), however, regarded lateral expansion of the entoplastron, and its subsequent development into a T-shaped structure, as a synapomorphy common to all dermochelyoids (an epifamily including Dermochelydae and Protostegidae sensu Hirayama, 1998). The possible absence of the posterior process on the entoplastron of *Cratochelone* is, therefore, significant (although it has yet to be conclusively confirmed) and may represent a key diagnostic feature of the taxon.

Cratochelone berneyi Longman, 1915, p. 24, pls. 12, 13, figs. 1, 2.

Holotype. QM F550, incomplete shoulder girdle and partial forelimb, plastron fragments.

Type locality. Unknown locality, Hughenden area, northern Queensland, Australia.

Stratigraphic horizon. Exact stratigraphic horizon is not known for the holotype due to absence of detailed locality data. However the specimen is generally regarded as being derived from the Toolebuc Formation (Rolling Downs Group), Eromanga Basin. This unit corresponds to the latest mid to Upper Albian *P. ludbrookiae* Zone/upper *C. paradoxa*-*P. pannosus* Zone (Moore et al., 1986; McMinn and Burger, 1986).

Diagnosis. As for genus.

Remarks. Despite the very fragmentary condition of the holotype, Gaffney (1981) recommended retention of *C. berneyi* (for the type specimen only) as a valid taxon primarily because of its large size in comparison to all other Australian Cretaceous chelonioid remains. This has also been advocated by many subsequent workers (e.g. Molnar, 1982a, 1991; Gaffney, 1991; Long, 1998) and is followed herein pending discovery of further material.

Genus *Notochelone* (Owen, 1882)

Type species. *Notochelone costata* (Owen, 1882), p. 178, figs. 1, 2, by subsequent designation of Lydekker, 1889b, p. 70.

Diagnosis. Characters follow Zangerl (1960), Gaffney (1981), Gaffney and Meylan (1988), Moody (1997) and Hirayama (1994, 1998). Small protostegid turtle with plastron length <1 m. Skull with nasals present and large temporal vacuity. High lingual ridge of maxilla exposed from lateral ridge; medial process of jugal absent. Prefrontal-postorbital in contact and barely allowing the frontals to reach the orbital rims. Interorbital bridge wide. Parietal-squamosal contact absent. Foramen caroticum laterale and canalis carotici interni not noticeably larger in diameter than the foramen anterius canalis carotici interni and the medial branch of the canalis caroticus internus; canalis caroticus lateralis small in diameter compared to the canalis caroticus internus. Rod-like rostrum basisphenoidale. Possibly amphicoelous cervical vertebrae. Carapace with marked neural keel; plastron with very large central and peripheroplastral fontanelles, reducing the hyoplastral-hypoplastral contact to a narrow projection; xiphiplastra much broader than long and medially curved with a large mid-line fontanelle. Scapular angle wide. Coracoid longer than humerus. Lateral process of humerus restricted to anterior portion of shaft (not visible in ventral view) and bearing a medial concavity.

Remarks. Lydekker (1889b) erected the genus *Notochelone* as a replacement for the preoccupied '*Notochelys*' *costata* established by Owen (1882). Zangerl (1960) briefly reviewed the taxon, listing comparisons with the dermochelyid *Corsochelys* Zangerl, 1960 from the Lower Campanian of Alabama, USA. Gaffney and Meylan (1988) later suggested a close, probable sister-taxon relationship between *Notochelone* and the Turonian genus *Desmatochelys* Williston, 1894, placing both within an unnamed clade referred to as 'D10'. Hirayama (1994, 1997, 1998), however, reassigned *Notochelone* to an expanded Protostegidae, recognising similarities in cranial morphology and structure of the forelimb. Despite this, others, such as Elliott et al. (1997) and Moody (1997), have suggested that the 'D10' taxa of Gaffney and Meylan (1988) should be regarded as a distinct family Desmatochelydae Williston, 1894.

Notochelone costata (Owen, 1882).

1882 *Notochelys costata* Owen, p. 178, figs. 1, 2.

Holotype. AM F67326, incomplete anterior portions of carapace (Fig. 7 A) and plastron, parts of shoulder girdle.

Type locality. Unknown locality, Flinders River region, northern Queensland, Australia.

Stratigraphic horizon. Exact stratigraphic horizon is not known for the holotype; however, the specimen is generally regarded as being derived from the Toolebuc Formation (Rolling Downs Group), Eromanga Basin. This unit corresponds to the latest mid to Upper Albian *P. ludbrookiae* Zone/upper *C. paradoxa*–*P. pannosus* Zone (Moore et al., 1986; McMinn and Burger, 1986). Molnar (1982a, 1991) and Long (1998) also reported *N. costata* as occurring in the overlying Allaru Mudstone, mid–Upper Albian *P. ludbrookiae* Zone/upper *C. paradoxa*-*P. pannosus*/*C. denticulata* zones (Krieg and Rodgers, 1995).

Diagnosis. As for genus.

Remarks. *Notochelone costata* represents one of the most common fossil tetrapods from the Upper Albian deposits of Queensland. Despite this, most remains attributed to the taxon are currently undescribed. Gaffney (1981) provided a list of the then recognised material including an incomplete anterior carapace and plastron recorded by Owen (1882), and an associated skull, carapace and partial plastron (QM F2249) from the Toolebuc Formation of Julia Creek in Queensland (see Fig. 1). Gaffney (1981) utilised both these specimens to create a tentative restoration of the complete shell of *N. costata*. This was later modified by Hirayama (1997) and is reproduced here in Fig. 7B.

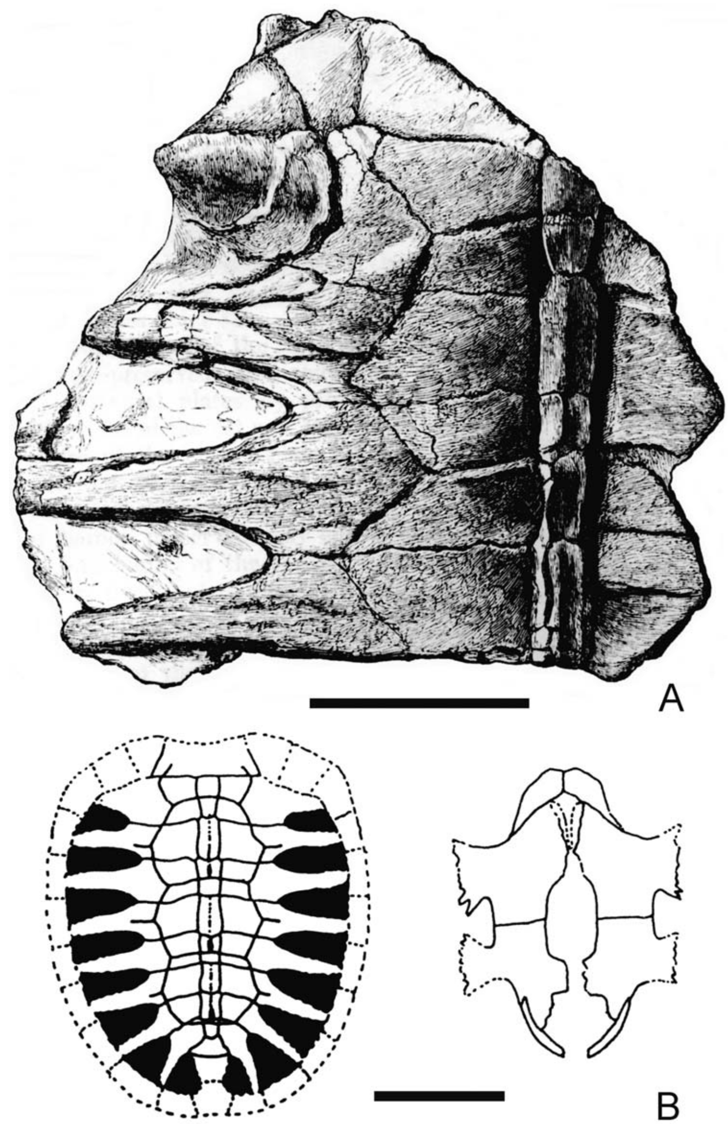


Fig. 7. *Notochelone costata* (Owen, 1882) from the Lower Cretaceous (Upper Albian) deposits of Queensland, Australia. A, partial carapace of holotype specimen (AM F67326) (after Owen, 1882); scale bar represents 100 mm. B, reconstructed carapace and plastron of *Notochelone costata* (Owen, 1882) from Hirayama (1997) based upon the holotype and partial specimen QM F2249 (see text); scale bar represents 300 mm.

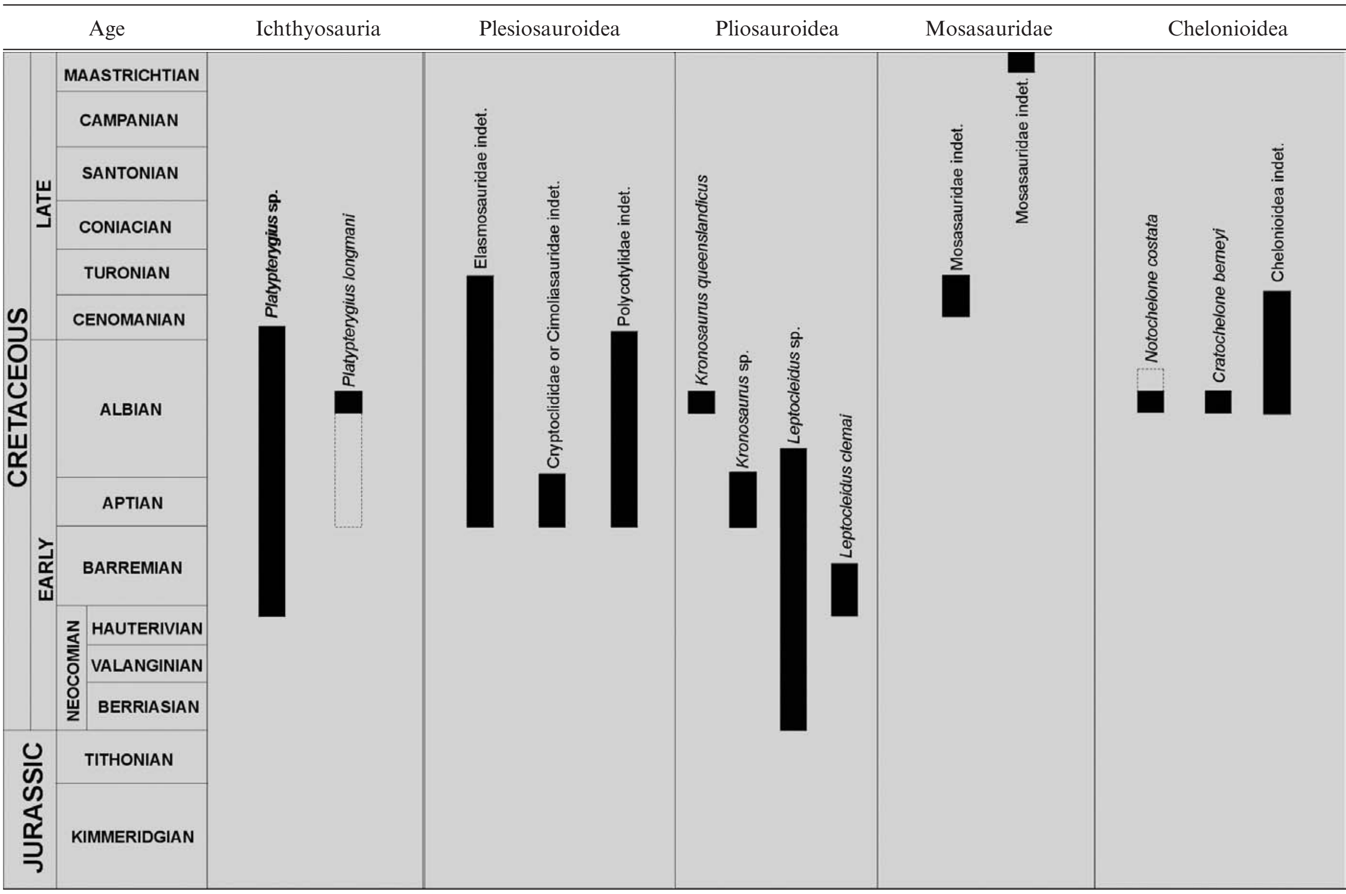
To date, *N. costata* is the only small-bodied chelonioid taxon known from Australia. However, Molnar (1991) recorded the carapace and vertebrae of a possibly distinct form from Cretaceous deposits (probably Toolebuc Formation) near Boulia in Queensland (Fig. 1). This material has yet to be studied but could indicate a greater taxonomic diversity in Australian Cretaceous marine turtles than is currently suspected.

5. Conclusions

Well-preserved marine reptile fossils are common in the Cretaceous epicontinental and continental-margin marine rocks of Australia. Despite this, most taxa remain very poorly understood and few detailed palaeoenvironmental or stratigraphic studies have been undertaken on the specific localities from which they originate. As a result, considerable potential exists for future work on all aspects of the Australian Cretaceous marine reptile fauna.

To date, the vast majority of remains have been recovered from the Aptian–Albian epicontinental marine units of the Eromanga Basin in Queensland, New South Wales and South Australia. Fragmentary and/or isolated specimens have also been recorded from the Berriasian, Hauterivian–Barremian, Albian–Cenomanian, Cenomanian–Turonian and Maastrichtian marine rocks of Western Australia, Aptian or Albian continental margin sediments of the Northern Territory and Aptian–Albian freshwater facies of New

Table 6
Stratigraphic distribution of Australian Cretaceous marine reptile taxa.



South Wales and Victoria. Interestingly, many of these deposits represent Cretaceous high latitude-polar environments and some (particularly the Aptian units of the southern Eromanga Basin and coastal ranges of Victoria) include palaeoclimatic indicators suggesting very cold to near freezing conditions.

As currently known, the Australian Cretaceous marine reptile fauna comprises one family of ichthyosaurs (Ophthalmosauridae), as many as five families of plesiosaur (Rhomaleosauridae, Pliosauridae, Polycotylidae, Elasmosauridae and possibly Cryptoclididae or Cimoliasauridae sensu O'Keefe, 2001), one family of chelonioid sea turtle (Protostegidae) and indeterminate mosasaurids. Although few named species may be regarded as valid, the stratigraphic distribution of these family-level taxa does provide some indication of broad trends in local faunal composition over time. For example (see Table 6), plesiosaurs and ichthyosaurs dominate Lower Cretaceous deposits with plesiosaurs showing a high taxonomic diversity (including the earliest known polycotylids), particularly in the Aptian. Albian faunas see the advent of chelonioid turtles with a corresponding reduction in plesiosaur diversity (through the loss of rhomaleosaurids) and a marked increase in the numbers of ichthyosaur remains. Upper Cretaceous units have yielded only fragmentary specimens of primarily plesiosaurs and mosasaurs with ichthyosaurs limited to rocks of Cenomanian age. This distribution compares well with that known from contemporary deposits elsewhere, which show a similar progressive decline in plesiosaur family-level diversity throughout the Cretaceous and a rapid radiation of mosasaurs following the apparent extinction of ichthyosaurs at the Cenomanian/Turonian boundary (Bakker 1993; Bardet 1994; Massare 1997).

Acknowledgements

I am indebted to Tim Flannery of the South Australian Museum for his continuous support and enthusiasm for the study of Australian Cretaceous faunas, floras and environments. Robert Jones of the Australian Museum, Pat Rich and Lesley Kool of Monash University, Dirk Megirian of the Museum and Art Gallery of the Northern Territory, Charles Schaff of the Museum of Comparative Zoology, Harvard University, Tom Rich of Museum Victoria, Ralph Molnar, Jo Wilkinson and Scott Hocknull of the Queensland Museum, Bruce Erickson of the Science Museum Minnesota, Neville Pledge of the South Australian Museum, Henk Godthelp of the University of New South Wales, John Long of the Western Australian Museum, the National Opal Collection, Cody Opal Pty. Ltd and many private individuals all generously assisted in making information and specimens available. The manuscript benefited greatly from the comments of Nathalie Bardet and Ryosuke Motani. Robert Hamilton-Bruce, South Australian Museum, contributed to production of the figures. The South Australian Museum, Origin Energy, The Advertiser, The Waterhouse Club, the Coober Pedy Tourism Association, Commercial and General Capital Ltd and Kenneth J. Herman Inc. gave financial support for this research.

References

Agassiz, L., 1857. North American Testudinata. In Contributions to the natural history of the United States. Volume 1, Part 2. Little, Brown and Co, Boston, pp. 223–425.

Alexander, E.M., Sansome, A., 1996. Lithostratigraphy and environments of deposition. In: Alexander, E.M., Hibbert, J.E. (Eds.). The petroleum geology of South Australia. Volume 2: Eromanga Basin, South Australia. Department of Mines and Energy Report Book, 96/20, pp. 49–86.

Alley, N.F., Pledge, N.S., 2000. The plants, animals and environments of the last 280 (290) million years. In: Slaytor, W.J.H. (Ed.). Lake Eyre Monograph Series. Volume 5. Royal Geographic Society of South Australia, Adelaide, pp. 35–82.

Andrews, C.W., 1911. Description of a new plesiosaur (*Plesiosaurus capensis*, sp. nov.) from the Uitenhage Beds of Cape Colony. Ann. S. Afr. Mus. 7, 309–322.

Andrews, C.W., 1922. Description of a new plesiosaur from the Weald Clay of Berwick (Sussex). Quart. J. Geol. Soc., London 78, 285–295.

Anonymous, 2001. Geological Survey donates plesiosaur to S.A. (South Australian) Museum. MESA J. 22, 17–17.

Arkhangelsky, M.S., 1998. On the ichthyosaurian genus *Platypterygius*. Paleontol. Zh. 32, 65–69. [In Russian].

Bakker, R.T., 1993. Plesiosaur extinction cycles – events that mark the beginning, middle and end of the Cretaceous. In: Caldwell, W.G.E., Kauffman, E.G. (Eds.). Evolution of the Western Interior Basin. Geological Association of Canada, Special Paper, 39, pp. 641–664.

Bardet, N., 1992. Stratigraphic evidence for the extinction of ichthyosaurs. Terra Nova 4, 649–656.

Bardet, N., 1994. Extinction events among Mesozoic marine reptiles. Hist. Biol. 7, 131–324.

Bardet, N., Godefroit, P., Sciau, J., 1999. A new elasmosaurid plesiosaur from the Lower Jurassic of southern France. Palaeontology 42, 927–952.

Bardet, N., Mazin, J.-M., Cariou, E., et al., 1991. Les Plesiosauria du Jurassique supérieur de la province de Kachchh (Inde). Comptes Rend. Acad. Sci. Paris, Sér. 313 2, 1343–1347.

Barron, E.J., Washington, W.M., 1982. Cretaceous climate: a comparison of atmospheric simulations with the geologic record. Palaeogeogr., Palaeoclimatol., Palaeoecol. 40, 103–133.

Baur, G., 1887. Uber die Ursprung der Extremitäten der Ichthyopterygia. Ber. Versamm. Oberr. Ver. 20, 17–20.

Belford, D.J., 1958. Stratigraphy and micropalaeontology of the Cretaceous of Western Australia. Geolog. Rundsch. 47, 629–647.

Benton, M.J., 1997. Vertebrate Palaeontology, Second Edition, Blackwell Science, Oxford.

Blainville de, H.M.D., 1835. Description de quelques espéces de reptiles de la Californie, précédée de l'analyse d'un systéme générale Erpetologie et d'Amphibiologie. Nouv. Ann. Mus. Hist. Nat., Paris 4, 233–296.

Broili, F., 1907. Ein neuer *Ichthyosaurus* aus der Norddeutschen Kreide. Palaeontographica 54, 139–162.

Brown, D.S., 1981. The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. Bull. Br. Mus. (Nat. Hist.) Geol. Ser. 35, 253–347.

Brown, D.S., 1993. A taxonomic reappraisal of the families Elasmosauridae and Cryptoclididae (Reptilia, Plesiosauroidea). Rev. Paléobiol. 7, 9–16.

Brown, D.S., Cruickshank, A.R.I., 1994. The skull of the Callovian plesiosaur *Cryptoclidus eurymerus*, and the sauropterygian cheek. Palaeontology 37, 941–953.

Burger, D., 1978. Appendix 1. Palynological examination of outcrop samples and subsurface sections in the Bathurst Island, Melville Island, Cobourg Peninsula and Darwin Sheet areas. In: Hughes, R.J. (Ed.). The geology and mineral occurrences of the Bathurst Island, Melville Island and Cobourg Peninsula, Northern Territory. Bureau of Mineral Resources, Geology and Geophysics, Bulletin, 177, pp. 58–61.

Burger, D., 1980. Palynology of the Lower Cretaceous Surat Basin. Bur. Min. Res., Geol Geophys, Bull 189, 1–106.

Burger, D., 1988. Early Cretaceous environments in the Eromanga Basin: palynological evidence from GSQ Wyandra-1 corehole. Mem. Assoc. Australas. Palaeontol. 5, 173–186.

Burton, G.R., Mason, A.J., 1998. Controls on opal localisation in the White Cliffs area. Quart. Notes. Geol. Surv. NSW 107, 1–11.

Carroll, R.L., 1988. Vertebrate Paleontology and Evolution, Freeman, San Francisco.

Carpenter, K., 1989. *Dolichorhynchops* does not equal *Trinacromerum* (Reptilia, Plesiosauria). J. Vert. Paleontol. 9, 15A.

Carpenter, K., 1996. A review of short-necked plesiosaurs from the Cretaceous of the Western Interior, North America. Neues Jahrb. Geol. Paläontol. Abhandl. 201, 259–287.

Carpenter, K., 1997. Comparative cranial anatomy of two North American Cretaceous plesiosaurs. In: Callaway, J.M., Nicholls, E.L. (Eds.). Ancient marine reptiles. Academic Press, San Diego, pp. 191–216.

Chapman, F., 1914. Australasian fossils, George Robertson, Melbourne.

Chatterjee, S., Small, B.J., 1989. New plesiosaurs from the Upper Cretaceous of Antarctica. In: Crame, J.A. (Ed.). Origins and evolution of the Antarctic biota. Geological Society of London, Special Publication, 47, pp. 197–215.

Choo, B., 1999. Cretaceous ichthyosaurs from Western Australia. Rec. W. Aust. Mus. Suppl. 57, 207–218.

Condon, M.A., 1968. The geology of the Carnarvon Basin, Western Australia. Bur. Min. Res., Geol. Geophys. Bull. 77, 1–191.

Constantine, A., Chinsamy, A., Vickers-Rich, P., et al., 1998. Periglacial environments and polar dinosaurs. S. Afr. J. Sci. 94, 137–141.

Cope, E.D., 1868. Remarks on *Clidastes iguanavus, Nectoportheus validus and Elasmosaurus*. Proc. Acad. Nat. Sci. Philadelphia 20, 181.

Cope, E.D., 1869a. Synopsis of the extinct Batrachia and Reptilia of North America, part 1. Trans. Am. Phil. Soc. 14, 1–235.

Cope, E.D., 1869b. On the reptilian orders Pythonomorpha and Streptosauria. Proc. Boston Soc. Nat. Hist. 12, 250–256.

Cope, E.D., 1872. On the geology and paleontology of the Cretaceous strata of Kansas. Ann. Rep. US Geol. Sur. Montana Adj. Terr. 5, 318–349.

Cragin, F., 1888. Preliminary description of a new or little known saurian from the Benton of Kansas. Am. Geol. 2, 404–407.

Cruickshank, A.R.I., 1997. A Lower Cretaceous pliosauroid from South Africa. Ann. S. Afr. Mus. 105, 207–226.

Cruickshank, A.R.I., Long, J.A., 1997. A new species of pliosaurid reptile from the Early Cretaceous Birdrong Sandstone of Western Australia. Rec. W. Aust. Mus. 18, 263–276.

Cruickshank, A.R.I., Fordyce, R.E., 1998. High latitude late Cretaceous plesiosaurs in Gondwana. J. Afr. Earth Sci. 27, 50–51.

Cruickshank, A.R.I., Fordyce, R.E., 2002. A new marine reptile (Sauropterygia) from New Zealand: further evidence for a Late Cretaceous austral radiation of cryptoclidid plesiosaurs. Palaeontology 45, 557–575.

Cruickshank, A.R.I., Fordyce, R.E., Long, J.A., 1999. Recent developments in Australasian sauropterygian palaeontology (Reptilia: Sauropterygia). Rec. W. Aust. Mus. Suppl. 57, 201–205.

Day, R.W., 1969. The Early Cretaceous of the Great Artesian Basin. In: Campbell, K.S.W. (Ed.). Stratigraphy and palaeontology. Essays in honour of Dorothy Hill. Australian University Press, Canberra, pp. 140–173.

Day, R.W., Whitaker, W.G., Murray, C.G., Wilson, I.H., Grimes, K.G., 1983. Queensland Geology. A companion volume to the 1:2 500 000 scale geological map (1975). Geol. Surv. Queensland Publ. 383, 1–194.

Delair, J.B., 1959. The Mesozoic reptiles of Dorset. Part 2. Proc. Dorset Nat. Hist. Archaeol. Soc. 80, 52–90.

De Lurio, J.L., Frakes, L.A., 1999. Glendonites as a palaeoenvironmental tool: implications for Early Cretaceous high latitude climates in Australia. Geochim. Cosmochim. Acta 63, 1039–1048.

Dettmann, M.E., Playford, G., 1969. Palynology of the Australian Cretaceous: a review. In: Campbell, K.S.W. (Ed.). Stratigraphy and palaeontology. Essays in honour of Dorothy Hill. Australian University Press, Canberra, pp. 174–210.

Dettmann, M.E., Molnar, R.E., Douglas, J.G., et al., 1992. Australian Cretaceous terrestrial faunas and floras: biostratigraphic and biogeographic implications. Cret. Res. 13, 207–262.

Elliott, D.K., Irby, G.V., Howard Hutchinson, J., 1997. *Desmatochelys lowi*, a marine turtle from the Upper Cretaceous. In: Callaway, J.M., Nicholls, E.L. (Eds.). Ancient marine reptiles. Academic Press, San Diego, pp. 243–258.

Embleton, B.J.J., 1984. Australia's global setting: past global settings. In: Veevers, J.J. (Ed.). Phanerozoic Earth history of Australia. Clarendon Press, Oxford, pp. 11–17.

Embleton, B.J.J., McElhinny, M.W., 1982. Marine magnetic anomalies, palaeomagnetism and the drift history of Gondwanaland. Earth Plan. Sci. Lett. 58, 141–150.

Etheridge, R., 1888. On additional evidence of the occurrence of *Plesiosaurus* in the Mesozoic rocks of Queensland. Proc. Linn. Soc. NSW 2, 410–413.

Etheridge, R., 1897. An Australian sauropterygian (*Cimoliasaurus*), converted into precious opal. Rec. Aust. Mus. 3, 21–29.

Etheridge, R., 1904. A second sauropterygian converted into opal from the Upper Cretaceous of White Cliffs, New South Wales. With indications of ichthyopterygians at the same locality. Rec. Aust. Mus. 5, 306–316.

Frakes, L.A., Francis, J.E., 1988. A guide to Phanerozoic cold polar climates from high-latitude ice-rafting in the Cretaceous. Nature 333, 547–549.

Frakes, L.A., Francis, J.E., 1990. Cretaceous palaeoclimates. In: Ginsberg, R.N., Beaudoin, B. (Eds.). Cretaceous resources, events and rhythms. Kluwer Academic Publishers, Dortrecht, pp. 273–287.

Frakes, L.A., Krassay, A.A., 1992. Discovery of probable ice-rafting in the Late Mesozoic of the Northern Territory and Queensland. Aust. J. Earth. Sci. 39, 115–119.

Frakes, L.A., Alley, N.F., Deynoux, M., 1995. Early Cretaceous ice rafting and climate zonation in Australia. Int. Geol. Rev. 37, 567–583.

Freytag, I.B., 1964. Reptilian vertebral remnants from Lower Cretaceous strata near Oodnadatta. Geol. Surv. S. Aust. Quart. Geol. Notes 10, 1–2.

Fürbringer, M., 1900. Zur vergleichenden Anatomie des Brustschulterapparates und der Schultermuskeln. Jen. Zeitsch. Naturwissen. 34, 215–718.

Gaffney, E.S., 1981. A review of the fossil turtles of Australia. Am. Mus. Nov. 2720, 1–38.

Gaffney, E.S., 1991. The fossils turtles of Australia. In: Vickers-Rich, P., Monaghan, J.M., Baird, R.F. et al., (Eds.). Vertebrate palaeontology of Australasia. Pioneer Design Studio, Monash University, Melbourne, pp. 703–720.

Gaffney, E.S., Meylan, P.A., 1988. A phylogeny of turtles. In: Benton, M.J. (Ed.). The phylogeny and classification of tetrapods, Volume 1: amphibians, reptiles, birds. Syst. Assoc. Spec., Volume 35A. Clarendon Press, Oxford, pp. 157–219.

Gervais, P., 1853. Observations relatives aux reptiles fossiles de France. Comptes Rend. Acad. Sci. Paris 36, 374–377.

Gray, J.E., 1825. A synopsis of the genera of reptiles and Amphibia, with a description of some new species. Ann. Phil. 10, 193–217.

Gregory, R.T., Douthitt, C.B., Duddy, I.R., et al., 1989. Oxygen isotopic composition of carbonate concretions from the Lower Cretaceous of Victoria, Australia: implications for the evolution of meteoric waters on the Australian continent in a paleopolar environment. Earth Plan. Sci. Lett. 92, 27–42.

Gürich, G., 1901. Jura- und Devon- fossilien von White Cliffs Australien. Neues Jahrb. Beil. 14, 492–495.

Hampe, O., 1992. Ein grosswuechsiger pliosauride (Reptilia, Plesiosauria) aus der Unterkreide (oberes Aptium) von Kolumbien. Cour. Forschung. Sencken. 145, 1–32.

Hector, J., 1874. On the fossil Reptilia of New Zealand. Trans. NZ Inst. 6, 333–358.

Helby, R., Morgan, R., Partridge, A.D., 1987. A palynological zonation of the Australian Mesozoic. Mem. Aust. Assoc. Palaeontol. 4, 1–94.

Henderson, R.A., 1990. Late Albian ammonites from the Northern Territory, Australia. Alcheringa 14, 109–148.

Henderson, R.A., 1998. Eustatic and palaeoenvironmental assessment of the mid-Cretaceous Bathurst Island Group of the Money Shoals Platform, northern Australia. Palaeogeogr., Palaeoclimat., Palaeoecol. 138, 115–138.

Henderson, R.A., McNamara, K.J., 1985. Maastrichtian nonheteromorph ammonites from the Miria Formation, Western Australia. Palaeontology 28, 35–88.

Henderson, R.A., Crampton, J.S., Dettmann, M.E., et al., 2000. Biogeographical observations on the Cretaceous biota of Australasia. Mem. Austr. Assoc. Palaeontol. 23, 355–404.

Hirayama, R., 1994. Phylogenetic systematics of fossil sea turtles. Isl. Arc. 3, 270–284.

Hirayama, R., 1997. Distribution and diversity of Cretaceous chelonioids. In: Callaway, J.M., Nicholls, E.L. (Eds.). Ancient marine reptiles. Academic Press, San Diego, pp. 225–241.

Hirayama, R., 1998. Oldest known sea turtle. Nature 392, 705–708.

Hocking, R.M., Moors, H.T., van de Graff, W.J.E., 1987. Geology of the Carnarvon Basin. Geol. Surv. W. Aust. Bull. 133, 1–289.

Hooks III, G.E., 1998. Systematic revision of the Protostegidae, with a redescription of *Calcarichelys gemma* Zangerl, 1953. J. Vertebr. Palaeontol. 18, 85–98.

Howchin, W., 1928. The building of Australia and the succession of life. Part 2, Government Printer, Adelaide.

Huene von, F., 1922. Die Ichthyosaurier des Lias und ihre Zusammenhänge, Gebrüder Borntraeger, Berlin.

Idnurm, M., 1985. Late Mesozoic and Cenozoic palaeomagnetism of Australia – I. A redetermined apparent polar wander path. Geophys. J. R. Astron. Soc. 83, 399–418.

Jack, R.L., Etheridge, R., 1892. Geology and palaeontology of Queensland and New Guinea with sixty-eight plates and a geological map of Queensland, Dulau and Co, London.

Johns, R.K., 1968. Geology and mineral resources of the Andamooka-Torrens area. Geol. Surv. S. Aust. Bull. 41, 7–103.

Kear, B.P., 2001. Elasmosaur (Reptilia, Plesiosauria) basicranial remains from the Early Cretaceous of Queensland. Rec. S. Aust. Mus. 34, 127–133.

Kear, B.P., 2002a. Darwin Formation (Early Cretaceous, Northern Territory) marine reptile remains in the South Australian Museum. Rec. S. Aust. Mus. 35, 33–47.

Kear, B.P., 2002b. Dental caries in an Early Cretaceous ichthyosaur. Alcheringa 25, 387–390.

Kear, B.P., 2002c. Reassessment of the Early Cretaceous plesiosaur *Cimoliasaurus maccoyi* Etheridge, 1904 (Reptilia, Sauropterygia) from White Cliffs, New South Wales. Aust. J. Zool. 50, 671–685.

Krieg, G.W., Rodgers, P.A., 1995. Stratigraphy – marine succession. In: Drexel, J.F., Preiss, W.V. (Eds.). The geology of South Australia. Volume 2. The Phanerozoic. Geological Survey of South Australia Bulletin, 54, pp. 112–123.

Kuhn, O., 1961. Die Familien der rezenten und fossilen Amphibien und Reptilien, Verlaghaus Meisenbach, Bamberg.

Linnaeus, C., 1758. Systema naturae, per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima. Stokholm.

Leidy, J., 1851. Description of fossils. Proc Acad Nat Sci Philadelphia 5, 325–328.

Long, J.A., 1998. Dinosaurs of Australia and New Zealand and other animals of the Mesozoic Era, University of New South Wales Press, Sydney.

Long, J.A., 1999. Prehistoric sea monsters of the west. Nat. Aust. 26, 46–53.

Long, J.A., Cruickshank, A.R.I., 1998. Further records of plesiosaurian reptiles of Jurassic and Cretaceous age from Western Australia. Rec. W. Aust. Mus. 19, 47–55.

Longman, H.A., 1915. On a giant turtle from the Queensland Lower Cretaceous. Mem. Queensland Mus. 3, 24–29.

Longman, H.A., 1922. An ichthyosaurian skull from Queensland. Mem. Queensland Mus. 7, 246–256.

Longman, H.A., 1924. A new gigantic marine reptile from the Queensland Cretaceous, *Kronosaurus queenslandicus* new genus and species. Mem. Queensland Mus. 8, 26–28.

Longman, H.A., 1930. *Kronosaurus queenslandicus*. A gigantic Cretaceous pliosaur. Mem. Queensland Mus. 10, 1–7.

Longman, H.A., 1932. Restoration of *Kronosaurus queenslandicus*. Mem. Queensland Mus. 10, 98.

Longman, H.A., 1935. Palaeontological notes. Mem. Queensland Mus. 10, 236–239.

Longman, H.A., 1943. Further notes on Australian ichthyosaurs. Mem. Queensland Mus. 12, 101–104.

Ludbrook, N.H., 1966. Cretaceous biostratigraphy of the Great Artesian Basin in South Australia. Geol. Surv. S. Aust. Bull. 40, 7–223.

Lundelius, E., Warne, S.St.J., 1960. Mosasaur remains from the Upper Cretaceous of Western Australia. J. Paleontol. 34, 1215–1217.

Lydekker, R., 1889a. On the remains and affinities of five genera of Mesozoic reptiles. Quart. J. Geol. Soc. London 45, 41–59.

Lydekker, R., 1889b. Catalogue of the fossils Reptilia and Amphibia in the British Museum (Natural History). Part III, The Order Chelonia, British Museum, London.

Maisch, M.W., Matzke, A.T., 2000. The Ichthyosauria. Stutt. Beitr. Nat. Ser. B (Geol. Paläontol.) 298, 1–159.

Massare, J.A., 1997. Introduction – faunas, behaviour and evolution. In: Callaway, J.M., Nicholls, E.L. (Eds.). Ancient marine reptiles. Academic Press, San Diego, pp. 401–421.

McConachie, B.A., Dunster, J.N., Wellman, P., et al., 1997. Carpentaria Lowlands and Gulf of Carpentaria regions. In: Bain, J.H.C., Draper, J.J. (Eds.). North Queensland Geology. Australian Geological Survey Organisation Bulletin, 240, pp. 365–398.

McCoy, F., 1867. On the occurrence of *Ichthyosaurus* and *Plesiosaurus* in Australia. Ann. Mag. Nat. Hist. 19, 355–356.

McGowan, C., 1972. The systematics of Cretaceous ichthyosaurs with particular reference to the material from North America. Cont. Geol. Univ. Wyoming 11, 9–29.

McGowan, C., Motani, R., 2003. Ichthyopterygia. Handbuch der Paläoherpetologie Part 8, Verlag Dr. Friedrich Pfeil, München.

McLoughlin, S., Haig, D.W., Backhouse, J., et al., 1995. Oldest Cretaceous sequence, Giralia Anticline, Carnarvon Basin, Western Australia: late Hauterivian–Barremian. J. Aust. Geol. Geophys. 15, 445–468.

McMinn, A., Burger, D., 1986. Palynology and palaeoenvironment of the Toolebuc Formation (sensu lato) in the Eromanga Basin. In: Gravestock, D.I., Moore, P.S., Pitt, G.M. (Eds.). Contributions to the geology and hydrocarbon potential of the Eromanga Basin. Geological Society of Australia Special Publication, 12, pp. 139–154.

McWae, J.R.H., Playford, P.E., Lindner, A.W., et al., 1958. The stratigraphy of Western Australia. J. Geol. Soc. Aust. 4, 1–161.

Molnar, R.E., 1982a. Australian Mesozoic reptiles. In: Rich, P.V., Thompson, E.M. (Eds.). Vertebrate palaeontology of Australasia. Monash University, Clayton, pp. 170–220.

Molnar, R.E., 1982b. A catalogue of fossil amphibians and reptiles in Queensland. Mem. Queensland Mus. 20, 613–633.

Molnar, R.E., 1991. Fossil reptiles in Australia. In: Vickers-Rich, P., Monaghan, J.M., Baird, R.F. et al., (Eds.). Vertebrate palaeontology of Australasia. Pioneer Design Studio, Monash University, Melbourne, pp. 605–702.

Motani, R., 1999. Phylogeny of the Ichthyopterygia. J. Vertebr. Paleontol. 19, 473–496.

Moody, R.T.J., 1997. The paleogeography of marine and coastal turtles of the North Atlantic and Trans-Saharan regions. In: Callaway, J.M., Nicholls, E.L. (Eds.). Ancient marine reptiles. Academic Press, San Diego, pp. 259–278.

Moore, P.S., Pitt, G.M., 1985. Cretaceous subsurface stratigraphy of the southwestern Eromanga Basin: a review. S. Aust. Dep Mines Energy Spec. Publ. 5, 269–286.

Moore, P.S., Pitt, G.M., Dettman, M.E., 1986. The Early Cretaceous Coorikiana Sandstone and Toolebuc Formation: their recognition and stratigraphic relationship in the southwestern Eromanga Basin. In: Gravestock, D.I., Moore, P.S., Pitt, G.M. (Eds.). Contributions to the geology and hydrocarbon potential of the Eromanga Basin. Geological Society of Australia Special Publication, 12, pp. 97–114.

Morgan, R.P., 1980. Palynostratigraphy of the Australian Early and Middle Cretaceous. Geol. Surv. NSW, Mem. Palaeontol. 18, 1–153.

Mory, A.J., 1988. Regional geology of the offshore Bonaparte Basin. In: Purcell, P.G., Purcell, R.R. (Eds.). The North West Shelf of Australia. Petroleum Exploration Society of Australia, Melbourne, pp. 287–309.

Murray, P.F., 1985. Ichthyosaurs from Cretaceous Mullaman Beds near Darwin, Northern Territory. The Beagle 2, 39–55.

Murray, P.F., 1987. Plesiosaurs from Albian aged Darwin Formation siltstones near Darwin, Northern Territory, Australia. The Beagle 4, 95–102.

O'Keefe, F.R., 2001. A cladistic analysis and taxonomic revision of the Plesiosauria (Reptilia, Sauropterygia). Acta Zool. Fenn. 213, 1–63.

Oppel, M., 1811. Die Ordnungen, Familien und Gattungen der Reptilien, als Prodrom einer Natugeschichte derselben, Joseph Lindauer, München.

Osborn, H.F., 1903. The reptilian subclass Diapsida and Synapsida and the early history of the Diaptosauria. Mem. Am. Mus. Nat. Hist. 1, 449–507.

Owen, R., 1840. Report on British fossil reptiles. Rep. Br. Assoc. Advan. Sci. London 9, 43–126.

Owen, R., 1841. Report on British fossil reptiles, Part II. Rep. Br. Assoc. Advan. Sci. London 11, 60–65.

Owen, R., 1860. On the orders of fossil and recent Reptilia, and their distribution in time. Rep. Br. Assoc. Advan. Sci. London 29, 153–166.

Owen, R., 1882. On an extinct chelonian reptile (*Notochelys costata*, Owen) from Australia. Quart. J. Geol. Soc. London 38, 178–183.

Persson, P.O., 1960. Early Cretaceous plesiosaurians (Reptilia) from Australia. Lunds Univ. Årsskrift 56, 1–23.

Persson, P.O., 1963. A revision of the classification of the Plesiosauria with a synopsis of the stratigraphical and geographical distribution of the group. Lunds Univ. Årsskrift 59, 1–59.

Persson, P.O., 1982. Elasmosaurid skull from the Lower Cretaceous of Queensland (Reptilia, Sauropterygia). Mem. Queensland Mus. 20, 647–655.

Pirrie, D., Doyle, P., Marshall, J.D., et al., 1995. Cool Cretaceous climates – new data from the Albian of Western Australia. J. Geol. Soc. London 152, 739–742.

Pledge, N.S., 1980. Vertebrate fossils from South Australia. South Australia Yearbook 1980, Government Printer, South Australia.

Rich, T.H., 1996. Significance of polar dinosaurs in Gondwana. Mem. Queensland Mus. 39, 711–717.

Rich, P.V., Rich, T.H., 1985. Plesiosauridae, the Andamooka sea monster. In: Rich, P.V., van Tets, G.F. (Eds.). Kadimakara. Extinct vertebrates of Australia. Princeton University Press, Princeton, pp. 143–146.

Rich, T.H., Rich, P.V., 1989. Polar dinosaurs and biotas of the Early Cretaceous of southeastern Australia. Nat. Geogr. Soc. Res. Rep. 5, 15–53.

Rieppel, O., 2000. Sauropterygia I. Placodontia, Pachypleurosauria, Nothosauria, Pistosauria. Handbuch der Paläoherpetologie Part 12A, Verlag Dr. Friedrich Pfeil, München.

Robertson, R.S., Scott, D.C., 1990. Geology of the Coober Pedy precious stones field. Results of investigations, 1981–1986. Geol. Surv. S. Aust. Rep. Invest. 56, 1–55.

Rodgers, P.A., 1995. Stratigraphy – upper non-marine succession. In: Drexel, J.F., Preiss, W.V. (Eds.). The Geology of South Australia. Volume 2. The Phanerozoic. Geol. Sur S. Aust. Bull., 54, pp. 123–124.

Romer, A.S., Lewis, A.D., 1959. A mounted skeleton of the giant plesiosaur Kronosaurus. Breviora 112, 1–15.

Sato, T., Storrs, G.W., 2000. An early polycotylid plesiosaur (Reptilia, Sauropterygia) from the Cretaceous of Hokkaido, Japan. J. Paleontol. 74, 907–914.

Sauvage, H.E., 1873. Notes sur les reptiles fossils. Bull. Soc. Géol. France 1, 365–380.

Shafik, S., 1990. Late Cretaceous nannofossil biostratigraphy and biogeography of the Australian western margin. Bur. Min. Res., Geol. Geophys. Rep. 295, 1–164.

Seeley, H.G., 1874. Note on some of the generic modifications of the plesiosaurian pectoral arch. Quart. J. Geol. Soc. 30, 436–449.

Seeley, H.G., 1898. Note on plesiosaurian humerus from New South Wales opal mines. Quart. J. Geol. Soc. 54, 106.

Sheard, M.J., 1990. Glendonites from the southern Eromanga Basin in South Australia: palaeoclimatic indicators for Cretaceous ice. Geol. Surv. S. Aust. Quart. Geol. Notes 114, 17–23.

Siverson, M., 1999. A new large lamniform shark from the uppermost Gearle Siltstone (Cenomanian, Late Cretaceous) of Western Australia. Trans. R. Soc. Edinburgh: Earth Sci. 90, 49–66.

Skwarko, S.K., 1966. Cretaceous stratigraphy and palaeontology of the Northern Territory. Bur. Min. Res., Geol. Geophys. Bull 73, 1–135.

Skwarko, S.K., 1968. Mesozoic. In: Walpole, B.P., Dunn, P.R., Crohn, P.W. et al., (Eds.). Geology of the Katherine–Darwin region, Northern Territory. Bur. Min. Res., Geol. Geophy. Bull., 82, pp. 105–116.

Smart, J., Senior, B.R., 1980. Jurassic–Cretaceous basins of northeastern Australia. In: Henderson, R.A., Stephenson, P.J. (Eds.). The geology and geophysics of northeastern Australia. Geological Society of Australia, Queensland Division, Brisbane, pp. 315–318.

Smith, E., 1999. Black opal fossils of Lightning Ridge, Kangaroo Press, Sydney.

Stevens, G.R., Clayton, R.N., 1971. Oxygen isotope studies on Jurassic and Cretaceous belemnites from New Zealand and their biogeographic significance. NZ J. Geol. Geophys. 14, 829–897.

Storrs, G.W., 1999. An examination of the Plesiosauria (Diapsida, Sauropterygia) from the Upper Cretaceous Niobrara Formation of central North America. Univ. Kansas, Paleontol. Cont. (New Ser.) 11, 1–15.

Storrs, G.W., Arkhangelskii, M.S., Efimov, V.M., 2000. Mesozoic marine reptiles of Russia and other former Soviet republics. In: Benton, M.J., Shishkin, M.A., Unwin, D.M. et al., (Eds.). The age of Dinosaurs in Russia and Mongolia. Cambridge University Press, Cambridge, pp. 187–210.

Swinton, W.E., 1930. Preliminary account of a new genus and species of plesiosaur. Ann. Mag. Nat. Hist. 6, 206–209.

Teichert, C., Matheson, R.S., 1944. Upper Cretaceous ichthyosaurian and plesiosaurian remains from Western Australia. Aust. J. Sci. 6, 167–178.

Thulborn, T., Turner, S., 1993. An elasmosaur bitten by a pliosaur. Mod. Geol. 18, 489–501.

Vickers-Rich, P., 1996. Early Cretaceous polar tetrapods from the Great Southern Rift Valley, southeastern Australia. Mem. Queensland Mus. 39, 719–723.

Vine, R.R., Day, R.W., Casey, D.J., et al., 1967. Revised nomenclature of the Rolling Downs Group, Eromanga and Surat basins. Queensland Govern. Min. J. 68, 144–151.

Wade, M., 1984. *Platypterygius australis*, an Australian Cretaceous ichthyosaur. Lethaia 17, 99–113.

Wade, M., 1990. A review of the Australian Cretaceous longipinnate ichthyosaur *Platypterygius*, (Ichthyosauria, Ichthyopterygia). Mem. Queensland Mus. 28, 115–137.

Wagstaff, B.E., McEwen Mason, J., 1989. Palynological dating of Lower Cretaceous coastal vertebrate localities, Victoria, Australia. Nat. Geogr. Soc. Res. Rep. 5, 54–63.

Welles, S.P., 1943. Elasmosaurid plesiosaurs with a description of new material from California and Colorado. Univ. California Publ. Geol. Sci. 13, 125–215.

Welles, S.P., 1949. A new elasmosaur from the Eagle Ford Shale of Texas. S. Method. Univ. Fondr Sci 1, 1–28.

Welles, S.P., 1962. A new species of elasmosaur from the Aptian of Colombia, and a review of the Cretaceous plesiosaurs. Univ. California Publ. Geol. Sci. 44, 1–96.

White, T.E., 1935. On the skull of *Kronosaurus queenslandicus* Longman. Occ. Papers Boston Soc. Nat. Hist. 8, 219–228.

White, T.E., 1940. Holotype of *Plesiosaurus longirostris* Blake and classification of the plesiosaurs. J. Paleontol. 14, 451–467.

Williston, S.W., 1894. A new turtle from the Benton Cretaceous. Kansas Univ. Quart. 3, 5–18.

Williston, S.W., 1903. North American plesiosaurs. Part 1. Field Columbian Mus. Publ. Geol. 73, 1–77.

Williston, S.W., 1908. North American plesiosaurs: *Trinacromerum*. J. Geol. 16, 715–736.

Williston, S.W., 1925. Osteology of the Reptiles, Harvard University Press, Cambridge.

Woodward, H., 1895. Proceedings of the geological society of London Session 1894–1895. November 21st 1894. Quart. J. Geol. Soc. London 51, iii.

Wopfner, H., Freytag, I.B., Heath, G.R., 1970. Basal Jurassic–Cretaceous rocks of the western Great Artesian Basin, South Australia: stratigraphy and environment. Assoc. Aust. Petrol. Geol. Bull 54, 383–416.

Zangerl, R., 1960. The vertebrate fauna of the Selma Formation of Alabama. V. An advanced cheloniid sea turtle. Fieldiana: Geol. Mem. 3, 281–312.