

## Cretaceous marine amniotes of Australia: perspectives on a decade of new research

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### Abstract

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Cretaceous marine amniote fossils have been documented from Australia for more than 150 years, however, their global significance has only come to the fore in the last decade. This recognition is a product of accelerated research coupled with spectacular new discoveries from the Aptian–Albian epeiric sequences of the Eromanga Basin – especially the opal-bearing deposits of South Australia and vast *lagerstätten* exposures of central-northern Queensland. Novel fragmentary records have also surfaced in Cenomanian and Maastrichtian strata from Western Australia. The most notable advances include a proliferation of plesiosaurian taxa, as well as detailed characterization of the ‘last surviving’ ichthyosaurian *Platypterygius*, and some of the stratigraphically oldest protostegid sea turtles based on exceptionally preserved remains. Compositionally, the Australian assemblages provide a unique window into the otherwise poorly known Early Cretaceous marine amniote faunas of Gondwana. Their association with freezing high latitude palaeoenvironments is also extremely unusual, and evinces a climate change coincident diversity turnover incorporating the nascent radiation of lineages that went on to dominate later Mesozoic seas.

### Keywords

Plesiosauria, *Platypterygius*, Protostegidae, Mosasauroida, Aptian-Albian, Cenomanian, Maastrichtian.

### Introduction

Although Australia has anecdotal Triassic (Kear, 2004; Kear and Hamilton-Bruce, 2011) and rare Jurassic (Kear, 2012) marine amniote fossil occurrences, virtually all of its currently documented Mesozoic record is Cretaceous in age. The earliest historical publications date from the late 19<sup>th</sup> century (McCoy, 1867a, 1867b, 1869; Owen, 1882; Etheridge 1888, 1897), with only sporadic reports appearing between 1900–1940 (Etheridge, 1904; Longman, 1915, 1922, 1924, 1930, 1932, 1935, 1943; White, 1935; Teichert and Matheson, 1944), and in the last decades of the 20<sup>th</sup> Century (Romer and Lewis, 1959; Lundelius and Warne, 1960; Persson, 1960, 1982; McGowan, 1972; Gaffney, 1981; Murray, 1985, 1987; Wade, 1984, 1985, 1990; Molnar, 1991; Thulborn and Turner, 1993; Cruickshank and Long, 1997; Long and Cruickshank, 1998; Cruickshank et al., 1999; Choo, 1999). Kear (2003) provided the first comprehensive overview confirming the presence of elasmosaurid, possible cryptoclidid, polycotyloid, rhomaleosaurid, and pliosaurid plesiosaurians, the ubiquitous ophthalmosaurian ichthyosaurian *Platypterygius*, protostegid sea turtles, and enigmatic mosasaurids (fig. 1). Since then, a decade of intensive study has anatomically clarified and phylogenetically redefined many of these taxa, and added a plethora of new discoveries that emphasize the global palaeoecological and palaeobiological significance of the Australian Cretaceous assemblages. This paper provides both

an updated summary and bibliography of these finds, with the purpose of stimulating further investigation into this dynamic field of antipodean vertebrate palaeontology over the decade to come.

### Institutional abbreviations

AM, Australian Museum, Sydney, Australia; AOD, Australian Age of Dinosaurs Museum, Winton, Australia; NMV, Museum Victoria, Melbourne, Australia; NTM, Northern Territory Museum and Art Gallery, Darwin, Australia; QM, Queensland Museum, Brisbane, Australia; SAM, South Australian Museum, Adelaide, Australia; UWA, University of Western Australia, Perth, Australia; WAM, Western Australian Museum, Perth, Australia.

### Plesiosaurians

Australian Cretaceous plesiosaurian fossils are abundant, and in several rock units, exceptionally well preserved. Those from the Aptian opal-bearing strata of the Bulldog Shale at Coober Pedy and Andamooka in South Australia, and Wallumbilla Formation at White Cliffs, as well as the Albian Grimman Creek Formation in New South Wales (fig. 2), are perhaps the most unusual because they manifest diagenetic replacement of the bony tissue by opaline hydrated silica. Kear (2005a, 2006a, 2006b) revised the existing specimens and

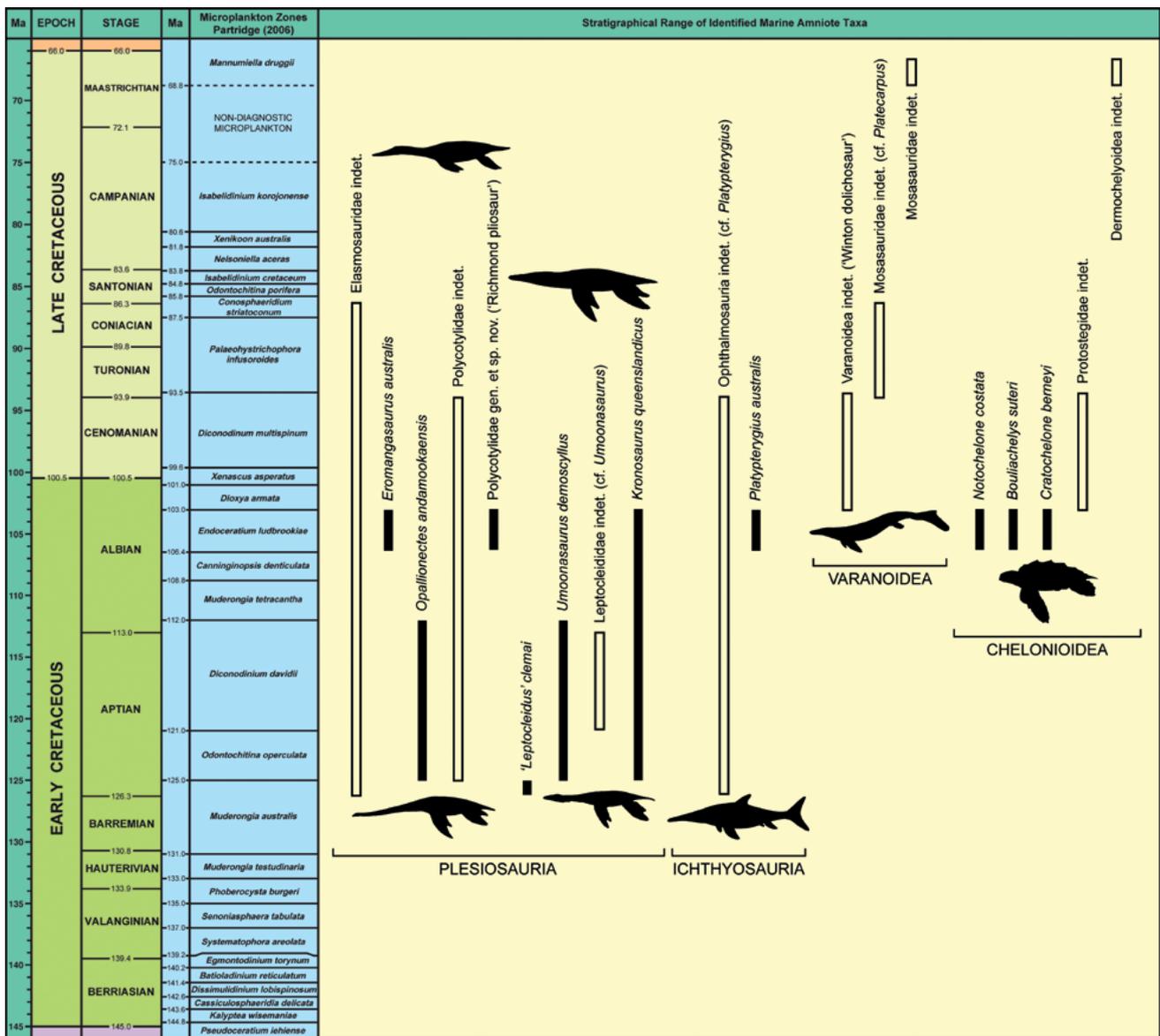


Figure 1. Stratigraphical distribution of Australian Cretaceous marine amniote taxa updated from Kear (2003). Australian standard microplankton (dinoflagellate) zonation is modified from Partridge (2006) to accommodate the emended geological timescale of Gradstein et al. (2012). Taxon ranges indicate named species (black bars) or indeterminate occurrences assigned to higher-level taxa (open bars).

recognized a diversity of taxa. These included indeterminate elasmosaurids, some of which were osteologically immature and of surprisingly small body-size – the most diminutive being less than 2 m in estimated maximum length (AM F9639–F9928; see Kear, 2002a). Their vertebral morphology showed characteristics of other Gondwanan elasmosaurids. For example, the lack of a pronounced ventral notch on the articular faces of the cervical centra (Kear, 2002a, p. 672, fig. 1) is typical of the Early Cretaceous *Callawayasaurus colombiensis* (Welles, 1962) from Colombia, as well as *Eromangasaurus australis* (Sachs, 2005) and the *nomen dubium* *Woolungasaurus glendowerensis* Persson, 1960

(Sachs, 2004) from Australia. Furthermore, the centrum proportions of these ‘juvenile’ elasmosaurids (Kear, 2002a, p. 673, table 1) are reminiscent of the austral high-latitude *Aristonectes parvidens* Cabrera, 1941 and *Kaiwhekia katiki* Cruickshank and Fordyce, 2002 (see O’Gorman et al., 2014) from Patagonia–Antarctica and New Zealand respectively. Note, though, that elasmosaurid cervical centrum proportions are intraspecifically variable and of uncertain taxonomic significance (O’Keefe and Hiller, 2006; Sachs et al., 2013).

Kear (2005b, 2007a) and Sachs (2005) reported on cranial material of *E. australis* from the middle–upper Albian Toolebuc Formation near Maxwelton in Queensland (fig. 2).

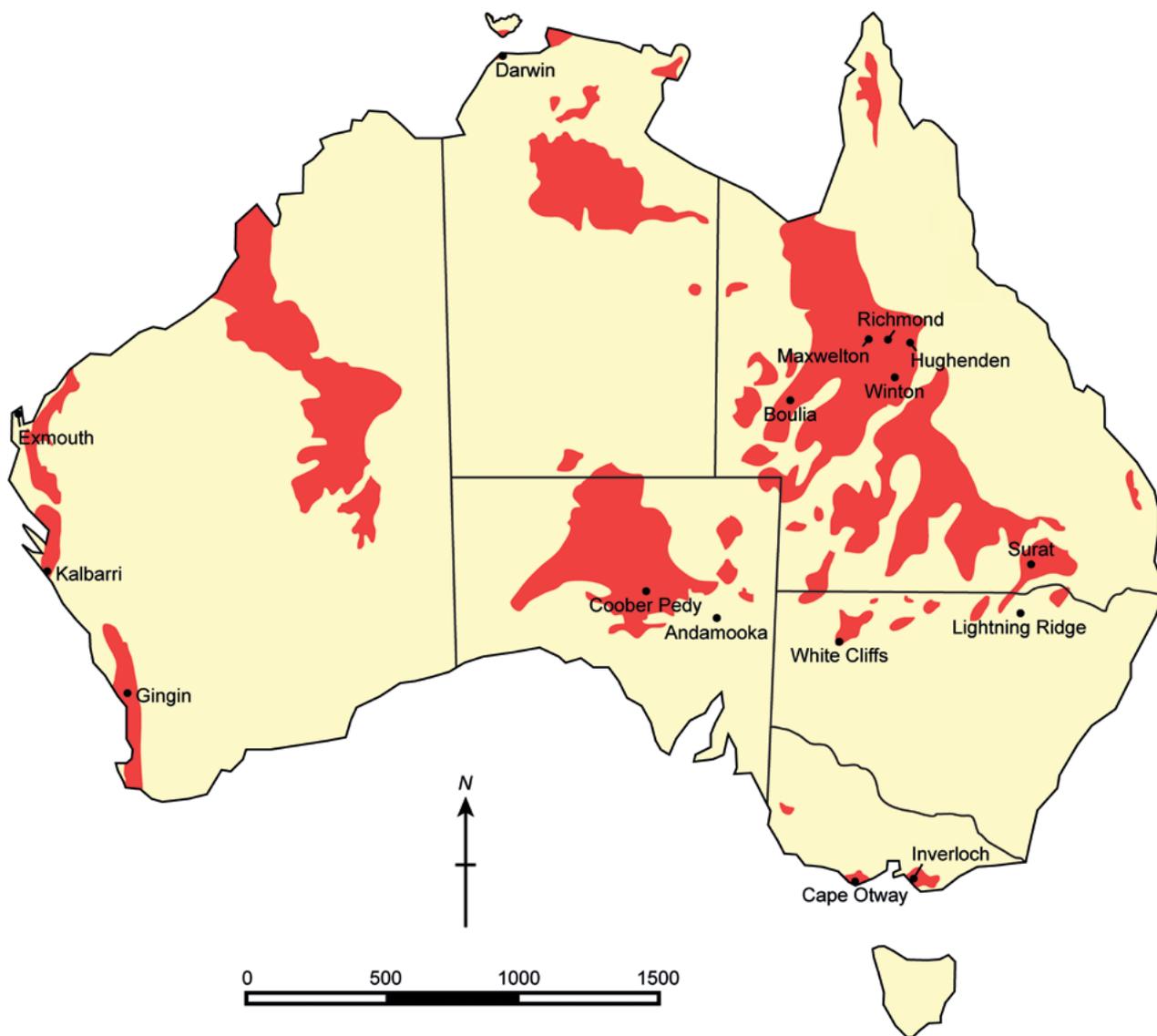


Figure 2. Diagrammatic map of Cretaceous rock outcrops on the Australian continent with state borders and specific locality references for fossil occurrences discussed in the text (developed from Kear and Hamilton-Bruce, 2011).

The Toolebuc Formation and overlying Allaru Mudstone are lagerstätten sequences that have yielded some of the most spectacular Early Cretaceous marine amniote fossils found worldwide. The holotype skull of *E. australis* (QM F11050; Kear, 2005b, p. 794, fig. 2A–C) is a classic example. It bears a series of depression fractures and crushing attributed to a bite from a gigantic predatory pliosauroid (Thulborn and Turner, 1993). Moreover, its phylogenetic character states include circular (non-compressed) tooth cross-sections and the possible presence of a pineal foramen, which suggest a basal position within Elasmosauridae (Benson and Druckenmiller, 2014), although, its topology within this clade is ambiguous (Sachs and Kear, 2015). Several other fragmentary

elasmosaurid skulls have also been found in the Toolebuc Formation (e.g. AM F87826; Kear, 2001a), one of which has a well-preserved premaxillary palate exposing the intracranial sinuses (SAM P40510; fig. 3A). A number of articulated elasmosaurid postcranial skeletons await adequate preparation and study. In addition, indeterminate isolated vertebrae occur in the Aptian Birdrong Sandstone (WAM 94.7.6), lower Albian Windalia Radiolarite (WAM 05.2.1), as well as the Cenomanian upper Gearle Siltstone (WAM 15.2.1) in Western Australia. McHenry et al. (2005) reported on a remarkable elasmosaurid specimen (QM F33037) from the Wallumbilla Formation (referred to as the Blackdown or Doncaster Formation in the Walsh Creek region of Queensland) that preserved an

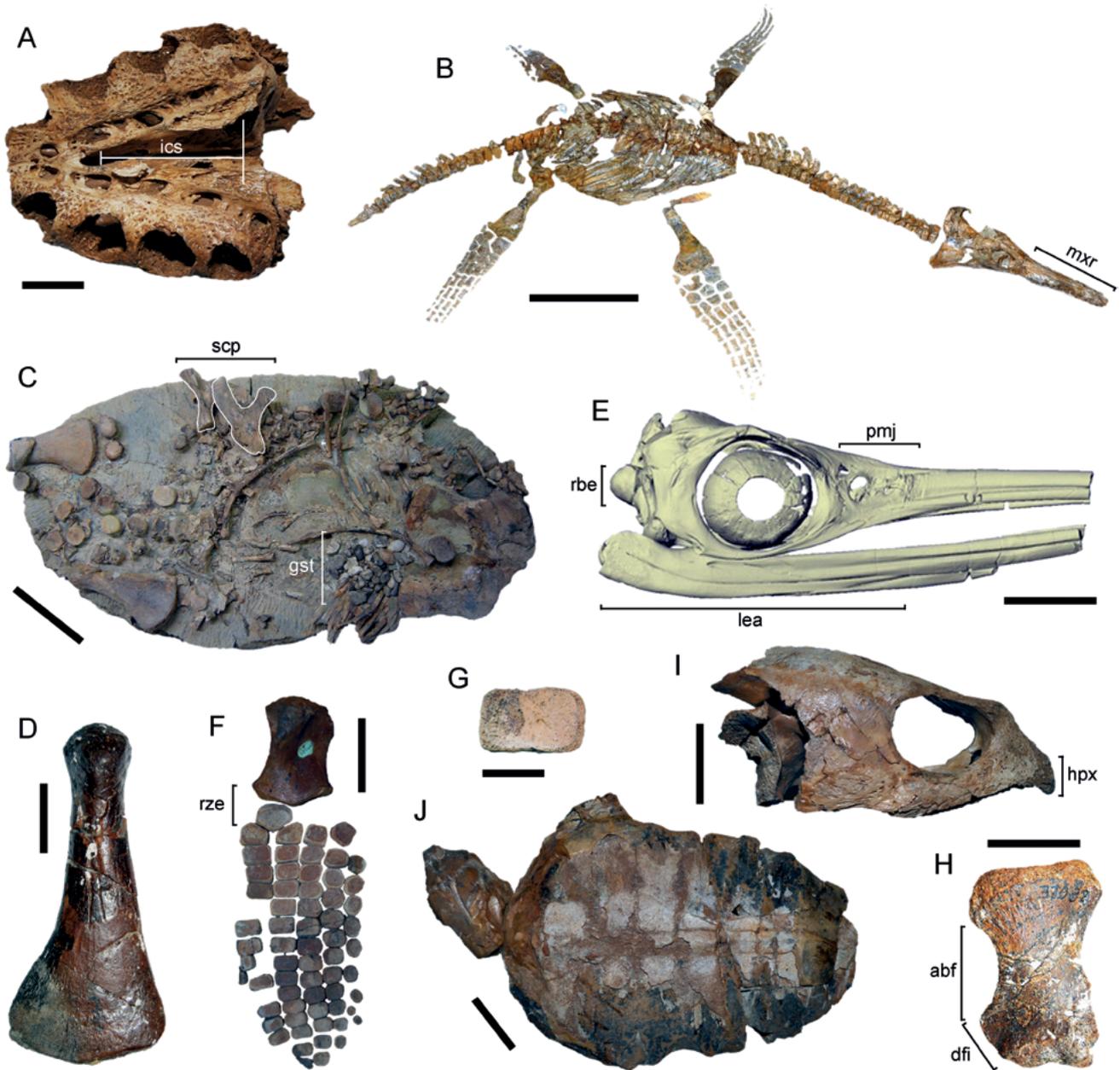


Figure 3. Marine amniote fossils from Cretaceous strata in Australia. A, elasmosaurid premaxillary palate (SAM P40510) exposing the vomerine contact and intracranial sinus. B, spectacular mounted skeleton (QM F18041) of the new polycotyloid popularly dubbed the ‘Richmond pliosaur’. C, partially disarticulated ‘juvenile’ postcranium referred to *Umoonasaurus demoscyllus*. Both scapulae (outlined) and an in situ gastrolith mass are indicated. D, ‘*Umoonasaurus*-like’ propodial from the late Aptian Darwin Formation, Northern Territory. E, CT rendering of an exceptionally preserved ‘juvenile’ *Platypterygius australis* cranium and mandible (AM F98273). Image compilation: Ben Hill (Adelaide). F, articulated humerus and distal forelimb elements (AM F107444) of a ‘juvenile’ *Platypterygius australis*. G, ophthalmosaurian phalanx (WAM 99.1.4) from the late Cenomanian Geale Siltstone, Western Australia. Image: Mikael Siverson (Western Australian Museum). H, mosasaurid ulna (UWA 37092) with antibrachial foramen and intermedium contact indicated. I, cranium of *Bouliachelys suteri* (SAM P41106) in lateral view. J, articulated cranium and carapace of *Bouliachelys suteri* (SAM P40525) in dorsal view. Scale bars represent 20 mm in A, G, H; 500 mm in B; 100 mm in C, J; and 50 mm in D–F, I. Abbreviations: abf – antibrachial foramen; dfi – distal facet for the intermedium; ics – intracranial sinus; gst – gastrolith mass; hpx – hooked premaxillae; lea – lateral exposure of angular; pmj – premaxillary, maxillary, and jugal contacts; rbe – reduced basioccipital extracondylar area; rze – position of radial zeugopodial element; scp – scapulae.

associated bromalite comprising belemnites and a high proportion of benthic bivalves and gastropods. This implied a propensity for bottom feeding, a habit advocated elsewhere from bite marks on bivalve shells (Kear and Godthelp, 2008).

Perhaps the most enigmatic Australian plesiosaurian named in recent years is *Opallionectes andamookaensis* Kear, 2006a from the Aptian Bulldog Shale of Andamooka. This taxon was identified from a single skeleton (SAM P24560), but an isolated tooth (privately owned) has since been found in coeval strata at Coober Pedy. Kear (2006a) noted features of the vertebrae, including craniocaudally short/broad cervical centra, the lack of a longitudinal ridge, and platycoelous to shallowly amphocoelous articular faces that might be homologous with those of the Late Cretaceous aristonectine elasmosaurids *Aristonectes* spp. and *K. katiki* (O’Gorman et al., 2013; O’Gorman et al., 2014). The absence of an intercoracoid embayment on the pectoral girdle (see Kear, 2006a, p. 843, fig. 3B), however, clearly differentiates *O. andamookaensis* from remains referred to *Aristonectes* (O’Gorman et al., 2013; Otero et al., 2014). Furthermore, a combination of its prominent caudolateral coracoid cornuae, distally expanded propodials, pre- and post-xial accessory ossicles in the epipodial row, and small labiolingually compressed teeth that lack enamel ridges is alternatively consistent with Late Jurassic – Early Cretaceous cryptocleidids – e.g. *Kimmerosaurus langhami* Brown, 1981, *Tatenectes laramiensis* (Knight, 1900) (O’Keefe and Street, 2009), and *Abyssosaurus nataliae* Berezin, 2011.

Australian polycotyliids are contentious and might incorporate the oldest stratigraphical exemplar of the group: a fragmentary opalized skeleton (AM F6266–F6298) from the Aptian Wallumbilla Formation at White Cliffs. Persson (1960) first mooted the polycotyliid affinity of this specimen, a conclusion supported by Kear (2005a) based on its characteristically slender, homodont teeth and cervical centra that were shorter than high with sharp mid-ventral keels and constricted lateral sides (see O’Keefe, 2004; Druckenmiller and Russell, 2008a; Schmeisser, McKean, 2012). Other features such as laterally flared dorsal apices on the neural spines (see Kear, 2005a, p. 775, fig. 4C) compare well with *Dolichorhynchops herschelensis* Sato, 2005. Craniad swelling of the median ventral edge of the articular facet rim is diagnostic for Polycotyliidae (Sato and Storrs, 2000) but also resembles the prominent ‘lip’ described in the leptocleidid *Hastanectes valdensis* Benson, Ketchum, Naish and Turner, 2013a.

Polycotyliid-like elements have been recovered in the Aptian Bulldog Shale (SAM P36356: Kear, 2006a), middle-late Albian Toolebuc Formation (SAM P41967), latest Albian–Cenomanian Mackunda Formation in Queensland (e.g. AOD F336), and late Cenomanian upper Gearle Siltstone (WAM 14.10.3.1–11). However, the only unequivocally diagnostic skeleton (QM F18041: fig. 3B) is the ‘Richmond pliosaur’ from the Allaru Mudstone of Richmond, Queensland (fig. 2). This sensational specimen represents one of the most complete Gondwanan plesiosaurian fossils yet discovered, and comprises a skull with characteristically elongate maxillary rostrum and symphyseal region of the mandible, incorporating a caudal extension of the splenial to the eighth tooth position. The splenial alternatively projects beyond the 10<sup>th</sup> tooth

position in most Late Cretaceous polycotyliids (Carpenter, 1996; Arkhangelsky et al., 2007). The palate of QM F18041 displays distinctively convex (= “dished” sensu O’Keefe, 2001) lateral palatal pterygoid surfaces bordering the posterior interpterygoid vacuities. Loss of the pineal foramen serves to differentiate QM F18041 from the only other named Early Cretaceous polycotyliid *Edgarosaurus muddi* Druckenmiller, 2002. Conspicuous ornamentation of ridges and grooves along the snout and mandible is further reminiscent of the Patagonian Campanian–Maastrichtian *Sulcusuchus erraini* Gasparini and Spalletti, 1990, and might have housed a dermal sensory system (O’Gorman and Gasparini, 2013; Foffa et al., 2014).

A second osteologically immature polycotyliid skeleton (QM F12719) from the Toolebuc Formation near Hughenden in Queensland (fig. 2) was considered a new leptocleidid by Glen and McHenry (2007) but is morphologically indistinguishable from QM F18041 and thus probably conspecific.

Cruickshank and Long (1997) named the first Australian leptocleidid plesiosaurian *Leptocleidus clemai* Cruickshank and Long, 1997 based on several partial skeletons (WAM 92.8.1, WAM 94.1.6) from the Aptian Birdrong Sandstone of Kalbarri in Western Australia (fig. 2). These were phylogenetically re-evaluated by Kear and Barrett (2011), who failed to resolve *L. clemai* with other *Leptocleidus* spp., and noted that the only discrete character state diagnosing the species – epipodials broader than long – was ubiquitous amongst polycotyliids and other Cretaceous plesiosaurians. Cruickshank and Long (1997) listed a 30% size increase relative to the type species *Leptocleidus superstes* Andrews, 1922 as another specifically differential feature, but failed to offer an explicit case for their generic referral to *Leptocleidus* (Kear and Barrett, 2011). Little else remains to distinguish *Leptocleidus clemai* except perhaps its robust propodials, which have a noticeably sigmoidal profile like polycotyliids (e.g. Albright et al., 2007; O’Keefe, 2008) and *L. superstes* (Kear and Barrett, 2011); although, the articular surface on the humeral head exhibits pronounced lateral flaring unlike the more cylindrical capitulum of *L. superstes* (compare Kear, 2003, p. 294, fig. 6A, B with Kear and Barrett, 2011, p. 673, fig. 4F–I).

Kear (2006b) documented isolated small pliosauroid bones and teeth that were similar to those of leptocleidids but occurred in non-marine strata of the Aptian–Albian Eumeralla Formation from Cape Otway to Inverloch in Victoria, and in the early-middle Albian Griman Creek Formation of Lightning Ridge, New South Wales and Surat in Queensland (fig. 2). New plesiosaurian elements from the Eumeralla Formation were figured by Benson et al. (2013b, p. 3, fig. 2), including NMV P198945, a large broken tooth (45 mm high) missing most of its enamel surface (Benson et al., 2013b, p. 2, fig. 1). Benson et al. (2013b) argued for plesiosaurian affinity based on remnants of three incomplete and irregularly spaced enamel ridges (the remaining intact surface was otherwise smooth), conical tooth shape, and the apparent absence of carinae. While these traits are certainly compatible with plesiosaurians, they are likewise similar to spinosaurid theropods (also recovered from the Eumeralla Formation: Barrett et al., 2011), which can express smooth or fluted enamel, conical tooth form, and reduced carinae (e.g. Dal Sasso et al., 2005; Medeiros, 2006; Richter et al., 2013).

The best-known leptocleidid taxon from Australia is *Umoonasaurus demoscyllus* Kear, Schroeder and Lee, 2006a from the Aptian Bulldog Shale of Coober Pedy. A number of skeletons have been discovered, including multiple small-bodied ‘juveniles’, one of which (SAM P15980; originally identified as cf. *Leptocleidus* sp. by Kear, 2007b) was proportionately scaled to the 2.5 m long holotype (AM F99374) and thereby estimated to be only 700 mm in maximum body length (Kear, 2007b). Another ‘juvenile’ specimen (SAM P33915) was also probably less than 1 m long and includes an in situ gastrolith accumulation, together with complete scapulae that display lateral shelves – a key leptocleidid synapomorphy (fig. 3C). Originally classified with Jurassic rhomaleosaurids (Kear et al., 2006a) or polycotyliids (Druckenmiller and Russell, 2008a), the leptocleidid affinity of *U. demoscyllus* has been iterated by recent phylogenies (Ketchum and Benson, 2010; Benson and Druckenmiller, 2014), but relies upon few states including the presence of a lateral shelf on the scapula (disparately occurring in Jurassic taxa: Sato et al., 2003; Sachs et al., 2014), and a triangular fossa extending from the pineal foramen to the sagittal crest on the dorsal surface of the parietal; evident elsewhere in the disputed leptocleidids *Nichollssaura borealis* (Druckenmiller and Russell, 2008b) and *Brancaasaurus brancai* Wegner, 1914 (Benson et al., 2013a). The skull of *U. demoscyllus* is, however, unique in its development of thin, high crests along the midline of the snout and above the orbits on the frontals (see Kear et al., 2006a, p. 617, fig. 1b). The function of these is unclear but they potentially represent display structures that might have been sexually dimorphic (Kear et al., 2006a).

Kear (2002b) reported on leptocleidid remains from the late Aptian Darwin Formation near Darwin in the Northern Territory (fig. 2). Further assessment of this material has revealed propodials (e.g. NTM P998-6; fig. 3D) and associated vertebrae that are indistinguishable from those of *U. demoscyllus* (see Kear, 2006a, supplemental fig. S7f, g) and might evidence this, or another closely related species inhabiting the Australian continental margin during the Early Cretaceous.

The gigantic pliosauroid *Kronosaurus queenslandicus* Longman, 1924 is the largest and most stratigraphically widespread plesiosaurian taxon thus far documented from Australia. Its conspicuous remains have been recovered from Aptian units throughout the Eromanga Basin, including the Bulldog Shale at Coober Pedy (Kear, 2006a), and the Wallumbilla Formation at both White Cliffs (Kear, 2005a) and near Richmond; this was the source of the famous Harvard University skeleton (MCZ 1285: Romer and Lewis, 1959). The holotype (QM F1609), however, derived from the Albian Toolebuc Formation at Hughenden, with a second flattened skull (QM F2446) that is thought to represent a separate species (Molnar, 1991). In contrast, McHenry (2009) considered all of the Australian *Kronosaurus* remains coherent with a monospecific morphotype, and thus presented a composite reconstruction of the cranium and mandible (see McHenry, 2009, p. 349, fig. 5-35) incorporating parts of a 10 m long skeleton (QM F10113) from the Toolebuc Formation near Hughenden.

Phylogenetic determinations have placed *K. queenslandicus* as a derived member of the Brachaucheninae (Benson and Druckenmiller, 2014), a Cretaceous pliosauroid radiation

notably characterised by loss of the subcentral foramina on the cervical vertebrae. Cranial modelling and inferred gastric residues also suggest that *K. queenslandicus* might have favoured smaller prey particularly marine turtles, elasmosaurid plesiosaurians, and possibly sharks (McHenry, 2009).

### Ichthyosaurians

Australian Cretaceous ichthyosaurian fossils have been intensively studied. Wade (1984) compiled a seminal review, recognizing a single species *Platypterygius australis* (McCoy, 1867a). Subsequent uncertainty over the holotype led to taxonomic conflict (Wade, 1990). However, Zammit (2010) resolved these issues with a reassessment of the original specimens described by McCoy (1869). These included a partial skull (MV P12989: Zammit, 2010, p. 6, fig. 2A), probably associated with the type vertebrae (Wade, 1985), that supported referral to the genus *Platypterygius* (via a reduced extracondylar area on the basioccipital: McGowan and Motani, 2003), and conformed with other exemplars of *P. australis* (which exhibit exclusion of the lacrimal from the external bony nasal aperture and the presence of accessory caudodorsal nasal foramina: Kear, 2005c). Fossils of *P. australis* are otherwise prolific and often excellently preserved, especially in the middle–late Albian Toolebuc Formation and Allaru Mudstone of Queensland. This unprecedented quantity and quality of material has facilitated comprehensive appraisals of craniodental (Kear, 2005c; Maxwell et al., 2011) and postcranial anatomy (Zammit et al., 2010) that are now a comparative standard for Cretaceous ichthyosaurian remains worldwide (e.g. Maxwell and Kear, 2010; Maxwell et al., 2012; Fischer et al., 2014). Moreover, functional analyses and feeding traces have permitted reconstruction of locomotory modes (Zammit et al., 2014), jaw musculature and sense organs (Kear, 2005c), and dietary specialisation towards small-bodied prey including bony fish (Wretman and Kear, 2014) and aquatic amniotes (e.g. hatchling turtles: Kear et al., 2003). Pathological elements have further afforded evocative glimpses into ichthyosaurian disease (dental caries: Kear, 2001b) and intraspecific behavioural interactions (Zammit and Kear, 2011). Exceptionally preserved foetal remains also infer a K-selection reproductive strategy favouring large young (around one meter long at parturition) that were born ‘tail first’ and probably precocial (Kear and Zammit, 2014).

The precise phylogenetic relationships of *P. australis* are ambiguous, but the taxon is undoubtedly an advanced ophthalmosaurian because of the restricted basicoccipital extracondylar area, extensive lateral exposure of the angular, and extra pre-radial zeugopodial element/digit articulating with the humerus (McGowan and Motani, 2003: fig. 3E, F). Kear and Zammit (2014) identified additional ontogenetically stable autapomorphies that were consistently expressed through an *in-utero* to osteologically mature ‘adult’ growth trajectory: premaxillary *processus supranarialis* having minimal contact with the bony nasal aperture; premaxillary *processus subnarialis* of subequal length to the *processus supranarialis* and extending across the external face of the maxilla; a well sutured jugal-maxilla contact; and absence of a squamosal (fig. 3E).

Other Australian *Platypterygius* occurrences are known from the Aptian Bulldog Shale, Wallumbilla Formation, Darwin Formation, and Birdrong Sandstone (Kear, 2002b, 2003, 2005a, 2006a), as well as the late Albian–Cenomanian Alinga Formation and Molecap Greensand of Western Australia (Choo, 1999; Kear 2003). Novel discoveries have extended this range into the mid-late Cenomanian upper-most Gearle Siltstone. This was based on an isolated phalanx (WAM 99.1.4: fig. 3G) from the Murchison River region west of Kalbarri, which is important because it could represent the stratigraphically youngest ichthyosaurian fossil thus far documented from the southern hemisphere (see Sachs and Grant-Mackie, 2003; Zammit, 2012).

### Aquatic squamates

Kear et al. (2005) summarized the Australian marine squamate record noting the presence of various indeterminate mosasaurids. These incorporated an ulna and phalanx (UWA 37092) which Lundelius and Warne (1960, p. 1216) thought similar to either *Platecarpus* Cope, 1869 or *Clidastes* Cope, 1868, but “perhaps closer to *Platecarpus*”. The ulna (fig. 3H) certainly has a compact shaft with shallowly concave edges suggesting an oval antebrachial foramen. However, the distal extremity appears to be offset for contact with the intermedium, which is more like *Clidastes* (Russell, 1967). UWA 37092 derived from the Molecap Greensand near Gingin (fig. 2), a slumped sequence of Cenomanian–Coniacian strata associated with a buried Cretaceous impact crater (Mory et al., 2005). Some mosasaurid dorsal vertebrae have been documented from this unit (WAM 98.7.1–10), and other mosasaurid vertebrae are known from the early Maastrichtian Korojon Calcarenite (UWA 133937), and late Maastrichtian Miria Formation (WAM 91.8.16) of Western Australia (see Kear et al., 2005, p. 309, fig. 2G–O).

Scanlon and Hocknull (2008) mentioned the surprising occurrence of a ‘dolichosaur-like’ presacral vertebra (QM F52673) in the non-marine latest Albian–Turonian Winton Formation at Winton in Queensland (fig. 2). The tapered centrum shape, “moderately prominent” synapophyses, and apparent absence of pachyostosis (evident in various aquatic varanoids: Houssaye et al., 2008) were advocated to support this assignment. The oval outline and cranial inclination of the cotyle (see Scanlon and Hocknull, 2008, p. 133, fig. 1F) are otherwise similar to varanids as well as basal mosasauroids (Carroll and De Braga, 1992; Makádi et al., 2012), yet the badly eroded condyle seems to lack a varanid-like precondylar constriction (Scanlon and Hocknull, 2008). The affinities of QM F52673 are thus unclear and the specimen is probably best interpreted as an indeterminate varanoid.

### Marine Turtles

Marine turtle fossils are frequently discovered in Australia, but are at present stratigraphically restricted to only a few units including the middle–late Albian Toolebuc Formation and Allaru Mudstone (Kear, 2003), together with the late Albian–Cenomanian Mackunda Formation (e.g. AOD F795), and late Maastrichtian Miria Formation (Kear and Siverson,

2010). Molnar (1991, p. 618) reported a possible marine, “or at least aquatic” turtle (listed as a “tortoise” by Molnar, 1991, p. 612) from an unspecified locality northwest of Winton (fig. 2) that was mapped within the non-marine Winton Formation. This specimen (QM F12413) consists of an internal cast of the carapace (Molnar, 1991, p. 690, pl. 1), but seems to show reduced costal plates and fontanelization consistent with Chelonioida (Wood et al., 1996; Lehman and Tomlinson, 2004). All other identifiable Winton Formation turtle remains pertain to chelids (Hocknull et al., 2009). However, the lower-most Albian section of the Winton Formation does produce typically marine vertebrates (e.g. ichthyodectiform teleosts: Berrell et al., 2014), and was deposited by a tidal fluvial system that could have accommodated euryhaline organisms.

Most Australian Cretaceous marine turtles are referred to the cosmopolitan clade Protostegidae, which might represent either a basal chelonioid lineage (Hirayama, 1998; Hooks, 1998; Kear and Lee, 2006; Bardet et al., 2013), or a more archaic radiation of marine cryptodires (Joyce, 2007). Three endemic Australian taxa have been named from the middle–late Albian Toolebuc Formation, and are amongst the oldest protostegids documented worldwide. Owen (1882) described the partial carapace and plastron (AM F67326) of *Notochelys costata* Owen, 1882, from an unknown location on the Thomson River in Queensland (see De Vis, 1911). Lydekker (1889) subsequently replaced the epithet ‘*Notochelys*’ with *Notochelone* Lydekker, 1889 because of synonymy, and De Vis (1911) referred additional elements that Kear (2003) used to compile an emended diagnosis. Kear and Lee (2006) listed the jugal-quadrate contact, extension of the pterygoid onto the articular condyle of the quadrate, and incorporation of the vomer into the upper triturating surface as states distinguishing *N. costata* from the larger-bodied (around 50%) coeval taxon *Bouliachelys suteri* Kear and Lee, 2006. This is known from several spectacular skulls (e.g. SAM P41106: fig. 3I) found near Boulia in Queensland (fig. 2). Kear and Lee (2006) phylogenetically placed both *N. costata* and *B. suteri* as basal protostegids. Parham and Pyenson (2010) further correlated the distinctive hooked premaxillae and poorly developed secondary palate of *B. suteri* with ‘shear’ feeding (as opposed to durophagy), and proposed protostegid convergence upon extant herbivorous cheloniids. Interestingly, Kear (2006c) identified both gastrolites/cololites and coprolites within multiple ‘*Notochelone*-like’ specimens that contained dense accumulations of *Inoceramus* bivalve shell. These were processed orally, implying benthic ‘grazing’ and an invertebrate-based diet in the earliest protostegids (Kear, 2006c).

Despite obvious character state differentiation, Myers (2007) suggested that *N. costata* and *B. suteri* might be synonymous because of proportional similarities in their crania. This warrants further exploration especially relative to their postcranial elements, which now include several articulated skeletons under preparation and study (e.g. SAM P40525: fig 3J).

The holotype (QM F14550: Kear, 2006d, p. 781, fig. 2A–R) and only specimen of the colossal (around four meters in length) Toolebuc Formation protostegid *Cratochelone berneyi* Longman, 1915 discovered near Hughenden, was re-evaluated

by Kear (2006d), and found to possess highly vascular limb bone surfaces compatible with the advanced protostegids *Archelon* Wieland, 1896 and *Protostega* Cope, 1872. Comparable microstructures occur in Australia's only Late Cretaceous chelonoid fossil, a dermochelyoid scapula (WAM 03.3.37: Kear and Siverson, 2010, p. 4, fig. 2E) from the late Maastrichtian Miria Formation southwest of Exmouth in Western Australia (fig. 2), and suggest that complex metabolic physiology repeatedly coupled with body size (see Rhodin, 1985) and perhaps pelagic lifestyles throughout marine turtle evolution.

### Conclusions and Future Research

Australian Cretaceous marine amniote fossils represent a significant resource for exploring the enigmatic vertebrate biodiversity of Gondwana. The astounding taxonomic richness, preservation quality, and sheer productivity of the documented source units, particularly those from the Aptian–Albian strata of the Eromanga Basin in Queensland and South Australia (Kear, 2003), mark them as some of the most important (although as yet under-popularized) Mesozoic marine vertebrate *lagerstätten* known worldwide. Their association with Early Cretaceous freezing high latitude palaeoenvironments is also unique, and has been linked with climate change coincident dispersals and cladogenic events that shaped later Cretaceous faunas (Kear et al., 2006b). Clearly this offers an exciting focus for on-going research, especially given the recent advances in quantitative modeling (e.g. Benson et al., 2010a), geochemical analyses (e.g. Bernard et al., 2010), bone microstructure visualization (e.g. Houssaye, 2013), and soft tissue reconstruction (e.g. Lindgren et al., 2014) that are changing the perspectives on Mesozoic marine amniote evolution. Nevertheless, such innovative approaches would not be possible without the pioneering studies undertaken over the last decade. These have provided not only a fundamental systematic framework but also posed an intriguing experimental question that can be used to frame future investigations – did Australia's Cretaceous marine amniotes experience high-latitude thermal isolation and low-temperature adaptation concomitant with the coeval continental record of inimitable relics (e.g. Thulborn and Turner, 2003; Smith and Kear, 2013), regional immigrants (e.g. Rich and Vickers-Rich, 2003; Smith et al., 2008; Hocknull et al., 2009; Rich et al., 2009; Agnolin et al., 2010; Benson et al., 2010b; Kellner et al., 2010; Barrett et al., 2011; Benson et al., 2012; Fitzgerald et al., 2012; Poropat et al., 2014; Poropat et al., 2015; Rich et al., 2014), and endemic progenitors (e.g. Pridmore et al., 2005; Salisbury et al., 2006; Rowe et al., 2008; Smith, 2010) whose descendants are still extant on the Australian landmass today?

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