

# Marine reptiles from the Lower Cretaceous (Aptian) deposits of White Cliffs, southeastern Australia: implications of a high latitude, cold water assemblage

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## Abstract

Marine reptile remains, represented by several fragmentary skeletons and isolated elements, are described from the Lower Cretaceous (Aptian) southern high latitude deposits (Doncaster Member, Wallumbilla Formation) of White Cliffs in southeastern Australia. The specimens are attributable to at least three families of plesiosaur (Elasmosauridae, Polycotyliidae and Pliosauridae) and probably one family of ichthyosaur (Ophthalmosauridae). Polycotyliid material from White Cliffs is amongst the oldest from anywhere in the world, and could point to an eastern Gondwanan origin for the group. Interestingly, the White Cliffs marine reptile fossils occur in association with palaeoclimatic indicators denoting seasonally very cold to near freezing conditions. This differs markedly from the climate regimes typically tolerated by modern aquatic reptiles but suggests that some Mesozoic taxa were able to cope with low temperature environments. Exactly what adaptations facilitated their survival is unknown. However, various strategies including elevated metabolic rates, rapid growth and/or seasonal migration/hibernation might have enabled their exploitation of cold water habitats along the southern coastal margin of the Australian Cretaceous epicontinental seaway.

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*Keywords:* Marine reptiles; Lower Cretaceous; Australia; White Cliffs; High latitude; Cold water

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## 1. Introduction

During the Early Cretaceous, what is now southeastern Australia was a peninsular region of eastern Gondwana located close to the southern polar circle. A shallow epicontinental sea inundated much of the current land-surface, and today is represented by extensive deposits of carbonate-rich shale and mudstone. These sediments crop out widely in the modern Eromanga Basin, an enormous depositional depression (whose boundaries roughly correspond to the southern and eastern shorelines of the Cretaceous seaway; see Frakes et al., 1987) that covers large areas of central and southwestern Queensland, northern New South Wales and South Australia.

Interestingly, palaeoclimatic indicators from Upper Neocomian–Lower Albian marine units along the southern margin of the Eromanga Basin suggest very cold to near freezing conditions (Frakes and Francis, 1988, 1990; Sheard, 1990; Frakes et al., 1995; De Lurio and Frakes, 1999), and are associated with a distinctive fossil fauna of invertebrates (e.g., Etheridge, 1902; Ludbrook, 1966; Day, 1969; Henderson et al., 2000) and vertebrates (e.g., Chapman, 1914; Ludbrook, 1966; Molnar, 1980; Molnar and Pledge, 1980; Alley and Pledge, 2000; Kear, 2003a,b, 2004), primarily marine reptiles. One particular deposit, the Aptian (Lower Cretaceous) opal-bearing Wallumbilla Formation (Doncaster Member) at White Cliffs in north-western New South Wales (Fig. 1; see also Burton and Mason, 1998, figs. 1, 2 for detailed geological and locality maps of the area), is of key interest because it has produced a number of important specimens, representing at least three families of plesiosaur (Elasmosauridae, Polycotyliidae and Pliosauridae)

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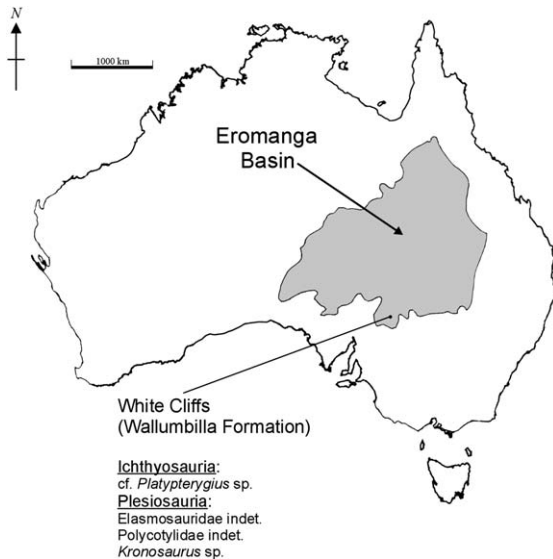


Fig. 1. Map showing location of White Cliffs with list of marine reptile taxa recovered (shaded area shows extent of Eromanga Basin).

and probably one family of ichthyosaur (Ophthalmosauridae). The earliest of these finds was reported by Woodward (1895), who mentioned several fragmentary elements and a large tooth, assigned to the European/North American Cretaceous pliosaurid *Polyptychodon* (now referred to the Australian taxon *Kronosaurus*; see Kear, 2003a). Etheridge (1897) described further material, notably the partial skeleton of a small-bodied plesiosauroid *Cimoliasaurus leucoscopelus* Etheridge. Other reports include Seeley (1898), who noted an isolated plesiosaur propodial, and Gürich (1901) who briefly discussed several vertebral centra belonging to a large plesiosaurian of uncertain affinity. Etheridge (1904) reassessed much of the then documented material assigning most plesiosaur specimens to the cosmopolitan genus *Cimoliasaurus* Leidy, 1851 (widely regarded as a non-diagnosable “waste-basket taxon”; see Storrs et al., 2000; Kear, 2002a) and describing a new species of plesiosauroid *Cimoliasaurus maccoyi* Etheridge (based on an incomplete skeleton). Etheridge (1904) also reported an incomplete ichthyosaurian centrum, purportedly showing similarity to those of “*Ichthyosaurus australis*” McCoy, 1867 (this taxon was referred to *Platypterygius longmani* Wade, 1990, now considered a junior synonym of *P. australis* sensu McGowan and Motani, 2003), from the Cretaceous Rolling Downs Group of northern Queensland. More recently, Ritchie (1979) recorded the discovery and excavation of a small (ca. 2.5 m) plesiosaur skeleton from White Cliffs. Unfortunately, this specimen is held in a private fossil display and unavailable for study.

Because opal mining at White Cliffs has largely ceased, almost no new discoveries of vertebrate fossils have been documented in recent years. Despite this, numerous reports have come from individual miners (although their validity in many cases has yet to be substantiated) and several partial skeletons are known to reside in inaccessible private collections. This paper aims to review some of the key marine reptile specimens from White Cliffs (mostly held in the collections of

the Australian Museum, Sydney) and give a preliminary assessment of their taxonomy and palaeoecology.

## 2. Abbreviations and terminology

Repository abbreviations: AM, Australian Museum, Sydney; SAM, South Australian Museum, Adelaide. Lithostratigraphic nomenclature follows Burton and Mason (1998) for the opal-bearing sediments of White Cliffs, New South Wales and Vine et al. (1967) for the Rolling Downs Group units. Systematic terminology follows Motani (1999) and McGowan and Motani (2003) for Ichthyosauria and O’Keefe (2001, 2004) for Plesiosauria except in the ranking of Sauropterygia and Plesiosauria, both of which follow the more conventional system of Carroll (1988), Benton (1997) and Rieppel (2000). Functional subdivision of the vertebral column in ichthyopterygians follows Buchholtz (2001), with designation of structural units as neck, trunk, tail stock and fluke. All measurements were taken using calipers and are in millimetres (mm).

## 3. Geological and palaeoenvironmental setting

The opal-bearing deposits of White Cliffs are typically characterised by weathering-bleached siltstones and claystones. These comprise part of the southeastern extension of the Doncaster Member of the Wallumbilla Formation (see Burton and Mason, 1998 for discussion), a predominantly near-shore-coastal shallow marine (possibly with anoxic bottom conditions) sequence that crops out extensively throughout the Eromanga Basin. The Wallumbilla Formation (which consists of the basal Doncaster Member and overlying Coreena Member) forms the lowermost unit of the Rolling Downs Group, an extensive series of epicontinental marine–paralic/fluviatile strata of Early Aptian–Cenomanian age. A summary of the Rolling Downs Group units, their ages, lithologies, depositional environments and marine reptile taxa is presented in Table 1.

The Doncaster Member of the Wallumbilla Formation is generally regarded as Early Aptian–Early Albian in age on the basis of palynological (Helby et al., 1987; Burger, 1988) and macroinvertebrate (Day, 1969) data. However, in the White Cliffs area, the unit is represented by rocks of predominantly Aptian age (see Burton and Mason, 1998). This broad age range is applied to all marine reptile fossils from the White Cliffs deposits and corresponds to the *Cyclosporites hughesii*–lowermost *Crybelosporites striatus* spore-pollen zones, and *Odontochitina operculata*–*Diconodinium davidii* dinoflagellate zones of Helby et al. (1987).

Determinations of palaeolatitude place the White Cliffs area as high as 70° S during the Early Cretaceous (Embleton and McElhinny, 1982; Embleton, 1984; Idnurm, 1985). Palaeoclimatic indicators including distinct growth-banded wood (Dettmann et al., 1992), potentially ice-rafted quartzite/porphyritic boulders (Frakes and Francis, 1988, 1990; Frakes et al., 1995) and glendonites (crystal aggregates pseudomorphing the calcium carbonate hexahydrate mineral ikaite; Sheard, 1990; De Lurio and Frakes, 1999) suggest predominantly cool,

Table 1

Stratigraphic chart of Rolling Downs Group units in the Eromanga Basin showing their ages (including palynological zonation), lithological features, environment of deposition and marine reptile taxa

Unit	Stage	Lithology	Depositional environment	Marine reptile taxa
Winton Formation	Cenomanian <i>A. distocarinatus</i> spore-pollen Zone	Labile sandstone, siltstone, mudstone, minor coal	Fluviatile	Possible marine turtle (Molnar, 1991)
Mackunda Formation	Late Albian–Early Cenomanian <i>P. ludbrookiae</i> / <i>P. pannosus</i> dinoflagellate zones, <i>A. distocarinatus</i> Zone	Labile glauconitic sandstone, siltstone, mudstone, minor limestone	Marginal marine/paralic	Polycotyliidae indet. (Kear, 2002b, 2003a)
Allaru Mudstone	Middle–Late Albian Upper <i>C. paradoxa</i> spore-pollen Zone, <i>P. pannosus</i> / <i>C. denticulata</i> / <i>P. ludbrookiae</i> dinoflagellate zones	Mudstone, siltstone, minor limestone, minor labile glauconitic sandstone	Shallow marine/paralic	<i>Platypterygius longmani</i> Wade, 1990; Elasmosauridae indet. (Kear, 2003a); <i>?Notochelone costata</i> (Long, 1998)
Toolebuc Formation	Latest middle–Late Albian <i>P. ludbrookiae</i> Zone, upper <i>C. paradoxa</i> Zone in southern Eromanga Basin, diachronously in Upper Albian <i>P. pannosus</i> Zone further north	Bituminous and calcareous shale, siltstone, limestone, some fine labile sandstone	Restricted shallow marine/offshore	<i>Platypterygius longmani</i> Wade, 1990; <i>Kronosaurus queenslandicus</i> Longman, 1924; Elasmosauridae indet. (= “ <i>Wollungasaurus</i> ” sp.; see Thulborn and Turner, 1993); Polycotyliidae indet. (see Cruickshank et al., 1999); <i>Notochelone costata</i> (Owen, 1882); <i>Cratochelone bernyi</i> Longman, 1915
Wallumbilla Formation	Early Aptian–middle Albian <i>C. hughesii</i> / <i>C. striatus</i> spore-pollen zones, <i>O. operculata</i> / <i>D. davidii</i> / <i>M. tetracantha</i> dinoflagellate zones	Mudstone, siltstone, minor labile glauconitic sandstone, limestone	Coastal-offshore shallow marine	<i>Platypterygius</i> sp. (Wade, 1990; this paper); <i>Kronosaurus ?queenslandicus</i> (see Thulborn and Turner, 1993); Elasmosauridae indet. (Welles, 1962 = <i>Woolungasaurus glendowerensis</i> Persson, 1960); Polycotyliidae indet. (this paper, = <i>?Dolichorhynchops</i> sp. Persson, 1960)

Lithostratigraphic nomenclature follows Vine et al. (1967). Stage/palynological zone correlation derived from Helby et al. (1987). Lithology and depositional environments follow interpretations of Day et al. (1983), McMinn and Burger (1986) and Burger (1988).

strongly seasonal conditions, possibly with winter freezing. This correlates with estimates of sea-level isotopic palaeotemperatures in the southwestern section of the Eromanga Basin, which have yield averages as low as 12.2 °C (Stevens and Clayton, 1971; Dettmann et al., 1992). Selwood et al. (1994), however, reported revised isotopic data supporting much cooler ocean temperatures during the Early Cretaceous. Indeed, Pirrie et al. (1995) indicated palaeotemperatures of around 10 °C from Lower Albian belemnites from the Carnarvon Basin, Western Australia, which lay near approximately 45° S palaeolatitude at that time. In contrast, Huber et al. (1995) and Huber and Hodell (1996) have argued that minimal pole to equator thermal gradients existed during much of the mid and Late Cretaceous. This observation was also discussed

by Henderson et al. (2000), who added that although Early Cretaceous palaeotemperatures at 70–80° latitude would certainly have been more equitable than they are today, strong evidence attests to the marked seasonality and winter freezing experienced along the inboard coastal margins of the Australian epicontinental seaway during the Late Neocomian–Early Albian.

Where documented, the marine reptile remains from White Cliffs are known to occur both as partially articulated skeletons and isolated elements. This compares well with the taphonomic models of Martill (1985, 1987), which suggest that disarticulated specimens are indicative of oxygenated shallow-water conditions, and frequently represent the remnants of carcasses that have come to rest on the sea floor following

a period of post-mortem drifting, with the body distended by decomposition gasses (established through comparisons with the disintegration patterns of large vertebrate carcasses in modern marine systems).

#### 4. Survey of key specimens

Subclass: Diapsida Osborn, 1903

Superorder: Ichthyopterygia Owen, 1840

Order: Ichthyosauria de Blainville, 1835

Family: Ophthalmosauridae Baur, 1887 (sensu McGowan and Motani, 2003).

Genus *Platypterygius* von Huene, 1922

cf. *Platypterygius* sp.

Fig. 2

1904 cf. *Ichthyosaurus australis* Etheridge, p. 307.

*Referred material.* AM L545, 546 (casts, AM records indicate that originals were held by the Mining and Geological Museum, Sydney, however current whereabouts of the specimens are unknown; R. Jones, pers. comm. 2002), two vertebral centra from tail stock (caudal) region (Table 2); AM F9924, 9925, two badly distorted trunk (dorsal) centra from a juvenile individual (Fig. 2A, Table 2).

*Description.* All of the centra examined are disc-like and anteroposteriorly compressed with the dorsal length sub-equal to the ventral length. Similar to other thunnosaurian ichthyosaurs, the tail stock centra exhibit a more marked degree of anteroposterior compression relative to those from the trunk region (see Table 2) and are nearly circular in outline (height being just slightly greater than the transverse width). The articular surfaces of both the trunk and tail stock centra are deeply

Table 2

Measurements (mm) of ichthyosaur vertebral centra from White Cliffs (\*centrum incomplete or †distorted)

Specimen	Length	Width	Height
AM L545	12.1	43.48	45.42
AM L546	12.21	42.81	43.36
†AM F9924	29.09	45.66	*37.49
†AM F9925	29.91	49.24	61.7

amphicoelous. Where preserved, both the diapophyses and parapophyses of the trunk centra are distinctly raised and sub-circular. This is unlike centra from the tail stock region, in which only the sub-rectangular diapophysis is present and positioned low on the lateral centrum surface. The ventral surfaces of the two recovered tail stock centra appear to possess weakly developed haemapophysial facets. These occur as paired lobate expansions of the articular surface rim towards the ventral transverse midline.

*Remarks.* Despite ichthyosaur fossils having been reported from White Cliffs as early as 1904 (Etheridge, 1904), their remains are relatively rare compared to those of other groups. To date most of the known material consists of isolated centra; however, the partial skeleton of a juvenile individual was excavated by opal miners in the late 1980s. This specimen currently resides in a private collection and is difficult to access (R. Jones, pers. comm. 2002).

Although none of the White Cliffs ichthyosaur material can be diagnosed beyond Ichthyosauria gen. et sp. indet., tentative assignment to cf. *Platypterygius* sp. is justifiable on the basis of: (1) overall similarity to *Platypterygius* vertebral material described from the Toolebuc Formation, Queensland (Wade, 1990), Darwin Formation, Northern Territory (Murray, 1985, 1987; Kear, 2002a) and Birdrong Sandstone, Western Australia (Choo, 1999); and (2) current recognition of *Platypterygius* as the only valid ichthyosaur genus known

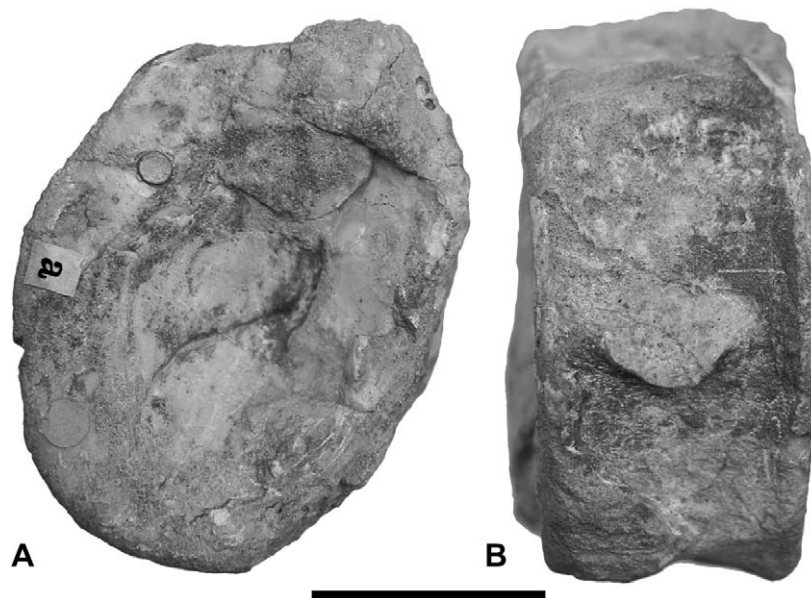


Fig. 2. Ichthyosaur vertebra AM F9924 from the Lower Cretaceous (Aptian) of White Cliffs. A, articular view. B, right lateral view. Scale bar represents 20 mm.

from the Cretaceous of Australia (McGowan, 1972; Arkhangel'sky, 1998; Maisch and Matzke, 2000; Kear, 2003a; McGowan and Motani, 2003). Interestingly, the White Cliffs tail stock centra (AM L545, 546) are distinctive in their possession of haemapophysial facets. Well-developed haemapophysial facets have been reported in *Platypterygius* tail stock centra from the Lower Cretaceous (probable Upper Aptian) Darwin Formation of the Northern Territory, Australia (Kear, 2002b). Maisch and Matzke (2000), however, suggested that haemapophysial facets were absent in all Late Jurassic and Cretaceous ichthyosaurs (indicating a probable reduction and/or loss of the haemapophyses), being present only in Triassic (Maisch and Matzke, 2000) and a few Jurassic taxa including *Eurinosaurus* (von Huene, 1928), *Leptonectes* (Owen, 1881), *Ichthyosaurus* (Owen, 1881), *Temnodontosaurus* (von Huene, 1922) and *Ophthalmosaurus* (Andrews, 1910). The presence of haemapophysial facets in ichthyosaur centra from the Cretaceous of Australia therefore suggests

that this character may be more variable in its development, and occur in a range of species-level taxa of Triassic–Cretaceous age (the possibility of the Australian forms representing localized relicts is not favoured because of homologies in the limb and cranial morphology shared with other ophthalmosaurs; see Choo, 1999; Wade, 1990).

Superorder: Sauropterygia Owen, 1860

Order: Plesiosauria de Blainville, 1835

Plesiosauria gen. et sp. indet.

Fig. 3A, B

*Referred material.* AM L968 (cast labelled “*Ichthyosaurus*” from registered mould T482, whereabouts of original specimen unknown), isolated propodial lacking posterodistal section (Fig. 3A); SAM P11530, isolated incomplete right propodial (Fig. 3B).

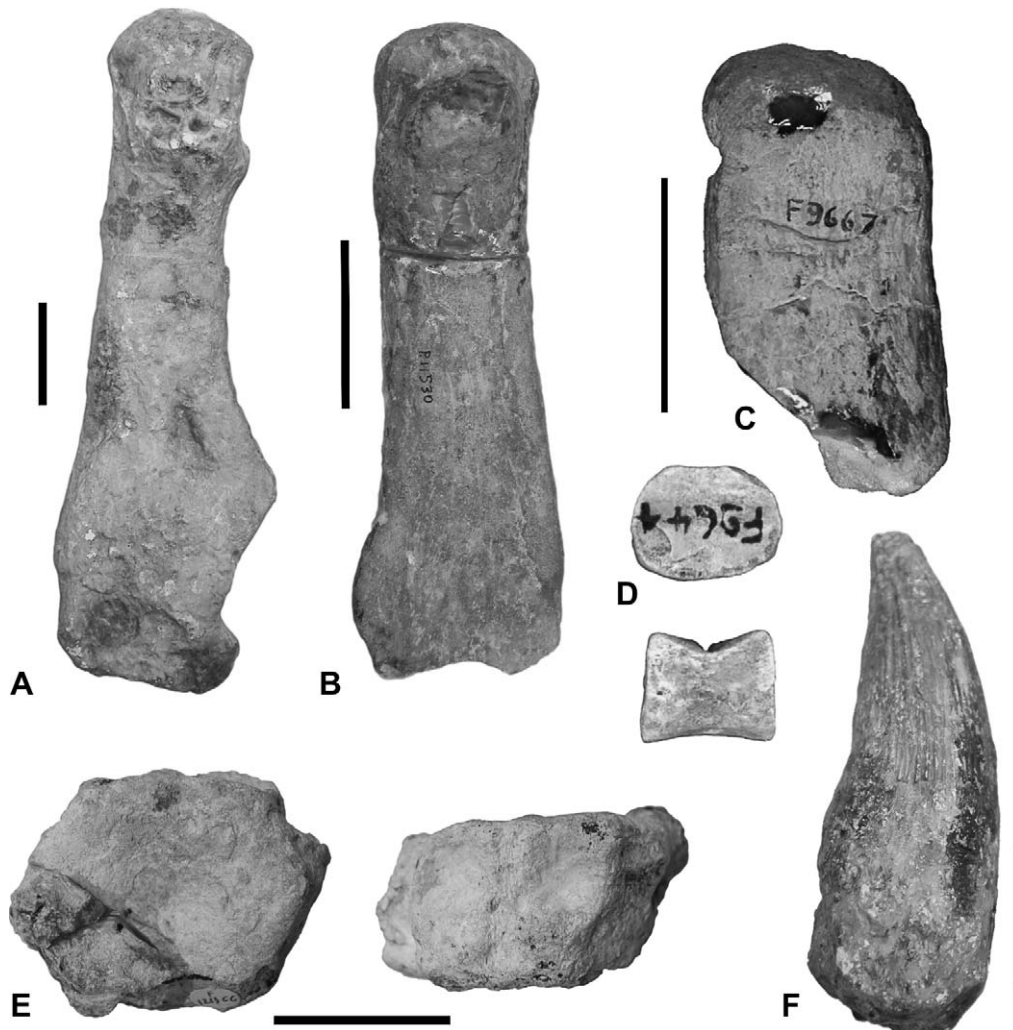


Fig. 3. Plesiosaurian elements from the Lower Cretaceous (Aptian) of White Cliffs. A, isolated propodial (AM L968) attributed to Plesiosauria indet. B, isolated propodial (SAM P11530) attributed to Plesiosauria indet. C, incomplete propodial (AM F9667) and D, anterior cervical vertebra (in anterior and lateral views) of (AM F9644) holotype specimen (AM F9630–9928) of *Cimoliasaurus maccoyi* Etheridge, 1904 (nomen dubium). E, isolated caudal vertebra (AM F121366) in anterior and dorsal views, specimen attributed to Elasmosauridae indet. F, cast of tooth (AM L508) attributed to *Kronosaurus* sp. Scale bars represent 300 mm in A, B and E, 40 mm in C and D, and 20 mm in F.

**Description.** AM L968 is nearly complete but lacks part of the posterodistal margin; SAM P11530 lacks most of its distal extremity. The dorsal tuberosities of both specimens are incomplete. Total length is (AM L968) 260.8 mm, (SAM P11530) 165 mm; total proximal length is (AM L968) 47.9 mm, (SAM P11530) 26.83 mm; total proximal height is (including trochanter) (AM L968) 51.5 mm, (SAM P11530) 36.44; width across base of dorsal trochanter is (AM L968) 37.2 mm, (SAM P11530) 17.75; total distal length (not including missing posterior margin) is (AM L968) 91.6 mm, (SAM P11530) 47.48 mm; total distal height is (AM L968) 25.9 mm, (SAM P11530) 16.12. The anterior edge of both propodials is nearly straight as is the posterior edge of SAM P11530. However, the posterior edge of AM L968 differs in being shallowly concave along its entire unbroken length. The proximal ends of both propodials are dorsoventrally expanded, with the articular head separated from the distal section by a constricted shaft. The dorsal tuberosities of both specimens are damaged but were clearly robust. They are separated from the hemispherical glenoid articular surfaces by shallow grooves. The propodial shafts are straight and ovoid in cross-section (becoming more elliptical distally); the proximal posterior margin of AM L968 bears a raised rugose tuberosity marking the insertion point for a muscle. The distal of AM L968 is incomplete (and is entirely missing in SAM P11530) but was probably quite broad. The distal articular surface is dorsoventrally compressed and shows a large facet for articulation with the radius.

**Remarks.** Despite being incomplete, both AM L968 and SAM P11530 are notable in their possession of dorsoventrally compressed, proportionately slender propodial shafts. This readily distinguishes them from the short, stout propodials of elasmosaurids (Brown, 1981; Murray, 1987) but is very similar to the propodials of polycotyliids and most pliosauroids (Andrews, 1913; Welles, 1943, 1962; Brown, 1981; Storrs, 1999). Indeed, Persson (1960) noted that SAM P11530 was potentially attributable to the polycotyliid *Cimoliasaurus leucoscopelus* (considered a nomen dubium; see Persson, 1960; Welles, 1962; Kear, 2003a). Because the posterodistal sections of both elements are missing, it is unknown whether any supernumerary ossifications are present in the propodial row (a key feature of polycotyliids; see O’Keefe, 2001). AM L968 and SAM P11530 are therefore provisionally referred to Plesiosauria gen. et sp. indet. pending discovery of more diagnostic material.

Superfamily: Plesiosauroidea Welles, 1943

Family: Elasmosauridae Cope, 1869a

Elasmosauridae gen. et sp. indet.

Fig. 3C–E

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. 3C, D); AM F121366, caudal centrum, juvenile (Fig. 3E).

**Description.** AM F9630–9928 represents the fragmentary skeleton of a very immature individual with an estimated body size (based on comparisons of vertebral column length with other elasmosaurs such as *Thalassomedon hanningtoni* Welles, 1943) of less than 2 m. Several authors including Etheridge (1904), Persson (1960) and Kear (2002a) have given adequate descriptions, figures and measurements of the remains.

AM F121366 is a damaged caudal centrum with comparable morphology to that of other elasmosaurs. The centrum body (length, 34.97 mm, width, 66.82 mm, height, 54.8 mm) is anteroposteriorly compressed with weakly amphicoelous articular surfaces. A shallow notochordal pit is present at the centre of the posterior articular surface (the anterior articular surface is obscured by silicified matrix). The dorsal surface bears two deep, teardrop-shaped neural arch facets separated by a narrow spool-shaped depression for the neural canal. The ventral surface of the centrum is damaged; however, the lateral surfaces bear remnants of prominent plateaus marking the articulations for the caudal ribs.

**Remarks.** Elasmosaurs are one of several plesiosaur groups known from the White Cliffs deposits. Interestingly, their remains were only recently recognised by Kear (2002a) following a re-examination of the enigmatic *Cimoliasaurus maccoyi*. This taxon was established by Etheridge (1904) and later revised by Persson (1960) who included it within the plesiosauroid family Cimoliasauridae (sensu Delair, 1959). Welles (1962), however, considered *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 by 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 (2002a) found Persson’s (1960) diagnostic characters 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; Gasparini et al., 2003a), which have largely excluded Cimoliasauridae (sensu Persson, 1960) leaving the group’s taxonomic status in doubt (Storrs, 1999). Indeed, the genus *Cimoliasaurus* has come to be regarded as a non-diagnosable “waste-basket taxon” (Storrs et al., 2000). In contrast, the most current comprehensive series of cladistic analyses and taxonomic revision of the Plesiosauria (O’Keefe, 2001, 2004) have revived the family designation but modified it to include the enigmatic *Kimmerosaurus* Brown, 1981 and *Aristonectes* Cabrera, 1941 [= *Morturneria* (Chatterjee and Small, 1989) in the

analysis of O’Keefe, 2001, 2004], taxa elsewhere regarded as either derived cryptoclidids (see Brown, 1981, 1993; Chatterjee and Small, 1989; Cruickshank and Fordyce, 1998, 2002) or elasmosaurids (*Aristonectes* only; see Bardet et al., 1991; Gasparini et al., 2003a). The relationship 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.

Family: Polycotyliidae Williston, 1908

Polycotyliidae gen. et sp. indet.

Fig. 4

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 isolated quadrate, teeth, partial vertebral column, rib fragments, limb elements (Fig. 4A–D, Table 3).

*Description.* The re-examination of AM F6266–6298 provided here is intended as a supplement to the initial description of Etheridge (1897). Other assessments have been given by Persson (1960), Welles (1962), Molnar (1982a, 1991), Long (1998) and Kear (2003a).

Although Etheridge (1897) stated that no cranial remains were present with AM F6266–6298, a single left quadrate (AM F6295) has been identified among the remains. The specimen (Fig. 4A, Table 3) is markedly longitudinally shortened and nearly triangular in outline with massive articular condyles. Its anterior surface is shallowly concave with the anterodorsal edge forming a narrow, transversely elongate facet for contact with the squamosal. Posteriorly the surface of the quadrate is inset, forming a broad transverse trough that undercuts the dorsal margin of the articular condyles. The medial surface is dominated by a highly rugose, rectangular facet for the quadrate ramus of the pterygoid (however, the pterygoid process itself is markedly reduced). The distal articular surface is composed of a small lateral and massive medial condyle separated by a slight constriction. The articular surfaces of both condyles are smooth and well formed with the medial condyle produced into a weak V-shaped ridge.

Etheridge (1897) recorded four teeth (AM F6273) with AM F6266–6298, noting their slender conical shape, striated

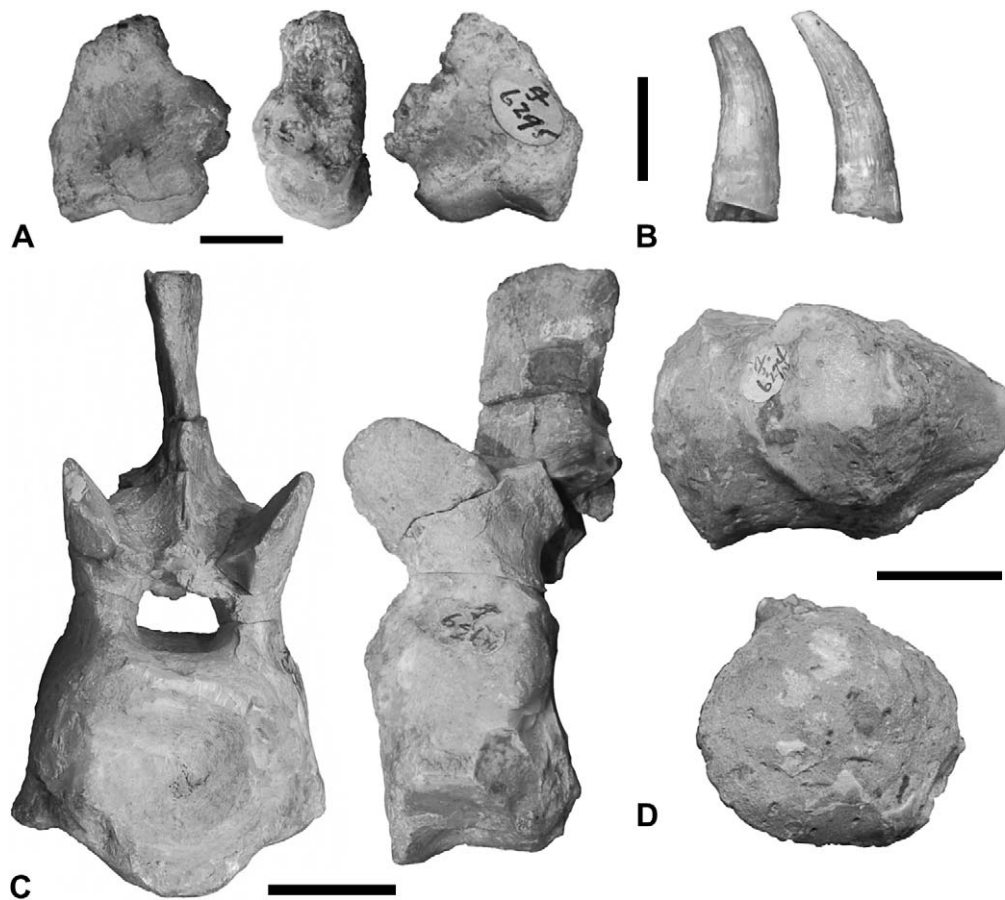


Fig. 4. Indeterminate polycotyloid remains attributed to *Dolichorhynchops* sp. (= *Cimoliasaurus leucoscopelus* Etheridge, 1897, nomen dubium) by Persson (1960) from the Lower Cretaceous (Aptian) of White Cliffs. A, quadrate (AM F6295) in posterior, lateral and anterior views. B, teeth (AM F6273). C, cervical vertebrae (AM F6269) in anterior and lateral views. D, propodial head (AM F6266) in dorsal and proximal views. Scale bars represent 10 mm in A and B, and 20 mm in C and D.

Table 3  
Measurements (mm) of polycotyloid elements from White Cliffs (\*specimen incomplete)

Element	Dimension	Measurement
Quadrate (AM F6295)	Total height	21.6
	Width across condyles	20.64
	Length medial condyle	13.81
	Height pterygoid facet	19.45
Teeth (AM F6273)	Total height	*14.09, 16.71, *16.95, *17.51, *18.93
	Width across base (anteroposteriorly)	5.41, 6.02, 6.63, 4.9, 6.96
Vertebrae (AM F6266, AM F6269, AM F6270, AM F6271, AM F6272, AM F10816)	Centrum length	21.74, 26.8, 25.32, 19.09, 22.97, 25.05, 16.19, 16.77, 17.84, 18.65, 24.07, 28.33, 22.32, 24.76
	Centrum width	37.78, 41.71, 43.26, *16.03, 43.62, 44.2, *35.96, 25.61, 29, 30.34, 31.92, *17.84, 34.36, 40.34
	Centrum height	31.07, 34.05, 35.61, 30.91, 35.27, 35.63, 51.66, 18.96, 21.96, 23.64, 25.29, 39.39, 36.07, 27.87, 32.37
Rib heads (AM F6281, AM F6282, AM F6283)	Height (articular facet)	22.64, 21.65, 24.93, 14.33, 18.75, 20.02
	Length (articular facet)	15.96, 16.71, 15.29, 13.44, 19.14, 18.53
Propodials (AM F6274)	Total length (head fragment)	50.15, 51.14, —
	Height (proximal articular surface)	61.5, 59.18, 63.86
Propodial shaft fragment (AM F6726)	Maximum height (dorsoventral)	33.69
	Maximum width (mediolateral)	56.78
	Maximum length (anteroposterior)	52.84
Distal propodial fragment (AM F6275)	Maximum height (dorsoventral)	37.25
	Maximum width (mediolateral)	*78.64
	Maximum length (anteroposterior)	57
Epidodials (AM F6284, AM F6285, AM F6286)	Total height	15.86, 12.94, 20.51, 11.06
	Total width (mediolaterally)	22.75, 23.64, 22.63, 25.9
	Total length (anteroposteriorly)	32.4, *18.17, 35.48, 29.9
Phalanges (AM F6289, AM F6290, AM F6291, AM F6292, AM F6293, AM F6294)	Total width (mediolaterally)	27.77, 25.54, 22, 25.67, 17.98, 16.92, *17.33, 17.75, 18.26, 18.72, 19.68, 20.34, 22.89, 26.12
		12.8, 14.46, 9.41, 11.6, 9.43, 6.82, 10.94, 10.48, 9.42, 14.54, 12.72, 9.16, 13.8, 12.73
	Length (at mid-section)	

enamel and lack of distinct carinae. Examination of the current material, however, indicates that five teeth are present, only one of which is complete. All of the teeth are small (see Fig. 4B, Table 3) and slender in general form with a distinctly ovoid cross-section. The crowns bear coarse, widely spaced striations that extend to the apex but are restricted to the lingual surface of each tooth. Where visible, the labial surfaces of the teeth are smooth and frequently show fine longitudinal cracks. Only one tooth has a complete apex. This is slender and preserves evidence of wear faceting. Estimated total crown height (based on the more complete teeth) is around half the height of the entire tooth (including root). Only two of the teeth bear reasonably complete roots. These are cylindrical in shape with an ovoid cross-section, and lack any visible surface ornamentation. A shallow conical resorption cavity (for a replacement tooth) is present on the posterolingual face of one tooth.

The postcranium of AM F6266–6298 includes mainly parts of the axial skeleton. Etheridge (1897) described the cervical vertebrae (AM F9637, 9638, 9643–51, 9655, 9659–64,

9928; Fig. 4C, Table 3; see also Etheridge, 1897, pl. 5, figs. 1–5, pl. 6, figs. 1–3) in some detail, noting the strong anteroposterior compression (length being less than half the height) of the centra, their amphicoelous articular surfaces and their lack of central mammillae and notochordal pits. The present examination indicates that the cervical centra also have markedly constricted mid-sections and articular surface rims that are elevated and expanded anteriorly. In addition, the neural arches are not fully fused to the centra. This contrasts with the observations of Etheridge (1897), who suggested that the cervical vertebrae of AM F6266–6298 showed extensive ankylosis, indicating the specimen's ontogenetic maturity. Close inspection reveals that many suture lines are still visible, and indeed most vertebral elements (e.g., centra, neural arches and cervical ribs) exhibit a complete lack of fusion. The left quadrate (AM F6295) also shows no evidence of fusion with the pterygoid or squamosal. AM F6266–6298 therefore appears to have been osteologically immature at the time of death and probably represents a large sub-adult individual.



The cervical neural arches of AM F6266–6298 enclose a small ovoid neural canal and bear zygapophyses that are orientated approximately 45° to the horizontal axis. The cervical rib facets are large and situated low on the lateral centrum surfaces. Some additional neural arch (AM F6298), transverse process (AM F6277, 6278, 6283, 6287) and neural spine (AM F6283, 6297) fragments may derive from the pectoral or anterior dorsal region. These, however, include only broken sections of the basal articular facets, all of which lack evidence of fusion with the centra.

Where preserved, the transverse processes of the pectoral/dorsal vertebrae (Etheridge, 1897, pl. 7, fig. 3) are markedly short and squat with bulbous articular heads. The articular surfaces are dorsoventrally deep and transversely narrow with fine surface pitting. Many of the accompanying neural spine fragments (which may also derive from the cervical series) are robust and rectangular in outline with markedly transversely expanded dorsal apices. In dorsal view the apex bears a convex, saddle-shaped surface (which is finely pitted and bordered by a continuous crennate margin) possibly for attachment of cartilage or ligaments.

Etheridge (1897) recorded the presence of numerous rib fragments with AM F6266–6298 and gave a lengthy description of the articular ends (AM F6281–6283, 6296, Table 3), noting that all were single-headed (a feature also remarked on by Persson, 1960). One rib section (AM F6280; Etheridge, 1897, pl. 7, fig. 4) differs in being markedly slender and tapering and may represent part of a gastralia.

None of the remains catalogued with AM F6266–6298 can be readily identified as limb girdle elements. Although a large, flat and slightly curved bone fragment (AM F6283, bulk registered with parts of the dorsal ribs, long axis height 64.77 mm, anteroposterior length at base 35.69 mm, width at mid-section 14.79 mm) may represent a broken section of the dorsal ramus of the scapula.

Etheridge (1897) reported the remains of two humeri with AM F6266–6298, describing only the excellently preserved propodial heads (Fig. 4D, Table 3; see also Etheridge, 1897, pl. 7, fig. 1). These are large and bear hemispherical glenoid articular surfaces with prominent dorsal tuberosities. Additional fragments (Table 3), probably representing the left humerus, are also present. These include parts of the distal extremity and propodial shaft (AM F6275, 6276). The shaft section is incomplete but clearly shows an elliptical distal cross-section, becoming more oval proximally. The distal propodial extremity appears to have been fan-shaped in dorsoventral outline with a weakly projecting anterodistal margin. The distal articular surface is damaged but preserves remnants of the large radial facet. It is impossible to discern the extent of the radial facet or the presence/absence of any supernumerary ossifications.

Etheridge (1897) briefly remarked on the distal limb elements of AM F6266–6298, including the epipodials, undifferentiated carpals (AM F6284–6286; Etheridge, 1897, pl. 6, figs. 6, 7) and numerous phalanges (AM F6289–6294; Etheridge, 1897, pl. 7, figs. 7–9). The epipodials and undifferentiated carpals (Table 3) are all flattened and slightly depressed in the middle. Their edges are rough and bordered by strongly

produced margins. Etheridge suggested that one element (probably AM F6286) might represent an intermedium. The bone is, however, disc-shaped unlike the distinctly pentagonal intermedia of most plesiosaurs (e.g., Andrews, 1911, 1913; Bardet et al., 1999) and could alternatively be one of the distal carpals. The other recovered proximal limb elements all appear to be derived from the distal carpal row, although one (AM F6285) may be the poorly ossified radiale.

The phalanges cannot be arranged with precision because the paddles were disarticulated during extraction by the opal miners. However, all are similarly elongate and dorsoventrally compressed with strongly constricted mid-section.

*Remarks.* The White Cliffs polycotyloid material is highly significant because it currently represents the oldest record of the group from anywhere in the world (Sato and Storrs, 2000). The sole specimen AM F6266–6298 was originally described as *Cimoliasaurus leucospelus* by Etheridge (1897) and 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. leucospelus* for convenience (Molnar, 1982a, 1991 also used the misspelled genus name “*Trinacromeron*”). 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 Polycotyloidea. AM F6266–6298 is, however, extremely fragmentary (generating rampant polytomies when included with existing data matrices, e.g., Bardet et al., 1999; O’Keefe, 2001, 2004; Gasparini et al., 2003a) and cannot be clearly allied with any current polycotyloid genus. For example, the teeth (Fig. 3B) 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, 1869 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. 3C). This is a condition regarded as characteristic for all members of the family Polycotyloidea (Sato and Storrs, 2000). Similarly, the vertebral centra are anteroposteriorly compressed with their length, being less than half the height, a feature that 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). Most unusually, the quadrate (Fig. 3A) has a markedly reduced pterygoid process resembling that of *D. osborni* (Storrs, 1999) and the neural spines have markedly transversely expanded dorsal apices. This is unlike any other member of the group and appears to represent a unique feature of the White Cliffs remains. Recently, Long (1998, citing A. Cruickshank, pers. comm. 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 do differ in key features, such as the presence of transversely expanded dorsal apices on the neural spines. The morphology of the quadrate and dentition also serves to distinguish AM F6266–6298 from all currently described species of *Leptocleidus* (for which cranial material is known). For example, the short, stocky quadrate of AM F6266–6298, with its anteroposteriorly bulbous articular condyles, is unlike that of *Leptocleidus* spp., in which the quadrate is large and elongate with a very wide, anteroposteriorly narrow, articular surface (evidenced by comparison with an undescribed skull AM F99374 from the Lower Cretaceous Bulldog Shale of South Australia, and published accounts of Andrews, 1911, 1922). Similarly, the dentition of AM F6266–6298 lacks the mesodistal carinae present on the teeth of some species of *Leptocleidus* [e.g., *L. capensis* (Andrews, 1911); see 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. In light of these differences, AM F6266–6298 is provisionally retained as Polycotylidae gen. et sp. indet. pending recovery of more diagnostic material.

Superfamily: Pliosauroida Welles, 1943 (sensu O'Keefe, 2001)

Family: Pliosauridae Seeley, 1874

Genus *Kronosaurus* Longman, 1924

*Kronosaurus* sp.

1904 *Cimoliasaurus* sp. Etheridge, p. 316 (AM L508 only).

2002a Pliosauridae Kear, p. 678 (AM L508 only).

*Referred material.* AM L508, isolated tooth with partial root (cast, original listed ca. 1904 as held in the private collection of a Mr. Goldstein, Sydney, current whereabouts of original specimen unknown); AM L1894 isolated tooth crown (cast, dated 1970, original in private ownership).

*Description.* Both AM L508 (Fig. 3F) and AM L1894 are large teeth being (AM L508) 76.22 mm, (AM L1894) 5.03 mm high, and (AM L508) 29.21 mm, (AM L1894) 21.08 mm wide (anteroposteriorly across base). Crowns are conical and slightly curved with ovoid base. Degree of curvature is greater in AM L1894 and tooth is proportionately more slender than AM L508. Distinct carinae are absent from both specimens. The ornamentation consists of numerous coarse striations; these are strongly raised in AM L508 and often branch towards base. AM L1894 is a shed crown (with internal resorption cavity); however, AM L508 retains a damaged remnant of the tooth root, perhaps indicating derivation from a floating carcass.

*Remarks.* The larger of the two recovered teeth, AM L508 (Fig. 3F), was initially described by Etheridge (1904), who

assigned it to *Cimoliasaurus* sp. Persson (1960) subsequently referred the specimen to Pliosauroida gen et sp. indet., a conclusion also followed by Kear (2002a), who suggested further attribution to Pliosauridae. The conical shape of the crown and absence of distinct carinae are here used to diagnose AM L508 as *Kronosaurus* sp. This is in accordance with Massare (1997), who suggested that conical tooth form and lack of distinct carinae were characteristic features of the dentition in the Cretaceous pliosaurids *Kronosaurus* and *Brachauchenius* Williston, 1903. This differs from the condition in most Jurassic taxa in which the teeth are more trihedral in shape because of the robust carinae on the anterolabial/posterolabial margins of the crown (Tarlo, 1960; Massare, 1987, 1997). Generic assignment of AM L508 to *Kronosaurus* sp. is also supported by the overall similarity to *Kronosaurus* dental remains described from the Wallumbilla Formation (Doncaster Member) and Toolebuc Formation of Queensland (Longman, 1924; White, 1935); and the current recognition of *Kronosaurus* as the only valid large pliosaurid genus from the Cretaceous of Australia (Molnar, 1982a,b, 1991; Thulborn and Turner, 1993; Long, 1998; Kear, 2003a, 2004). AM L1894 on the other hand, despite sharing the conical tooth form and absence of distinct carinae observable in currently recognised dental remains of *Kronosaurus*, is distinctly smaller with comparatively more slender proportions and a much less coarse striation pattern. It may, therefore, conceivably belong to another as yet unidentified pliosauroid or pliosauriform taxon. Although, derivation from the posterior portion of the jaw of *Kronosaurus*, or from a juvenile individual of that genus perhaps with differing dietary habits relative to the adults (a possible mechanism for avoiding intraspecific competition between sympatric age groups), cannot be ruled out. Consequently, AM L1894 is here tentatively referred to *Kronosaurus* sp., although confirmation of this assignment must await the discovery of more informative remains.

## 5. Discussion

The fossil marine reptiles of White Cliffs constitute one of several assemblages known from Cretaceous southern high-latitude deposits. Occurrences from elsewhere include ichthyosaurs and plesiosaurs from the Aptian–Albian Bulldog Shale of South Australia (Ludbrook, 1966; Alley and Pledge, 2000; Kear, 2003a,b, 2004), isolated plesiosaur teeth and rare bones from the Aptian–Albian Wonthaggi and Eumeralla formations of Victoria (Rich et al., 1988; Rich and Rich, 1989; Vickers-Rich, 1996) and Griman Creek Formation of northern New South Wales/southern Queensland (Kear, 2003a), numerous plesiosaur and mosasaur skeletons from Maastrichtian deposits in Patagonia (see Gasparini et al., 2003b for summary) and Antarctica, particularly the Lopez de Bertodano Formation of Seymour and Vega islands (Chatterjee and Zinsmeister, 1982; Chatterjee et al., 1984; Chatterjee and Small, 1989; Case et al., 2000; Martin, 2002; Martin et al., 2002; Novas et al., 2002), excellently preserved plesiosaur and mosasaur specimens from units including the Campanian–Maastrichtian Katiki Formation and Maastrichtian Maungataniwha

Sandstone of New Zealand (Welles and Gregg, 1971; Wiffen and Moisley, 1986; Bell et al., 1998; Cruickshank and Fordyce, 1998, 2002), and scattered plesiosaur elements from undifferentiated Upper Cretaceous strata of the Chatham Islands (Cruickshank and Fordyce, 2002). Marine reptile fossils (representing mainly mosasaurs and plesiosaurs) are also known from Cretaceous high latitude deposits in the Northern Hemisphere, most notably the Lower Campanian Smoking Hills Formation of the Canadian Northwest Territories (Russell, 1967; Nicholls and Russell, 1990).

Among the currently known Cretaceous high latitude localities White Cliffs (along with several others in southern and southeastern Australia) is unusual in that it preserves marine reptile fossils in direct association with palaeoclimatic indicators (e.g., glacial erratics, glendonites and growth-banded wood), representing seasonally very cold to near freezing conditions. This contrasts markedly with climate regimes typically tolerated by modern aquatic reptiles, but suggests that some Mesozoic taxa (including ichthyosaurs and plesiosaurs) were able to cope with extreme low temperature environments. Exactly what adaptations (if any) were present in these taxonomically diverse groups is unknown. However, a wide range of physiological mechanisms (perhaps including metabolic or mass dependent endothermy, the latter documented in the living Leatherback turtle *Dermochelys coriacea*; Paladino et al., 1990) or behavioural strategies (such as seasonal migration or short-term hibernation in smaller freshwater/coastal forms, vis-à-vis the American alligator *Alligator mississippiensis*; e.g., Brisbin et al., 1982) might have facilitated their exploitation of cold water habitats along the southern coastal margins of the Australian Cretaceous epicontinental seaway.

Of the marine reptile clades currently recorded from White Cliffs, plesiosaurs are by far the most diverse (including up to three families), and the group most frequently occurring as fossils. Plesiosaurs also form the dominant faunal element in Upper Cretaceous high latitude deposits in the Northern Hemisphere (Nicholls and Russell, 1990), Antarctica (Martin, 2002) and in the Lower Cretaceous Bulldog Shale of South Australia (in which as many as five families may be present, possibly including Polycotyliidae; see Kear, 2003a,b, 2004). This latter unit is a lateral equivalent of the Wallumbilla Formation, and exhibits a similar macroinvertebrate fauna (see Ludbrook, 1966; Johns, 1968; Day, 1969), as well as palaeoclimatic indicators including ice-rafted erratic boulders, glendonites and growth-banded fossil wood (Frakes and Francis, 1988, 1990; Sheard, 1990; Dettmann et al., 1992; Frakes et al., 1995; De Lurio and Frakes, 1999). The characteristic faunal composition of these Cretaceous high latitude deposits contrasts markedly with those typically occurring in contemporaneous (or closely approximating) low latitude marine reptile assemblages from elsewhere. For example, in Australia the Upper Albian Toolebuc Formation of northeastern Queensland preserves plesiosaurs in far fewer numbers (and with reduced taxonomic diversity although as many as three family-level clades are still present) relative to ichthyosaurs and

chelonoid turtles, which otherwise dominate the assemblage (Wade, 1990; Molnar, 1991; Kear, 2003a). The reasons for this dissimilarity in faunal composition are not yet fully understood, but may be related to a greater tolerance by certain clades and/or taxa (i.e. plesiosaurs) for colder water environments. Indeed, the prevalence of very cold to near freezing conditions in at least the southern reaches of the Australian Cretaceous epicontinental seaway during Late Neocomian–Early Albian (Frakes and Francis, 1988) may have provided an effective barrier to the successful dispersal of groups such as chelonoids, which do not appear in the Australian Cretaceous record prior to the uppermost Albian (Kear, 2002a, 2003a). Both Nicholls and Russell (1990) and Martin (2002) documented a similar pattern in the Upper Cretaceous deposits of North America and Antarctica respectively, in which chelonoids, some mosasaurid taxa and sharks (the latter in North American units only) showed distributions conforming to strict latitudinal boundaries (becoming rarer with increasing latitude). This was interpreted as a product of temperature-restricted distribution, particularly in the case of marine turtles, in which prevailing water temperature is a critical factor in controlling the availability of nesting sites (see Mrosovsky, 1980).

The taxonomic composition of the White Cliffs marine reptile fauna highlights its cosmopolitan nature and strong relationships with taxa known from elsewhere. For example, the ophthalmosaurid ichthyosaur *Platypterygius* has been documented from many localities around the world (McGowan, 1972), and the large pliosaurid *Kronosaurus* has been recorded from Aptian–Albian strata in both Australia and South America (Hampe, 1992). Interestingly, the White Cliffs marine reptile assemblage also includes some potentially endemic forms, in particular the earliest known polycotyliids (Sato and Storrs, 2000); this could suggest a potential origin for the group in the high latitude epicontinental seas of eastern Gondwana sometime in the Neocomian–Early Gallic. If this was the case, then polycotyliids appear to have undergone an explosive radiation into the Northern Hemisphere during the mid-Cretaceous, where their remains are known from as early as the Late Albian in North America (Sato and Storrs, 2000; Druckenmiller, 2002) and Cenomanian in Asia (Sato and Storrs, 2000) and Europe (Storrs et al., 2000).

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## References

- 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*, vol. 5. Royal Geographic Society of South Australia, Adelaide, pp. 35–82.
- Andrews, C.W., 1910. In: *A Descriptive Catalogue of the Marine Reptiles of the Oxford Clay*, vol. 1. British Museum (Natural History), London, 205 pp.
- Andrews, C.W., 1911. Description of a new plesiosaur (*Plesiosaurus capensis* sp. nov.) from the Uitenhage Beds of Cape Colony. *Annals of the South African Museum* 7, 309–322.
- Andrews, C.W., 1913. In: *A Descriptive Catalogue of the Marine Reptiles of the Oxford Clay*, vol. 2. British Museum (Natural History), London, 206 pp.
- Andrews, C.W., 1922. Description of a new plesiosaur from the Weald Clay of Berwick (Sussex). *Quarterly Journal of the Geological Society of London* 78, 285–295.
- Arkhangelsky, M.S., 1998. On the ichthyosaurian genus *Platypterygius*. *Paleontologicheskii Zhurnal* 32, 65–69.
- 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., Enay, R., Krishna, J., 1991. Les Plesiosaures du Jurassique supérieur de la province de Kachchh (Inde). *Comptes Rendus de l'Académie des Sciences de Paris, Série 2* 313, 1343–1347.
- Baur, G., 1887. Über die Ursprung der Extremitäten der Ichthyopterygia. *Berichte über die Versammlungen des Oberrheinischen Vereines* 20, 17–20.
- Bell, G.L., Caldwell, M.W., Holmes, R., Wiffen, J., McKee, J., 1998. Sea monsters of the South Pacific: on the Late Cretaceous mosasaurs from New Zealand. *Journal of Vertebrate Paleontology* 19, 37A.
- Benton, M.J., 1997. *Vertebrate Palaeontology*, second ed. Blackwell Science, Osney Mead, Oxford, 452 pp.
- de Blainville, H.M.D., 1835. Description de quelques espèces de reptiles de la Californie, précédée de l'analyse d'un système générale Erpetologie et d'Amphibiologie. *Nouvelles Annales du Muséum d'Historie Naturelle*, Paris 4, 233–296.
- Brisbin, I.L., Standora, E.A., Vargo, M.J., 1982. Body temperature and behavior of American alligators during cold winter weather. *American Midland Naturalist* 107, 209–218.
- Brown, D.S., 1981. The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. *Bulletin of the British Museum (Natural History), Geology Series* 35, 253–347.
- Brown, D.S., 1993. A taxonomic reappraisal of the families Elasmosauridae and Cryptoclididae (Reptilia, Plesiosauroidea). *Revue de Paléobiologie* 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.
- Buchholtz, E.A., 2001. Swimming styles in Jurassic ichthyosaurs. *Journal of Vertebrate Paleontology* 21, 61–73.
- Burger, D., 1988. Early Cretaceous environments in the Eromanga Basin: palynological evidence from GSQ Wyandra-1 corehole. *Memoirs of the Association of Australasian Palaeontologists* 5, 173–186.
- Burton, G.R., Mason, A.J., 1998. Controls on opal localisation in the White Cliffs area. *Quarterly Notes, Geological Survey of New South Wales* 107, 1–11.
- Cabrera, A., 1941. Un plesiosaurio nuevo del Cretáceo del Chubut. *Revista del Museo de La Plata* 2, 113–130.
- Carpenter, K., 1989. *Dolichorhynchops* does not equal *Trinacromerum* (Reptilia, Plesiosauria). *Journal of Vertebrate Paleontology* 9, 15A.
- Carpenter, K., 1996. A review of short-necked plesiosaurs from the Cretaceous of the Western Interior, North America. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 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.
- Carroll, R.L., 1988. *Vertebrate Paleontology and Evolution*. Freeman, San Francisco, 698 pp.
- Case, J.A., Martin, J.E., Chaney, D.S., Reguero, M., Marensi, S.A., Santillana, S.M., Woodburne, M.O., 2000. The first duck-billed dinosaur (Family Hadrosauridae) from Antarctica. *Journal of Vertebrate Paleontology* 20, 612–614.
- Chapman, F., 1914. *Australasian Fossils*. George Robertson, Melbourne, 341 pp.
- 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, London, Special Publication 47, 197–215.
- Chatterjee, S., Small, B.J., Nickell, M.W., 1984. Late Cretaceous marine reptiles from Antarctica. *Antarctic Journal of the United States* 19, 7–8.
- Chatterjee, S., Zinsmeister, W.J., 1982. Late Cretaceous marine vertebrates from Seymour Island, Antarctica. *Antarctic Journal of the United States* 17, 66.
- Choo, B., 1999. Cretaceous ichthyosaurs from Western Australia. *Records of the Western Australian Museum, Supplement* 57, 207–218.
- Cope, E.D., 1869. Synopsis of the extinct Batrachia and Reptilia of North America, part 1. *Transactions of the American Philosophical Society* 14, 1–235.
- Cruickshank, A.R.I., 1997. A Lower Cretaceous plesiosaur from South Africa. *Annals of the South African Museum* 105, 207–226.
- Cruickshank, A.R.I., Fordyce, R.E., 1998. High latitude late Cretaceous plesiosaurs in Gondwana. *Journal of African Earth Sciences* 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). *Records of the Western Australian Museum, Supplement* 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)*. Geological Survey of Queensland, Publication 383, 1–194.
- Delair, J.B., 1959. The Mesozoic reptiles of Dorset. Part 2. *Proceedings of the Dorset Natural History and Archaeological Society* 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. *Geochimica et Cosmochimica Acta* 63, 1039–1048.
- Dettmann, M.E., Molnar, R.E., Douglas, J.G., Burger, D., Fielding, C., Clifford, H.T., Francis, J., Jell, P., Rich, T., Wade, M., Rich, P.V., Pledge, N., Kemp, A., Rozefelds, A., 1992. Australian Cretaceous terrestrial faunas and floras: biostratigraphic and biogeographic implications. *Cretaceous Research* 13, 207–262.
- Druckenmiller, P.S., 2002. Osteology of a new plesiosaur from the Lower Cretaceous (Albian) Thermopolis Shale of Montana. *Journal of Vertebrate Paleontology* 22, 29–42.
- 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 and Planetary Science Letters* 58, 141–150.
- Etheridge, R., 1897. An Australian sauropterygian (*Cimoliasaurus*), converted into precious opal. *Records of the Australian Museum* 3, 21–29.

- Etheridge, R., 1902. A monograph of the Cretaceous invertebrate fauna of New South Wales. *Memoirs of the Geological Survey of New South Wales* 11, 1–98.
- 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. *Records of the Australian Museum* 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., Beudoin, B. (Eds.), *Cretaceous Resources, Events and Rhythms*. Kluwer Academic Publishers, Dordrecht, pp. 273–287.
- Frakes, L.A., Alley, N.F., Deynoux, M., 1995. Early Cretaceous ice rafting and climate zonation in Australia. *International Geology Review* 37, 567–583.
- Frakes, L.A., Burger, D., Apthorpe, M., Wiseman, J., Dettmann, M., Alley, N., Flint, R., Gravestock, D., Ludbrook, N., Backhouse, J., Skwarko, S., Schneiberova, V., McMinn, A., Moore, P.S., Bolton, B.R., Douglas, J.G., Christ, R., Wade, M., Molnar, R.E., McGowan, B., Balme, B.E., Day, R.A., 1987. Australian Cretaceous shorelines, stage by stage. *Palaeogeography, Palaeoclimatology, Palaeoecology* 59, 31–48.
- Gasparini, Z., Bardet, N., Martin, J.E., Fernandez, M., 2003a. The elasmosaurid *Aristonectes* Cabrera from the latest Cretaceous of South America and Antarctica. *Journal of Vertebrate Paleontology* 23, 104–115.
- Gasparini, Z., Salgado, L., Casadio, S., 2003b. Maastrichtian plesiosaurs from northern Patagonia. *Cretaceous Research* 24, 157–170.
- Gürich, G., 1901. Jura- und Devon- fossilien von White Cliffs Australien. *Neues Jahrbuch Beilage* 14, 492–495.
- Hampe, O., 1992. Ein grosswuechsiger pliosauride (Reptilia, Plesiosauria) aus der Unterkreide (oberes Aptium) von Kolumbien. *Courier Forschungsinstitut Senckenberg* 145, 1–32.
- Helby, R., Morgan, R., Partridge, A.D., 1987. A palynological zonation of the Australian Mesozoic. *Memoirs of the Australasian Association of Palaeontologists* 4, 1–94.
- Henderson, R.A., Crampton, J.S., Dettmann, M.E., Douglas, J.G., Haig, D., Shafik, S., Stilwell, J.D., Thulborn, R.A., 2000. Biogeographical observations on the Cretaceous biota of Australasia. *Memoirs of the Australasian Association of Palaeontologists* 23, 355–404.
- Huber, B.T., Hodell, D.A., 1996. Middle–Late Cretaceous climate of the southern high latitudes: stable isotopic evidence for minimal pole-to-equator thermal gradients. Reply. *Geological Society of America, Bulletin* 108, 1193–1196.
- Huber, B.T., Hodell, D.A., Hamilton, C.P., 1995. Middle–Late Cretaceous climate of the southern high latitudes: stable isotopic evidence for minimal pole-to-equator thermal gradients. *Geological Society of America, Bulletin* 107, 1164–1191.
- von Huene, F., 1922. Die Ichthyosaurier des Lias und ihre Zusammenhänge. *Gebrüder Borntraeger, Berlin*, 114 pp.
- von Huene, F., 1928. Ein neuer *Eurhinosaurus* aus dem oberen Lias von Holtzmaden. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage* 1928, 471–484.
- Idnurm, M., 1985. Late Mesozoic and Cenozoic palaeomagnetism of Australia – I. A redetermined apparent polar wander path. *Geophysical Journal of the Royal Astronomical Society* 83, 399–418.
- Johns, R.K., 1968. Geology and mineral resources of the Andamooka-Torrens area. *Geological Survey of South Australia, Bulletin* 41, 7–103.
- Kear, B.P., 2002a. Reassessment of the Early Cretaceous plesiosaur *Cimoliasaurus maccoyi* Etheridge, 1904 (Reptilia, Sauropterygia) from White Cliffs, New South Wales. *Australian Journal of Zoology* 50, 671–685.
- Kear, B.P., 2002b. Darwin Formation (Early Cretaceous, Northern Territory) marine reptile remains in the South Australian Museum. *Records of the South Australian Museum* 35, 33–47.
- Kear, B.P., 2003a. Cretaceous marine reptiles of Australia: a review of taxonomy and distribution. *Cretaceous Research* 24, 277–303.
- Kear, B.P., 2003b. Studies on the Mesozoic Marine Reptile Fauna of Australia. PhD dissertation, University of New South Wales, 605 pp.
- Kear, B.P., 2004. Biogeographic and biostratigraphic implications of Australian Mesozoic marine reptiles. *Australian Biologist* 17, 4–22.
- Leidy, J., 1851. Description of fossils. *Proceedings of the Academy of Natural Sciences, 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, 188 pp.
- Longman, H.A., 1915. On a giant turtle from the Queensland Lower Cretaceous. *Memoirs of the Queensland Museum* 3, 24–29.
- Longman, H.A., 1924. A new gigantic marine reptile from the Queensland Cretaceous, *Kronosaurus queenslandicus* new genus and species. *Memoirs of the Queensland Museum* 8, 26–28.
- Ludbrook, N.H., 1966. Cretaceous biostratigraphy of the Great Artesian Basin in South Australia. *Geological Survey of South Australia, Bulletin* 40, 1–223.
- Maisch, M.W., Matzke, A.T., 2000. The Ichthyosauria. *Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie)* 298, 1–159.
- Martill, D.M., 1985. The preservation of marine vertebrates in the Lower Oxford Clay (Jurassic) of central England. *Philosophical Transactions of the Royal Society of London, Series B* 311, 155–165.
- Martill, D.M., 1987. A taphonomic and diagenetic case study of a partially articulated ichthyosaur. *Palaeontology* 30, 543–555.
- Martin, J.E., 2002. Late Cretaceous Antarctic vertebrate fossils in the British Antarctic Survey collections, Cambridge, England. *Journal of Vertebrate Paleontology, Supplement* 22, 83A.
- Martin, J., Bell, G., Case, J., Chaney, D., Fernández, M., Gasparini, Z., Reguero, M., Woodburne, M., 2002. Mosasaurs (Reptilia) from the Late Cretaceous of the Antarctic Peninsula. In: Gamble, J.A., Skinner, D.N.B., Henrys, S. (Eds.), *Antarctica at the Close of a Millennium: Eighth International Symposium of Antarctic Earth Sciences*. Royal Society of New Zealand, *Bulletin* 35, 293–299.
- Massare, J.M., 1987. Tooth morphology and prey preference in Mesozoic marine reptiles. *Journal of Vertebrate Paleontology* 7, 121–137.
- 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.
- McCoy, F., 1867. On the occurrence of Ichthyosaurus and Plesiosaurus in Australia. *Annals and Magazine of Natural History* 19, 355–356.
- McGowan, C., 1972. The systematics of Cretaceous ichthyosaurs with particular reference to the material from North America. *Contributions to Geology, University of Wyoming* 11, 9–29.
- McGowan, C., Motani, R., 2003. *Ichthyopterygia*. *Handbuch der Paläoherpetologie Part 8*. Verlag Dr. Friedrich Pfeil, München, 101 pp.
- 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, 139–154.
- Molnar, R.E., 1980. Australian late Mesozoic terrestrial tetrapods: some implications. *Mémoires de la Société Géologique de France* 139, 131–143.
- Molnar, R.E., 1982a. Australian Mesozoic reptiles. In: Rich, P.V., Thompson, E.M. (Eds.), *The Fossil Vertebrate Record of Australasia*. Monash University, Clayton, pp. 170–225.
- Molnar, R.E., 1982b. A catalogue of fossil amphibians and reptiles in Queensland. *Memoirs of the Queensland Museum* 20, 613–633.
- Molnar, R.E., 1991. Fossil reptiles in Australia. In: Vickers-Rich, P., Monaghan, J.M., Baird, R.F., Rich, T.H. (Eds.), *Vertebrate Palaeontology of Australasia*. Pioneer Design Studio, Monash University, Melbourne, pp. 605–702.
- Molnar, R.E., Pledge, N.S., 1980. A new theropod dinosaur from South Australia. *Alcheringa* 4, 281–287.
- Motani, R., 1999. Phylogeny of the Ichthyopterygia. *Journal of Vertebrate Paleontology* 19, 473–496.
- Mrosovsky, N., 1980. Thermal biology of sea turtles. *American Zoologist* 20, 531–547.
- 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.
- Nicholls, E.L., Russell, A.P., 1990. Paleobiogeography of the Cretaceous Western Interior Seaway of North America: the vertebrate evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology* 79, 149–169.
- Novas, F.E., Fernández, M., Gasparini, Z.B., Liro, J.M., Nuñez, H.J., Puerta, P., 2002. *Lakumasaurus antarcticus*, n. gen. et sp., a new mosasaur (Reptilia, Squamata) from the Upper Cretaceous of Antarctica. *Ameghiniana* 39, 245–249.
- O'Keefe, F.R., 2001. A cladistic analysis and taxonomic revision of the Plesiosauria (Reptilia, Sauropterygia). *Acta Zoologica Fennica* 213, 1–63.
- O'Keefe, F.R., 2004. Preliminary description and phylogenetic position of a new plesiosaur (Reptilia: Sauropterygia) from the Toarcian of Holzmaden, Germany. *Journal of Paleontology* 78, 973–988.
- Osborn, H.F., 1903. The reptilian subclass Diapsida and Synapsida and the early history of the Diaptosauria. *Memoirs of the American Museum of Natural History* 1, 449–507.
- Owen, R., 1840. Report on British fossil reptiles. Reports of the British Association for the Advancement of Science, London 9, 43–126.
- Owen, R., 1860. On the orders of fossil and recent Reptilia, and their distribution in time. Reports of the British Association for the Advancement of Science, London 29, 153–166.
- Owen, R., 1881. Monograph on the fossil Reptilia of the Liassic Formations. Part 3. Ichthyopterygia. Palaeontographical Society Monograph 35, 83–134.
- Paladino, F.V., O'Connor, M.P., Spotila, J.R., 1990. Metabolism of leatherback turtles, gigantothermy, and thermoregulation of dinosaurs. *Nature* 344, 858–860.
- Persson, P.O., 1960. Early Cretaceous plesiosaurians (Reptilia) from Australia. *Lunds Universitets 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 Universitets Årsskrift* 59, 1–59.
- Pirrie, D., Doyle, P., Marshall, J.D., Ellis, G., 1995. Cool Cretaceous climates – new data from the Albian of Western Australia. *Journal of the Geological Society, London* 152, 739–742.
- Rich, P.V., Rich, T.H., Wagstaff, B.E., McEwan Mason, J., Douthitt, C.B., Gregory, R.T., Mason, E.A., 1988. Evidence for low temperatures and biologic diversity in Cretaceous high latitudes of Australia. *Science* 242, 1403–1406.
- Rich, T.H., Rich, P.V., 1989. Polar dinosaurs and biotas of the Early Cretaceous of southeastern Australia. *National Geographic Society, Research Reports* 5, 15–53.
- Rieppel, O., 2000. Sauropterygia I. Placodontia, Pachypleurosauria, Nothosauria, Pistosauria. *Handbuch der Paläoherpelologie Part 12A*. Verlag Dr. Friedrich Pfeil, München, 134 pp.
- Ritchie, A., 1979. Sea monster in opal – or the one that got away? *Australian Natural History* 19, 408–413.
- Russell, D.A., 1967. Cretaceous vertebrates from the Anderson River N.W.T. *Canadian Journal of Earth Sciences* 4, 21–38.
- Sato, T., Storrs, G.W., 2000. An early polycotyloid plesiosaur (Reptilia, Sauropterygia) from the Cretaceous of Hokkaido, Japan. *Journal of Paleontology* 74, 907–914.
- Seeley, H.G., 1898. Note on plesiosaurian humerus from New South Wales opal mines. *Quarterly Journal of the Geological Society* 54, 106.
- Selwood, B.W., Price, G.D., Valdes, P.J., 1994. Cooler estimates of Cretaceous temperatures. *Nature* 370, 453–455.
- Sheard, M.J., 1990. Glendonites from the southern Eromanga Basin in South Australia: palaeoclimatic indicators for Cretaceous ice. *The Geological Survey of South Australia Quarterly Geological Notes* 114, 17–23.
- Stevens, G.R., Clayton, R.N., 1971. Oxygen isotope studies on Jurassic and Cretaceous belemnites from New Zealand and their biogeographic significance. *New Zealand Journal of Geology and Geophysics* 14, 829–897.
- Storrs, G.W., 1999. An examination of the Plesiosauria (Diapsida, Sauropterygia) from the Upper Cretaceous Niobrara Formation of central North America. *University of Kansas, Paleontological Contributions (New Series)* 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., Kurochkin, E.N. (Eds.), *The Age of Dinosaurs in Russia and Mongolia*. Cambridge University Press, Cambridge, pp. 187–210.
- Tarlo, L.B., 1960. A review of the Upper Jurassic plesiosaurs. *Bulletin of the British Museum (Natural History)* 4, 147–189.
- Thulborn, T., Turner, S., 1993. An elasmosaur bitten by a plesiosaur. *Modern Geology* 18, 489–501.
- Vickers-Rich, P., 1996. Early Cretaceous polar tetrapods from the Great Southern Rift Valley, southeastern Australia. *Memoirs of the Queensland Museum* 39, 719–723.
- Vine, R.R., Day, R.W., Casey, D.J., Milligan, E.N., Casey, D.J., Galloway, M.C., Exon, N.F., 1967. Revised nomenclature of the Rolling Downs Group, Eromanga and Surat basins. *Queensland Government Mining Journal* 68, 144–151.
- Wade, M., 1990. A review of the Australian Cretaceous longipinnate ichthyosaur *Platypterygius*, (Ichthyosauria, Ichthyopterygia). *Memoirs of the Queensland Museum* 28, 115–137.
- Welles, S.P., 1943. Elasmosaurid plesiosaurs with a description of new material from California and Colorado. *University of California, Publications in Geological Sciences* 13, 125–215.
- Welles, S.P., 1962. A new species of elasmosaur from the Aptian of Colombia, and a review of the Cretaceous plesiosaurs. *University of California, Publications in Geological Sciences* 44, 1–96.
- Welles, S.P., Gregg, D.R., 1971. Late Cretaceous marine reptiles of New Zealand. *Records of the Canterbury Museum* 9, 1–111.
- Wiffen, J., Moisley, W.L., 1986. Late Cretaceous reptiles (Families Elasmosauridae and Pliosauridae) from the Mangahouanga Stream, North Island, New Zealand. *New Zealand Journal of Geology and Geophysics* 29, 205–252.
- Williston, S.W., 1903. North American plesiosaurs. Part 1. *Field Columbian Museum Publications in Geology* 73, 1–77.
- Williston, S.W., 1908. North American plesiosaurs: *Trinacromerum*. *Journal of Geology* 16, 715–736.
- White, T.E., 1935. On the skull of *Kronosaurus queenslandicus* Longman. *Occasional Papers of the Boston Society of Natural History* 8, 219–228.
- Woodward, H., 1895. Proceedings of the Geological Society of London. Session 1894–1895. November 21st 1894. *Quarterly Journal of the Geological Society of London* 51, iii.