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An archaic crested plesiosaur in opal from the Lower Cretaceous high-latitude deposits of Australia

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Umoonasaurus demoscyllus gen. et sp. nov. is a new small-bodied (approx. 2.5 m) pliosauroid plesiosaur from the Lower Cretaceous (Aptian–Albian) of southern Australia. It is represented by several partial skeletons (one with a near complete skull is the most complete opalized vertebrate fossil yet known), and is unique in having large crests on the skull midline and above the orbits. *Umoonasaurus* is surprisingly archaic despite its relatively late age (approx. 115 Myr ago)—being simultaneously the most basal (primitive) and last surviving rhomaleosaurid. Notably, it lacks the ‘pliosauro-morph’ features (large head, short neck, gigantism) typically characterizing many more derived Jurassic rhomaleosaurids; thus, reinforcing the suspected convergent evolution of the ‘pliosauro-morph’ hypercarnivore body plan. *Umoonasaurus* inhabited an Early Cretaceous high-latitude (approx. 70° S) inland seaway subject to seasonally near-freezing climatic conditions. This extreme environment supported a diverse range of plesiosaur taxa, suggesting that these marine reptiles might have possessed adaptations (e.g. heightened metabolic levels) to cope with cold-water temperatures. Indeed, survival of ancient endemic lineages such as *Umoonasaurus* is a common phenomenon in Australian Cretaceous vertebrate assemblages and might have been facilitated by isolation in low-temperature high-latitude regions.

Keywords: plesiosaur; archaic; rhomaleosaurid; cranial crests; Early Cretaceous; high latitude

1. INTRODUCTION

Plesiosaurs (Plesiosauria) are an extinct group of Mesozoic marine reptiles adapted for submarine locomotion using four paddle-like limbs. Current studies recognize two principal lineages (*sensu* O’Keefe 2001): Plesiosauroidea, characterized by small-headed, long-necked forms (‘pliosauro-morphs’; O’Keefe 2002); and Pliosauroidea, typified by shorter-necked, larger-headed taxa (‘pliosauro-morphs’; O’Keefe 2002). Much of the documented

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fossil history of plesiosaurs comes from Jurassic and Cretaceous rocks in the Northern Hemisphere (Brown 1981; Bakker 1993); in contrast, plesiosaur records from the Southern Hemisphere are comparatively sparse (reviewed by Kear 2005). Recent work in the Lower Cretaceous (Aptian–Albian, approx. 115 Myr ago) deposits of southern Australia has uncovered evidence of a diverse assemblage (see Kear (2003) for summary) inhabiting an unusual Early Cretaceous near-freezing sub-polar zone (approx. 70° S; Frakes & Francis 1988). This study reports on an unexpected new addition to this high-latitude, cold-water fauna; a primitive, crested rhomaleosaurid (Pliosauroidea) from the opal mines of Coober Pedy (and contemporaneous strata) in northern South Australia.

2. SYSTEMATIC PALAEONTOLOGY

Diapsida Osborn 1903; Sauropterygia Owen 1860; Plesiosauria de Blainville 1835; Pliosauroidea Welles 1943 (*sensu* O’Keefe 2001); Rhomaleosauridae Nopsca 1928 (*sensu* O’Keefe 2001).

Umoonasaurus demoscyllus gen. et sp. nov.

(a) Etymology

Umoona (Antakirinja) indigenous name for the Coober Pedy area, and *sauros* (Greek), lizard; *demos* (Greek), of the people, and *scyll* (Greek), a sea monster of classical mythology—referring to the type locality and purchase of the holotype specimen by public donations.

(b) Holotype, locality and horizon

Holotype: Australian Museum F99374, opalized skeleton including skull from the Zorba Extension Opal Field, west of Coober Pedy. Referred specimens: South Australian Museum P23841 (opalized) from the Andamooka opal fields; P31050 from the Curdimurka area, Lake Eyre South; P410550 (juvenile) from the Neales River region, Oodnadatta. Stratigraphy: All localities are from the Bulldog Shale (Marree Subgroup) of northern South Australia. This unit is correlated with the Lower Aptian–Lower Albian, *Cyclosporites hughesii*, *Crybelosporites striatus* zones/*Odontochitina operculata*, *Diconodinium davidii* and *Muderongia tetracantha* zones (Alexander & Sansome 1996).

(c) Diagnosis

Identical for genus and species due to monotypy. *Umoonasaurus* possesses the unique-derived features (within Plesiosauria) of thin, arching crests on the midline of the snout (an elaboration of the midline ridge) and above the orbits, a large triangular pineal opening bordered by high fluted, crest-like margins. It further differs from all other plesiosaurs in displaying a distinctive mosaic of primitive and derived features (see character matrix in electronic supplementary material).

3. DESCRIPTION

Remains attributable to *Umoonasaurus* include three partial skeletons from adult individuals (*sensu* Brown 1981) of around 2.5 m maximum length (based on AM F99374). One additional osteologically immature specimen (SAM P410550) probably represents a

juvenile less than 1 m long. The holotype, dubbed 'Eric' in the popular press (see Cruickshank *et al.* 1999), is the most complete opalized vertebrate fossil yet known and is preserved in three dimensions with minimal distortion.

The skull of *Umoonasaurus* (figure 1) is small (222 mm maximum length, 130 mm maximum width) and triangular in outline with a short rostrum (narrow but lacking a distinct constriction at the premaxillary-maxillary suture). There is a high, blade-like crest extending along the skull midline (premaxilla, parietal) from snout to past the pineal foramen; this is highest around the level of the external nares. Another pair of strongly arched crests is also present on the frontals (and possibly postfrontals), above the orbits. These structures have not been reported in other plesiosaurs; although premaxillary midline ridges have been described in some taxa (*Rhomaleosaurus*, *Leptocleidus* and elasmosaurids; see Taylor 1992; Cruickshank 1997; Kear 2005), they are not as high or narrow as in *Umoonasaurus*. Function of the cranial crests in *Umoonasaurus* remains speculative; however, they appear too fragile for use in skull reinforcement, defence or male combat (see Molnar 2005). Their heavily sculpted surfaces suggest a horny covering in life; this would have substantially increased the crest height and perhaps (together with colour) made them effective display structures for species recognition and/or mating behaviours.

The snout of *Umoonasaurus* bears a premaxillary rosette with sockets for five enlarged procumbent fangs. There are at least 10 tooth sockets on the maxillae, with the 4th–6th housing additional large caniniform fangs. The remaining teeth are small and gracile (10–20 mm in crown height) with ornamentation (consisting of coarse, widely spaced striations) restricted to the lingual surface (see electronic supplementary material for figures). The small bony nasal openings are situated close to the anterior orbital margins. The orbits themselves are large with raised anterior borders. The postorbital bars are missing in the holotype; however, the temporal fenestrae appear to have occupied around one-third of the total skull length.

The anterior skull roof (formed by the parietals) is lanceolate in outline with a large, triangular pineal foramen. Unusually, the edges of the pineal foramen are raised, forming high fluted crests (a unique-derived feature of *Umoonasaurus*); these are continuous anteriorly and posteriorly with the midline crest. The palate has a large anterior interpterygoid vacuity (separated from the posterior interpterygoid vacuity by a closed midline suture) and vomers that do not extend far posteriorly beyond the internal nares (see O'Keefe (2001) for distribution of palate characters in other pliosauroids). The parasphenoid is keeled along its entire length and subdivides the narrow posterior interpterygoid vacuity. The adjacent postero-ventral pterygoid surfaces are dished (concave in ventral view); this is an unexpected feature traditionally regarded as a synapomorphy for Polycotylidae (Plesiosauroidea) (O'Keefe 2004). The posterior pterygoid edges bear squared lappets that underlie the quadrate pterygoid flanges. Notable features of the

basicranium include gracile paroccipital processes, robust basioccipital tubera, and exposure of the basioccipital posterior to the posterior pterygoid suture.

The postcranial skeleton of *Umoonasaurus* (see electronic supplementary material for figures) is rather generalized, but includes some novel and/or derived traits (shared with various other plesiosaurs) such as cervical centra with length < height, laterally compressed blade-like neural spines, cervical zygapophyses that are subequal to the centrum in width, single-headed ribs, a 'pygostyle-like' structure (formed from at least five fused caudal vertebrae) at the end of the tail, and epipodials that are broader than long.

4. PHYLOGENY AND EVOLUTION

Phylogenetic analysis using the most comprehensive published phylogenetic dataset of Plesiosauroidea (O'Keefe 2004) places *Umoonasaurus* as the most basal rhomaleosaurid pliosauroid (figure 2). Rhomaleosaurid affinities are supported by several strong synapomorphies (see matrix in electronic supplementary material; *subscript numbering* refers to character numbers in this matrix; character list follows O'Keefe (2004)): squared pterygoid lappets₅₉, presence of premaxillary fangs₁₀₁, cervical centra with length < height₁₁₂, cervical zygapophyses subequal to centrum in width₁₂₀. *Umoonasaurus*, however, lacks key synapomorphies characterizing all other more advanced rhomaleosaurids (grooves leading into external naris₃₇, robust paroccipital process₄₆, basioccipital covered posterior to pterygoid suture₆₄, robust teeth with large roots and wear₁₀₃), making it the most basal form. It also possesses a unique combination of primitive and derived states variably developed in other plesiosaurs (small skull₁, short rostrum₈, unconstricted snout₉, dished pterygoids₆₇, caniniform maxillary teeth₁₀₂, tooth ornament restricted to lingual surface₁₀₅, single-headed ribs₁₁₇, laterally compressed neural spines₁₃₀, epipodials broader than long₁₆₁). Rhomaleosaurids are morphologically conservative; thus, relationships between more advanced taxa (*Rhomaleosaurus*, *Macroplata*, *Simolestes* and *Leptocleidus*) are weakly resolved. Notably, *Umoonasaurus* fails to group with *Leptocleidus* (the taxon to which it has been previously attributed; Kear 2003). However, bootstrap frequencies are relatively weak due to missing data, and constraining these two taxa to form a clade does not result in a significantly worse tree (best constrained trees are only two steps longer, non-parametric test in PAUP $p > 0.40$; Swofford 2002).

Derived Jurassic rhomaleosaurids possess 'pliosauromorph' features (large heads, robust teeth, short necks and gigantism) hypothesized to be convergent with those in pliosaurids and polycotylids (the latter now removed to Plesiosauroidea; O'Keefe 2004). The absence of these traits in the most basal rhomaleosaurid (*Umoonasaurus*) reinforces this view, suggesting not only a preference for small-bodied prey (evidenced by preserved gut contents consisting of small teleosts; see electronic supplementary material), but also that the 'pliosauromorph' hypercarnivore body plan evolved

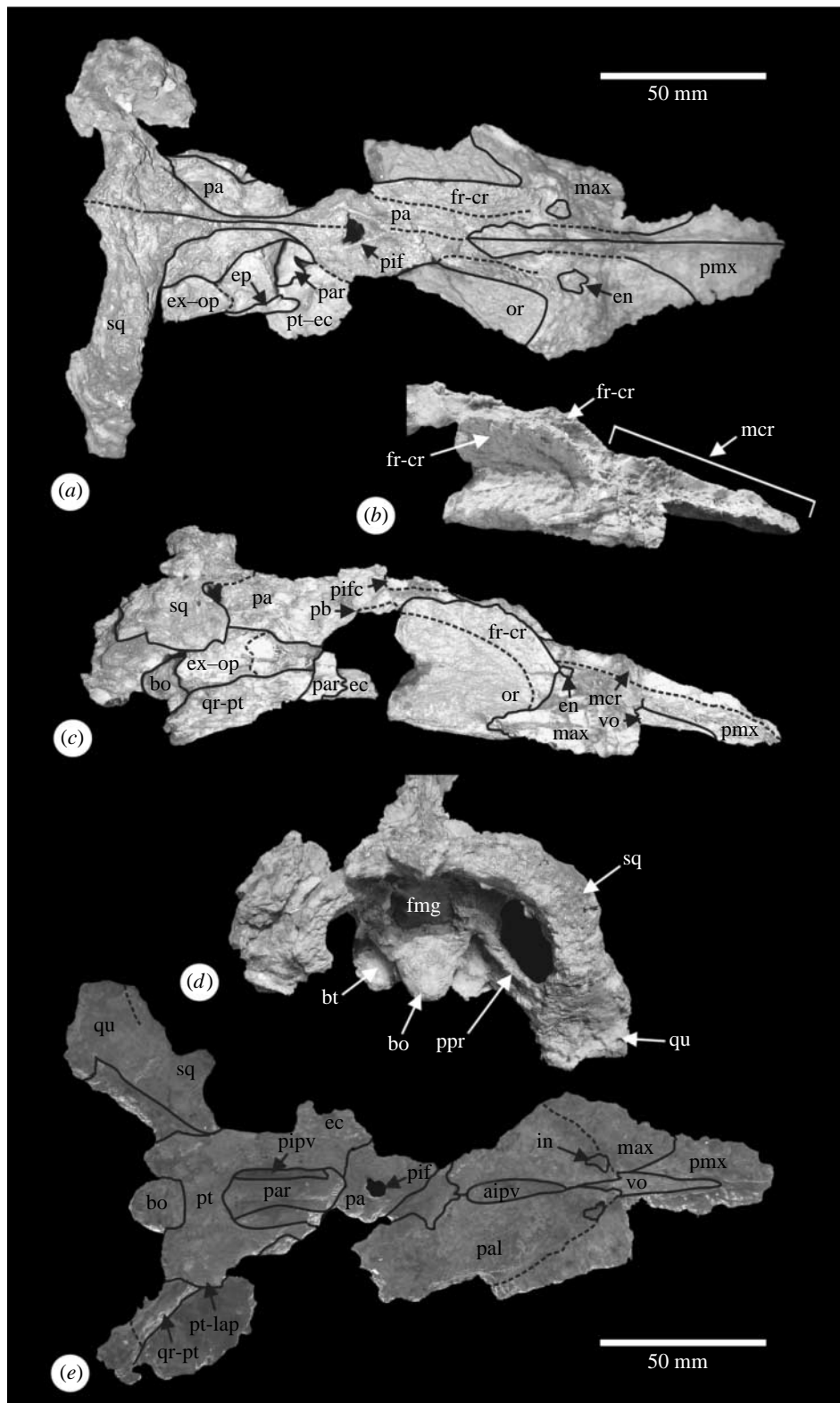


Figure 1. *Umoonasaurus demoscyllus* (AM F99374) skull in (a) dorsal, (b) anterolateral snout region showing crests, (c) lateral, (d) posterior and (e) palatal views (palate image is from a cast, original specimen is fixed to a display base and thus inaccessible). Abbreviations: aipv, anterior interpterygoid vacuity; bo, basioccipital; bt, basioccipital tuber; ec, ectopterygoid; en, external naris; ep, epipterygoid; ex-op, exoccipital-opisthotic; fmg, foramen magnum; fr-cr, frontal crest; in, internal naris; max, maxilla; mcr, midline crest (premaxilla); or, orbit; pa, parietal; pal, palatine; par, parasphenoid; pb, postorbital bar base; pif, pineal foramen; pifc, pineal foramen crest; pmx, premaxilla; ppr, paroccipital process; pt, pterygoid; pt-ec, pterygoid-ectopterygoid complex; pt-lap, pterygoid lappet; qr-pt, quadrate ramus of pterygoid; qu, quadrate; sq, squamosal; vo, vomer.

more than once even within Pliosauroida (O'Keefe 2002), in both pliosaurids and rhomaleosaurids.

Umoonasaurus lived (together with ichthyosaurs and a range of other plesiosaur taxa; Kear 2003) in

an extreme Early Cretaceous high-latitude palaeo-environment subject to seasonally near-freezing conditions (evidenced by glacial erratics, glendonites and densely growth-banded wood; Frakes & Francis

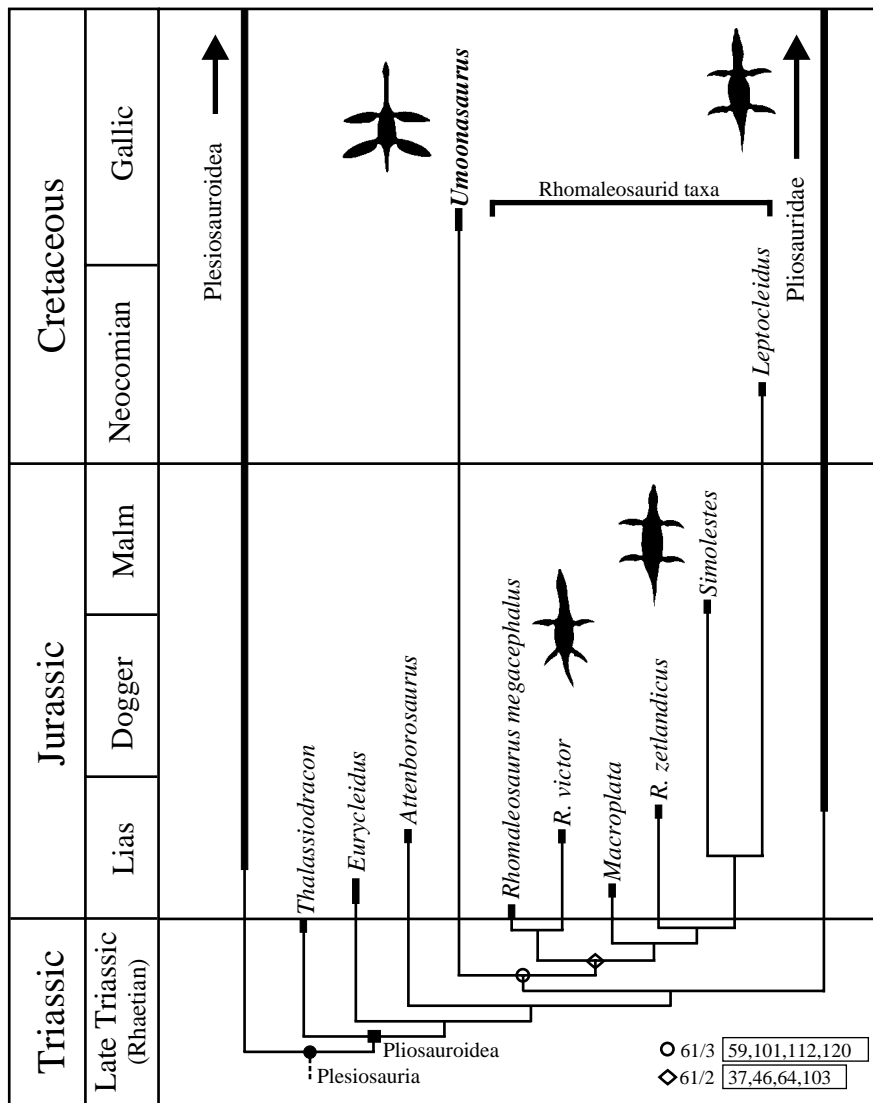


Figure 2. Phylogeny and stratigraphic record of (filled circle) Plesiosauria illustrating relationships among (filled square) plesiosauroidea including *Umoonasaurus* (see electronic supplementary material). *Umoonasaurus* and taxa exhibiting the 'plesiosauroid' body plan (*Rhomaleosaurus*, *Simolestes*, Plesiosauridae) are indicated by icons. Boxed numbers for selected nodes denoting (open circle) Rhomaleosauridae and (open diamond) advanced rhomaleosaurid taxa refer to synapomorphies discussed in the main text. Other numbers refer to bootstrap/Bremer support.

1988; De Lurio & Frakes 1999). This contrasts markedly with climate regimes typically tolerated by modern aquatic reptiles but suggests that some Mesozoic forms were able to cope with low-average water temperatures, perhaps via specialized physiological mechanisms (e.g. endothermy or inertial homeothermy) and/or behavioural strategies (e.g. seasonal migration). *Umoonasaurus* is also one of the several plesiosaur taxa apparently endemic to the high-latitude deposits (Bulldog Shale) of southern Australia (Kear 2003). Despite being the last surviving rhomaleosaurid, it is also the most basal form. This implies a long period of biogeographic isolation and is consistent with its unusual morphology. Indeed, such unique endemics are common in Australian Cretaceous marine and terrestrial assemblages (Rich *et al.* 1988; Thulborn & Turner 2003), suggesting that isolating barriers such as climate might have been shaping the evolution of a distinctive Australian Cretaceous biota long before actual physical separation from Antarctica occurred in the Early Tertiary.

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