

# MARINE REPTILES FROM THE LOWER CRETACEOUS OF SOUTH AUSTRALIA: ELEMENTS OF A HIGH-LATITUDE COLD-WATER ASSEMBLAGE

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**Abstract:** The Lower Cretaceous rocks of South Australia have yielded a diverse marine reptile assemblage of up to five families of plesiosaur (including a new cryptoclidid or cimoliasaurid, indeterminate elasmosaurids, a possible polycotyloid, rhomaleosaurids, and pliosaurid) and one family of ichthyosaur (ophthalmosaurid). Other common associated vertebrates include chimaerids and osteichthyans. Sharks, dipnoans and dinosaurs are uncommon and marine turtles are notably absent. The main fossil-producing strata belong to the Lower Aptian–Lower Albian Bulldog Shale although the Upper Albian Oodnadatta Formation has produced isolated elements. Both these units comprise finely laminated shaly mudstones and claystones deposited in a transgressive shallow coastal, epicontinental marine environment. Estimates of palaeolatitude place South Australia between 60° and 70°S, in the late Early Cretaceous. Sedimentary structures (including limestones boulders and glendonites), fossils, isotope data and climatic modelling also indicate that seasonally cool–cold conditions (possibly with winter freezing) prevailed during deposition of the Bulldog Shale. This con-

trasts markedly with climate regimes typically tolerated by modern aquatic reptiles but suggests that some of the South Australian Mesozoic taxa may have possessed adaptations (including elevated metabolic levels and/or annual migration) to cope with low temperatures. A high proportion of juvenile plesiosaur remains in the Bulldog Shale might also indicate that nutrient-rich cold-water coastal habitats functioned as both ‘safe calving grounds’ and refuges for young animals prior to their entering the open sea as adults. The occurrence of plesiosaurs and ichthyosaurs in the high-latitude Lower Cretaceous of southern Australia, along with plesiosaurs and mosasaurs in the Upper Cretaceous of South America, Antarctica, New Zealand and the Chatham Islands, demonstrates that Mesozoic marine reptiles utilized southern high-latitude environments over a considerable period of time, and that these records do not represent casual occupation by isolated taxa.

**Key words:** Plesiosauria, Ichthyosauria, South Australia, Lower Cretaceous, high latitudes, cold climates.

MESOZOIC marine reptiles are poorly known in Australia, hence the recovery of a diverse Early Cretaceous assemblage from several localities in central and northern South Australia (Text-fig. 1A–B) adds significantly to the understanding of fossil marine reptiles from the continent. Even more important is the fact that the South Australian fauna lived as far south as 60–70°S (Embleton and McElhinny 1982; Embleton 1984; Idnurm 1985), and endured environments with highly seasonal, cool to cold conditions (Stevens and Clayton 1971; Frakes and Francis 1988, 1990; Sheard 1990; Dettmann *et al.* 1992; Selwood *et al.* 1994; Frakes *et al.* 1995; De Lurio and Frakes 1999; Henderson *et al.* 2000). The fossils include ichthyosaurs and a diverse range of plesiosaurs. These are represented mainly by cosmopolitan genera (*Platypterygius*, *Leptocleidus*, *Kronosaurus*), although the presence of some poten-

tially endemic forms (such as a new cryptoclidid/cimoliasaurid *sensu* O’Keefe 2001) suggests that isolating barriers (perhaps including climate) were in effect.

Remains have been recovered from two principal units, the Lower Aptian–Lower Albian Bulldog Shale and mid–Upper Albian Oodnadatta Formation. These are separated by poorly fossiliferous strata of the Lower–mid Albian Coorikiana Sandstone and together comprise the Marree Subgroup, an epicontinental marine shaly interval that crops out extensively in the south-western Eromanga Basin. Marine reptile specimens are most common in the Bulldog Shale, and occur as articulated, partly disarticulated and isolated fossils. Material from the Oodnadatta Formation is sporadic and known only from a few isolated vertebrae. Comparisons with the taphonomic models of Martill (1985, 1987) suggest that remains typically

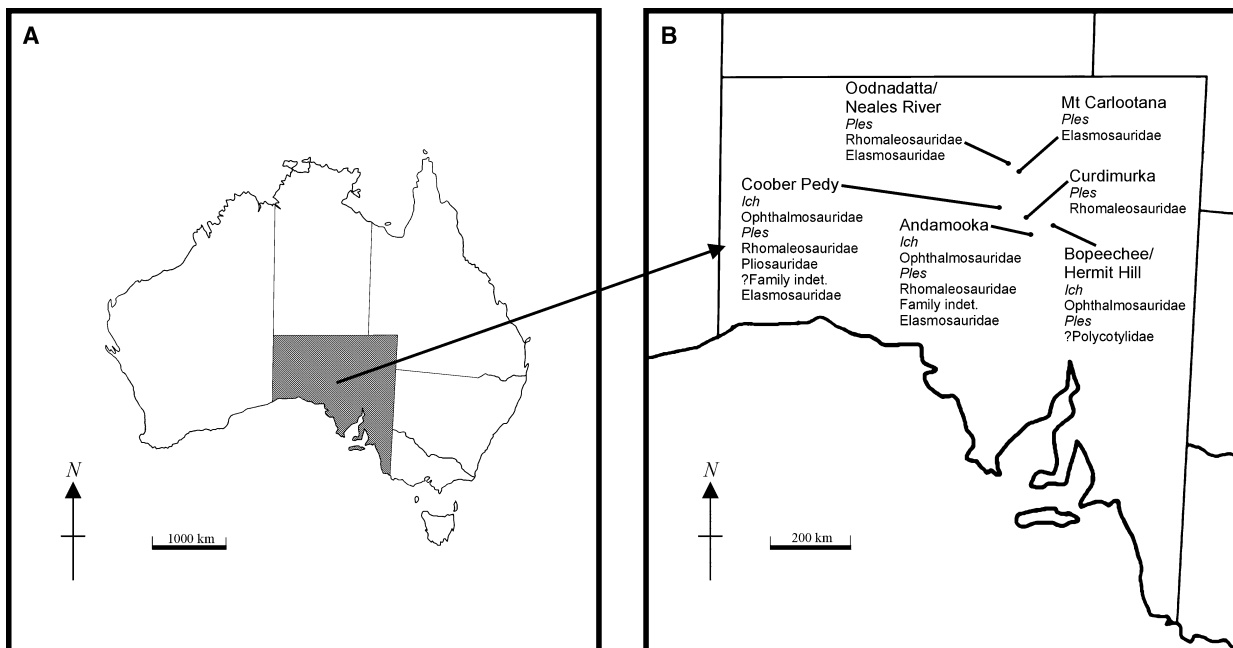
accumulated in oxygenated shallow-water conditions, in which carcass remnants came to rest on the sea floor following a period of post-mortem drifting, with the body distended by decomposition gasses.

Invertebrate and plant fossils occur in association with marine reptiles in both the Bulldog Shale and Oodnadatta Formation. Ludbrook (1966) described a diverse range of microfossils, bivalve molluscs, gastropods, ammonites and belemnites. The presence of large quantities of wood is consistent with an inferred proximity to land. The remains of vertebrates are common in the few localities that have been regularly sampled. Osteichthyan fish, chimaerids and a single lungfish tooth plate have been recorded from the opal-bearing deposits of Coober Pedy (Alley and Pledge 2000). Probable teleost fish and chimaerid elements have also been recovered from localities around Lake Eyre and the Neales River (Ludbrook 1966). Unusually, shark remains are unknown from the Bulldog Shale and Oodnadatta Formation although they do occur in the Coorikiana Sandstone. Rare dinosaur bones, representing both theropods and ornithopods, have been recovered from the opal beds at Andamooka and Coober Pedy (Molnar 1980; Molnar and Pledge 1980; Alley and Pledge 2000).

Sedimentological studies of the Bulldog Shale have identified the presence of often large (up to 3 m across) quartzite/porphyritic erratic boulders and glendonites (crystal aggregates pseudomorphing the calcium carbonate hexahydrate mineral ikaite). These are reliable indicators

of palaeoclimate and suggest predominantly cool to very cold conditions, possibly with winter freezing and ice build-up along coastal margins (Frakes and Francis 1988; Sheard 1990; Frakes *et al.* 1995; De Lurio and Frakes 1999). Estimates of Cretaceous sea-level isotopic palaeotemperatures for the Australian region also indicate cool to cold conditions. For example, Stevens and Clayton (1971) and Dettmann *et al.* (1992) recorded averages as low as 12.2°C in the south-west Eromanga Basin. Pirrie *et al.* (1995), however, indicated colder palaeotemperatures of around 10°C based on Lower Albian belemnites from the Carnarvon Basin, Western Australia (which lay at approximately 45°S palaeolatitude at that time). This observation was also discussed by Henderson *et al.* (2000), who remarked that although Cretaceous palaeotemperatures at 60–80°S would have been more equitable than they are today, strong seasonality and winter freezing probably characterised inboard coastal margins of the Australian epicontinental seaway at least during the Late Neocomian–Early Albian.

To date, little documented research has been undertaken on marine reptile fossils from South Australia. Howchin (1928) gave one of the earliest reports, briefly describing a series of elasmosaur vertebrae (SAM P6181) from an unspecified locality near the Neales River. Persson (1960) later re-examined this material, assigning it to the dubious taxon '*Woolungasaurus*' (considered a *nomen dubium* by Welles 1962; Kear 2003a). Freytag (1964) and Ludbrook (1966) attributed other remains to '*Woolunga-*



**TEXT-FIG. 1.** Map of South Australia showing localities that have produced Cretaceous marine reptile fossils. Abbreviations: *Ich*, Ichthyosauria; *Ples*, Plesiosauria.

*saurus*', including several isolated vertebrae from the Oodnadatta Formation near Oodnadatta and Mt Carlostana. Ludbrook (1966) also figured several small ichthyosaur vertebrae (SAM P39619) from Bulldog Shale sediments at Andamooka. Pledge (1980) illustrated plesiosaur material from this same locality, including a near-complete elasmosaurid hind limb (part of a partial skeleton, SMM P71.1.1, attributed to '*Woolungasaurus*') and a small pliosauroid humerus (SAM P15980). In addition, Pledge (1980) recorded an isolated large pliosaurid tooth (SAM P22525) from the Bulldog Shale at Coober Pedy, and a fragmentary ichthyosaur snout (SAM P31049) from equivalent deposits at Bopeechee Siding.

More recent South Australian finds include a purported elasmosaurid (SAM P24560) from Andamooka (a popular account of which was given by Rich and Rich 1985), a near-complete skeleton (AM F99374) attributable to the rhomaleosaurid *Leptocleidus* from Coober Pedy (Ritchie 1991; Cruickshank and Long 1997; Long 1998; Cruickshank *et al.* 1999; Alley and Pledge 2000; Kear 2003a), and possible cryptoclidid or cimoliasaurid (*sensu* O'Keefe 2001) material from the opal-bearing deposits of Coober Pedy and Andamooka, respectively (Cruickshank *et al.* 1999; Kear 2002a, 2003a).

This paper provides (1) a description of a new cryptoclidid or cimoliasaurid (*sensu* O'Keefe 2001) plesiosaur from the Bulldog Shale, and (2) a review of marine reptiles from the Cretaceous deposits of South Australia with preliminary interpretations of taxonomy and palaeoecology.

## GEOLOGICAL SETTING

The stratigraphy and geology of most marine reptile fossil sites in South Australia are poorly known. This is largely because of limited locality data, a result of many specimens being discovered serendipitously and extracted during opal mining. Accounts of regional geology (including maps) and depositional environments have been given by Johns (1968), Robertson and Scott (1990), Krieg and Rogers (1995) and Alexander and Sansome (1996).

All of the currently known South Australian marine reptile fossils are derived from the Marree Subgroup. This unit comprises the basalmost fossiliferous Bulldog Shale, a finely laminated series of mudstones and claystones (commonly pyritic and carbonaceous) deposited under transgressive coastal, shallow marine conditions (Ludbrook 1966; Moore and Pitt 1985; Krieg and Rogers 1995; Alexander and Sansome 1996). The presence of dark organic-rich shale layers and low microplankton diversity indicate dysaerobic bottom-waters (Krieg and Rogers 1995). Regular coquinoid layers (probably representing swell lags), isolated sandy deposits (Krieg and Rogers 1995) and disarticulated bones also suggest deposition

below normal wave base but probably within storm wave base. This differs from the fine-grained feldspathic and glauconitic proximal marine sandstones of the overlying Coorikiana Sandstone, which shows large-scale low-angle cross-bedding, ripple marks, and thin conglomerate layers interfingering with shoreface sands (interpreted as gravel, bars, beaches and river outlet channel deposits), consistent with deposition during regressive phases of the epicontinental seaway. The uppermost Oodnadatta Formation, which conformably overlies the Coorikiana Sandstone and represents the youngest unit in the Marree Subgroup, preserves a similar lithology to the Bulldog Shale (including finely laminated claystones and siltstones), and represents a secondary transgressive marine incursion.

Characteristically, some horizons of the Bulldog Shale are severely leached and bleached white or varicoloured by weathering. This is best seen in the areas of Andamooka and Coober Pedy, where bleaching may extend to a depth of around 40–50 m (Robertson and Scott 1990) and incorporate extensive deposits of opal (hydrated silica,  $\text{SiO}_2 \cdot n\text{H}_2\text{O}$ ). The opal at Andamooka and Coober Pedy commonly occurs along cracks, faults or within cavities left by fossil remains. It may also on occasion directly replace fossilized organic remnants (probably secondarily), as evidenced by the frequent preservation of internal and soft tissue structures. The process of opal formation is poorly understood, although it may be linked here to cyclical fluctuations in regional water tables (prompting dissolution of opal from silica-rich ground water) during the middle–late Tertiary (Robertson and Scott 1990).

Where bleaching is absent, the Bulldog Shale is dominated by organic-rich shaly horizons containing widespread gypsum and fossiliferous carbonate limestone concretions. These also occur in the Oodnadatta Formation and are typically elliptical in shape and up to 3 m in diameter. In the Bulldog Shale, the concretions are distinctively dark grey to khaki green colour and occasionally occur in association with limestones boulders and glendonites (Frakes and Francis 1988, 1990; Sheard 1990; Frakes *et al.* 1995; De Lurio and Frakes 1999). These palaeoclimatic indicators do not occur in overlying sediments, and tend to characterise mainly the lower (Aptian) depositional stages of the Bulldog Shale (Alley and Pledge 2000).

Rich macroinvertebrate (Ludbrook 1966; Johns 1968; Day 1969) and palynomorph (Moore and Pitt 1985; Moore *et al.* 1986; Krieg and Rodgers 1995; Alexander and Sansome 1996) assemblages have been used to determine the age of the Bulldog Shale as Early Aptian–Early Albian. Correlations based on the Australian Cretaceous palynological zonation of Helby *et al.* (1987) place the unit within the *Cyclosporites hughesii* and *Crybelosporites striatus* spore-pollen zones, and *Odontochitina operculata*,

*Diconodinium davidii* and *Muderongia tetracantha* dinoflagellate zones. Because of severe weathering, most microfossil remains have been leached from the opal-bearing strata at Coober Pedy and Andamooka. Consequently, an accurate palynomorph zonation cannot be established for deposits at these localities. However, a predominantly Aptian age can be suggested on the basis of key macroinvertebrate index taxa such as the bivalve molluscs *Maccoyella*, *Cyrenopsis*, the gastropod *Euspira* and the belemnite *Peratobelus* (Ludbrook 1966; Johns 1968; Day 1969; Henderson *et al.* 2000). Age ranges for the overlying Coorikiana Sandstone and Oodnadatta Formation can be derived from their palynomorph assemblages, the Coorikiana Sandstone correlating with the middle Albian *Coptospora paradoxa* spore-pollen Zone and *M. tetracantha* and *Canninginopsis denticulata* dinoflagellate zones (Krieg and Rodgers 1995), and Oodnadatta Formation with the middle–Late Albian *C. paradoxa* and *Phimnopollenites pannosus* spore-pollen zones and *Pseudoceratum ludbrookiae* and *C. denticulata* dinoflagellate zones. The Oodnadatta Formation also preserves a distinctive Albian macroinvertebrate fauna including the ammonites *Myloceras* and *Labeceras*, and belemnite *Dimitobelus* (Ludbrook 1966; Day 1969; Henderson *et al.* 2000).

## METHODS AND TERMINOLOGY

Lithostratigraphic nomenclature for South Australian Lower Cretaceous deposits follows Wopfner *et al.* (1970). Plesiosaur systematic terminology follows O’Keefe (2001, 2004) except in the ranking of Sauropterygia and Plesiosauria, both of which follow the more conventional system of Carroll (1988), Benton (1997) and Rieppel (2000). Data for comparative analysis of marine reptile assemblages from the Bulldog Shale and Toolebuc Formation, Queensland, are derived from examination of museum collections (Australian Museum, Sydney; Queensland Museum, Brisbane; National Museum Victoria, Melbourne; South Australian Museum, Adelaide) and literature surveys. Methods for analysis follow Nicholls and Russell (1990), who acknowledged the influence of preservational and collecting biases when using specimen counts from museum collections (this generally produces underestimates of relative abundance for common forms and overestimates for the relative abundance of rarer taxa; see Nicholls and Russell 1990, p. 152 for discussion). All measurements were taken using digital callipers and are in millimetres (mm).

*Institutional abbreviations.* AM, Australian Museum, Sydney; SAM, South Australian Museum, Adelaide; SMM, Science Museum Minnesota, Saint Paul.

## SYSTEMATIC PALAEOLOGY

Subclass DIAPSIDA Osborn, 1903  
 Superorder SAUROPTERYGIA Owen, 1860  
 Order PLESIOSAURIA de Blainville, 1835  
 Superfamily PLESIOSAUROIDEA Welles, 1943  
 Family indet.

Genus OPALLIONECTES gen. nov.

*Derivation of name.* Greek, combination of *opallios* (opal) and *nektes* (swimmer), alluding to the holotype specimen’s discovery in an opal mine and replacement of the fossil bone by opal.

*Type and only known species.* *Opallionectes andamookaensis* sp. nov.

*Diagnosis.* As for species.

*Opallionectes andamookaensis* gen. et sp. nov.

Text-figures 2–3, Tables 1–2

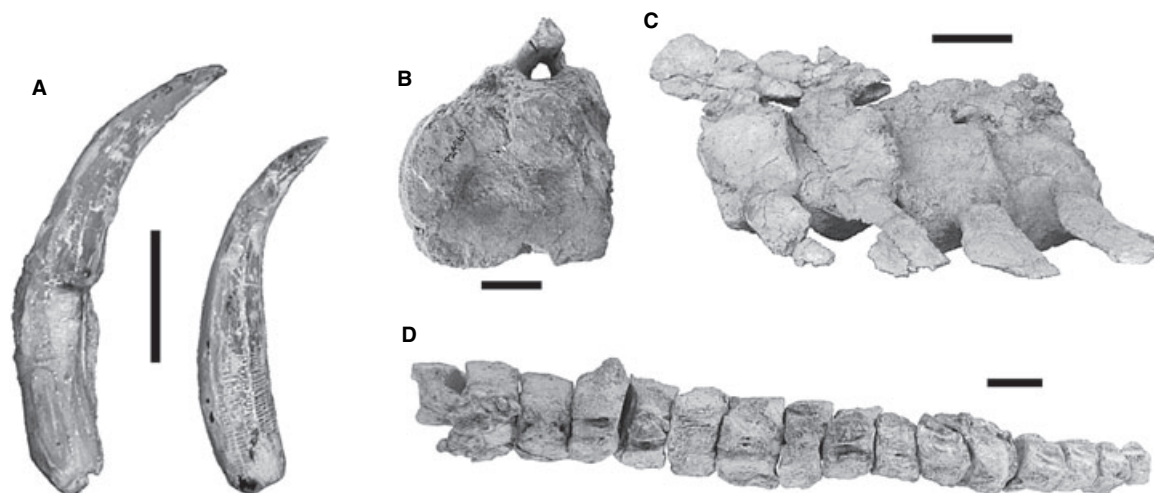
*Derivation of name.* Combination of the type locality name *Andamooka* and the suffix *-ensis* (Latin: of or from), referring to derivation of the holotype specimen from near the opal-mining township of Andamooka.

*Material.* Holotype and only known specimen, SAM P24560, partial articulated skeleton (mounted for display) including teeth; continuous series of 26 cervical, three pectoral and ten dorsal vertebrae; separate caudal series of 16 vertebrae; associated ribs; gastralia; partial right scapula; fragment of left scapula; left and right coracoid; left humerus, radius, ulna, carpal and metacarpal elements, phalanges; right proximal humerus; right femur, 107 associated gastroliths.

*Locality.* Lunatic Hill opal field, near Andamooka, west of Lake Torrens, Eromanga Basin, north-eastern South Australia.

*Horizon and age.* Bulldog Shale (Marree Subgroup), Lower Aptian–Lower Albian, *C. hughesii* and *C. striatus* zones/*O. operculata*, *D. davidii* and *M. tetracantha* zones (Krieg and Rodgers 1995; Alexander and Sansome 1996). The Andamooka opal fields are correlated with the lower–middle (Aptian) section of the unit (Ludbrook 1966; Johns 1968; Day 1969; Alley and Pledge 2000).

*Diagnosis.* Large plesiosauroid probably around 5 m in length distinguished by the following combination of features. Small needle-like teeth that are distinctly ovoid (labiolingually compressed) in cross-section and lack any surface ornamentation. Cervical centra with length less than height; platycoelous articular surfaces markedly ovate (ventral groove absent) and bearing prominent central mammillae surrounding the notochordal pit. Lateral sur-



**TEXT-FIG. 2.** *Opallionectes andamookaensis* gen. et sp. nov. holotype (SAM P24560). A, teeth in anterior view. B, anterior cervical vertebrae in posterior view. C, series of posterior cervical vertebrae in lateral view. D, articulated caudal series in dorsal view. Scale bars represent 10 mm in A, 20 mm in B and 50 mm in C and D.

faces of cervical centra lack any trace of a lateral longitudinal ridge but bear prominent facets for the single-headed cervical ribs. Longitudinal pectoral bar poorly preserved but apparently formed by scapula and coracoid only. Coracoids unite medially along their entire length (intercoracoid embayment absent) and bear prominent posterior coruna. Humerus massive with slender shaft and marked distal expansion. Supernumerary ossifications present in the epipodial row along the anterior margin of the carpus.

*Remarks.* Specific character states differentiating *Opallionectes andamookaensis* from all other related taxa are summarised below in the section on relationships.

#### Description

SAM P24560 is a partial skeleton lacking the skull, pelvic girdle, vertebrae from the sacral region and some limb elements. The specimen was found lying on its back with the posterior cervical vertebra, anterior dorsals, associated ribs/gastralia and pectoral girdle in articulation. The left forelimb, femur and caudal series had become slightly displaced prior to burial but were still in close association with the main part of the specimen. Several scattered teeth were recovered from the vicinity of the anteriormost cervical vertebrae. These probably belong to SAM P24560 because they possess complete roots (and thus are not likely to have been shed by scavengers feeding on the corpse) and show no evidence of damage from post-mortem processes such as transport, prolonged weathering on the seafloor or digestion (all of which produce characteristic patterns of wear and breakage; see Martill 1985). The nature of the specimen's discovery in an open-cut opal mine might explain the loss of some sections of the skeleton with bones being either destroyed by heavy machin-

ery or broken up for precious opal before the significance of the material was recognised.

*Size and ontogenetic stage.* Despite its large size (approximately 5 m based on comparative estimates of vertebral column length with *Cryptocleidus eurymerus* and *Muraenosaurus leedsi*), SAM P24560 exhibits features (such as a lack of fusion between the vertebral centra, neural arches and ribs and incompletely ossified articular surfaces on the girdle elements, humerus and femur *sensu* Brown 1981) consistent with osteological immaturity. This, coupled with the presence of well-developed posterolateral cornua on the coracoids, suggests that the individual was probably a young adult at the time of death.

*Dentition.* Five teeth were recovered in association with the specimen (Text-fig. 2A; Table 1). They are all small (around 21–32 mm in height) and needle-like in overall form with a distinctly ovoid (labiolingually compressed) cross-section. The crowns lack any surface ornamentation and are quite smooth. Where complete, the apex tapers to a fine point, which shows no evidence of faceting by wear. The crown represents almost two-thirds of the total height of each tooth. The roots are cylindrical in shape and subcircular in cross-section. Their surfaces are ornamented by fine concentric grooves and bear shallow elliptical resorption cavities for replacement teeth on the posterolingual face.

*Axial skeleton.* The vertebral column is incomplete (and in places poorly preserved) but includes 26 anterior and posterior cervical vertebra, three pectorals, 12 anterior-middle dorsals and a continuous section of 16 vertebrae constituting a partial caudal series. Most of the posterior cervical, pectoral and dorsal vertebrae were found in articulation with the anterior cervical and caudal series recovered as separated units (Table 1). The anteriormost cervical, posterior dorsal, sacral and anterior caudal series are missing. The articular surfaces of the more anter-

**TABLE 1.** Vertebral measurements (mm) of *Opallionectes andamookaensis* gen. et sp. nov., holotype (SAM P24560). Because vertebral centra from the pectoral and dorsal series are poorly preserved and unable to be measured with accuracy, their dimensions are not recorded in this table. Abbreviations: C, cervical; Ca, caudal (\*centrum incomplete).

No.	Length	Width	Height	No.	Length	Width	Height
C1	46.41	*-	*-	Ca1	50.37	*-	*-
C2	60.75	*-	*-	Ca2	56.26	96.49	68.99
C3	53.23	80.36	*-	Ca3	54.51	92.55	77.62
C4	63.56	79.82	56.35	Ca4	53.13	94.64	80.84
C5	63.04	*81.54	61.88	Ca5	54.72	93.55	81.77
C6	61.62	90.81	60.36	Ca6	54.51	94.89	72.39
C7	60.26	*-	*-	Ca7	58.51	91.5	72.61
C8	61.6	*-	*-	Ca8	54.04	82.01	73.02
C9	60.27	*-	*-	Ca9	49.07	70.84	70.21
C1	62.37	98.72	73.33	Ca10	48.05	67.87	64.16
C1	60.05	89.75	74.27	Ca11	56.17	68.68	59.7
C12	59.92	*-	63.65	Ca12	47.68	54.66	54.93
C13	65.1	100.32	74.41	Ca13	47.44	48.12	53.11
C14	63.78	93.9	95.27	Ca14	37.88	39.67	40.01
C15	60.27	94.95	76.21	Ca15	37.43	40.03	42.83
C16	64.17	97.42	67.61	Ca16	29.51	31.49	35.63
C17	66.83	95.93	80.78				
C18	67.82	*97.59	91.07				
C19	66.72	103.45	73.32				
C20	61.17	102.52	80.8				
C21	69.51	116.82	79.86				
C22	*51.73	111.64	74.16				
C23	63.89	109.55	67.96				
C24	64.14	*-	*-				
C25	59.73	*-	*-				
C26	69.49	108.69	*-				

ior cervicals are very slightly amphicoelous (Text-fig. 2B), becoming platycoelous in the remainder of the precaudal vertebrae (Text-fig. 2C). The caudal series exhibits weakly amphicoelous articular surfaces throughout (Text-fig. 2D). The size of the cervical vertebrae decreases steadily towards the head (Text-fig. 3A; Table 1). The centra are anteroposteriorly short with their length exceeding height only on the anteriormost vertebrae. All centra are markedly transversely broad. The articular surfaces are ovoid in outline and lack any trace of a ventral groove. They also bear prominent central mammillae surrounding the notocordal pits. The articular surface margins form an abrupt angle with the lateral centrum sides. There is no evidence of a lateral keel on any of the cervical vertebrae recovered. The ventral paired nutritive foramina are large and situated close to the mid-line in the more anterior cervicals but become more laterally placed in the more posterior vertebrae. The ventral surfaces of all cervical centra are convex and lack any evidence of a mid-line keel. The subcircular apophyses are set low on the lateral centrum surface throughout the cervical series. Neural arches are low and bear a high rectangular neural spine with a concave, fluted dorsal apex. The spines are all laterally compressed and bear both anterior neural flanges and posterior articulations for the succeeding neural spine. The zygapophyses are small and orientated in a horizontal plane. The pectoral vertebrae are poorly preserved and partly obscured

by overlying ribs and the underlying pectoral girdle. The visible articular surfaces are ovoid, similar to the cervical vertebrae, and platycoelous with the margins forming an abrupt angle with the lateral centrum sides. Most of the neural arches and all of the neural spines are missing. Like the pectoral vertebrae, the dorsals are poorly preserved and largely obscured by surrounding bones (Text-fig. 3A–B). They are, however, characterised by lateral apophyses located on the neural arch and borne on robust, distally flared, transverse processes. Although none of the neural arches is preserved, a continuous series of caudal centra are present (Text-fig. 2D; Table 1). These show a marked progressive decrease in size from the anteriormost to the posteriormost vertebrae. The anterior caudal centra are markedly anteroposteriorly compressed and bear prominent circular apophyses high on the lateral centrum surface. The ventral surfaces of the centra exhibit distinct facets for the haemal arches on both their anterior and their posterior margins. The distal caudal centra are somewhat cylindrical in shape and lack any clear trace of a neural arch, lateral caudal rib facets or haemal arch facets.

A few cervical, pectoral and dorsal ribs are preserved in SAM P24560. The cervical ribs are all single-headed with the anteriormost being markedly flattened compared with the posterior cervical ribs, which are large and elongate, becoming flattened towards their apices. The dorsal ribs are single-headed and

somewhat dorsoventrally flattened with rounded articular heads. A single possible sacral rib is present. This is short with a blunt distal margin for contact with the dorsal apex of the ilium (not recovered with the specimen). The gastralia are all poorly preserved (a result of the skeleton's 'belly up' orientation) and are too distorted to determine much of their morphology.

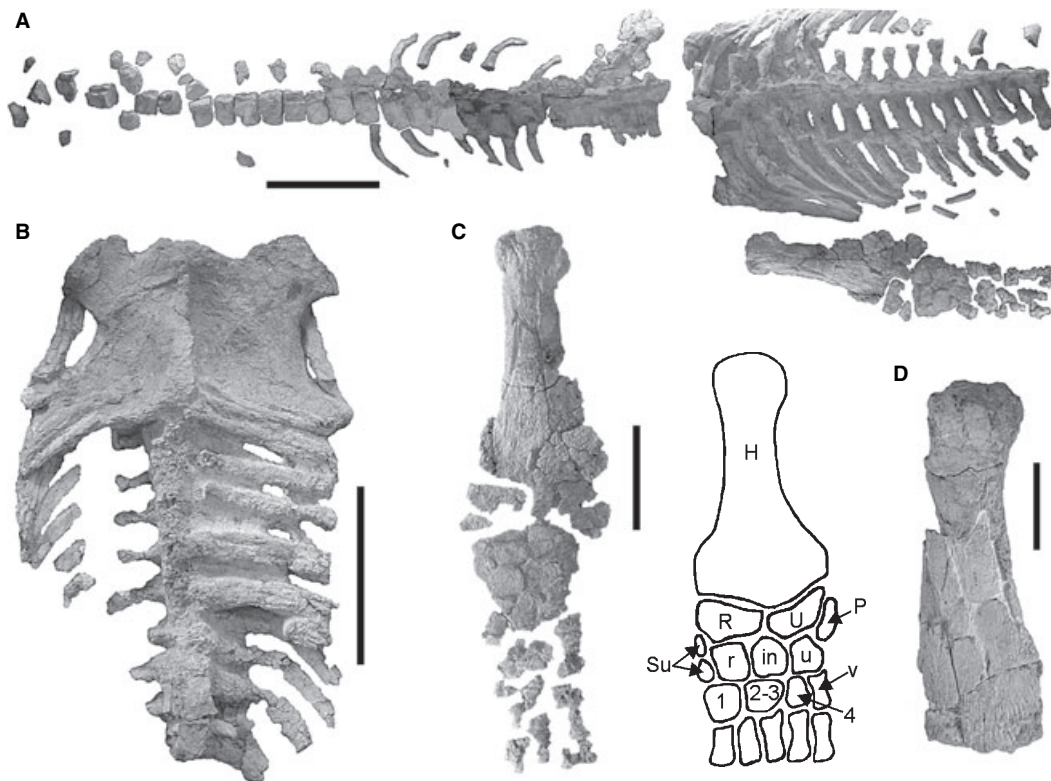
*Limb girdles.* The recovered pectoral girdle consists of a severely crushed right scapula, glenoid fragment of the left scapula and both coracoids. All elements are slightly displaced relative to each other with the scapula shifted forward beneath the posterior cervical vertebrae. The coracoids are preserved roughly in position, but are vertically displaced along the intercoracoid contact (see Text-fig. 3B). This suggests that the anterior section of the torso had decayed and collapsed before final burial. There is no trace of the pelvic girdle.

The scapulae of SAM P24560 (Table 2) are very poorly preserved but permit some reconstruction of their general shape. The more complete right scapula is crushed beneath the posterior cervical vertebrae and has suffered damage from weathering. Details of the posterior and ventral rami are lost but appear to have formed an elongate symphysis, contributing to a longitudinal pectoral bar probably formed by scapula and coracoid only. The dorsal ramus of the scapula is thin (with the anterior and posterior borders being roughly parallel) and relatively long with a slightly flared suprascapular border.

The coracoids (Text-fig. 3B; Table 2) are large, broad plates of bone, which unite medially along their entire length (intercoracoid embayment absent). The intercoracoid contact is deep with an irregular surface suggesting the presence of cartilage. The posterior border of each coracoid is straight and the posterolateral cornua are well developed, giving the lateral border of the coracoid a deeply concave outline. The width across the cornuae is approximately 15 per cent greater than the interglenoid width. The glenoid surface is ovoid in outline, shallowly concave and anterolaterally directed. The degree of preservation does not allow for any differentiation between the glenoid and scapular articular surfaces.

*Limbs.* The right forelimb and left femur are preserved disarticulated from the main body section. The proximal head of the left humerus remains in articulation with the coracoid and glenoid portion of the left scapula. Most of the distal elements of the right forelimb are lost although the main epipodial/carpal section and proximal phalanges are preserved as an articulated unit in association with the humerus (Text-fig. 3A, C).

The humerus (Text-fig. 3A, C; Table 2) is massive, elongate and pendulous with an expanded distal extremity. Both its anterior and its posterior borders are straight (giving a symmetrical dorsal outline), with the shaft being narrow and ovoid in cross-section along most of its length. A poorly developed rugosity part way along the ventral portion of the shaft marks



**TEXT-FIG. 3.** *Opallionectes andamookaensis* gen. et sp. nov. holotype (SAM P24560). A, articulated neck and anterior body section in dorsal view (as displayed in the South Australian Museum). B, anterior body section in ventral view showing articulated coracoids. C, articulated humerus and proximal forelimb (with interpretive reconstruction) in dorsal view. D, femur in dorsal view. Scale bars represent 500 mm in A and B, 200 mm in C and 100 mm in D.

the insertion for the m. coracobrachialis. The distal portion of the shaft is comparatively dorsoventrally flattened. The complete anterodistal margin is expanded to support an elongate radial facet. The posterodistal margin is mostly broken away although its remnant suggests considerable posterior expansion of the ulnar facet. The humeral head (crushed on the left humerus but well preserved on the right) is massive, weakly convex and

poorly ossified, suggesting the presence of a thick cartilage cap in life. There is only limited differentiation between the dorsal tuberosity and glenoid articular surface.

The radius and ulna (Text-fig. 3A, C; Table 2) are poorly preserved but give some idea of their general structure. The radius is broken into two sections, which when reassembled indicate an element that was distinctly broader than long. Its

**TABLE 2.** Measurements (mm) of various elements of *Opallionectes andamookaensis* gen. et sp. nov., holotype (SAM P24560) (\*element incomplete).

Element	Dimension	Measurement
Teeth	Maximum height	*32.06, 31.71, *23.98, 25.6, *21.67
	Width (labiolingual)	*6.55, 5.43, 5.67, 5.03, 5.43
Scapula	Maximum length (whole element)	236
	Maximum width	305
Coracoids	Maximum width across coruna (2x elements)	733
	Maximum width post glenoid (2x elements)	624
	Maximum width across coruna (1 element)	289
	Maximum width post glenoid (1 element)	386
	Maximum length whole element	457
	Maximum height articular surface	59.08
Humerus	Maximum width articular surface	53.67
	Maximum length (proximodistal)	452, *184
	Maximum width (distal extremity)	135.63, *-
	Height (proximal articular surface)	92.86, 85.61
	Width (proximal articular surface)	86.08, 64.33
Femur	Maximum length (proximodistal)	440
	Maximum width (distal extremity)	159
	Height (proximal articular surface)	125
	Width (proximal articular surface)	102.78
Radius	Maximum height	27.62
	Maximum width	60.47
	Maximum length	124.25
Ulna	Maximum height	41.93
	Maximum width	61.11
	Maximum length	87.88
Pisiform	Maximum height	21.33
	Maximum width	49.47
	Maximum length	37.87
Radiale	Maximum height	30.03
	Maximum width	64.17
	Maximum length	71.23
Radius	Maximum height	27.62
	Maximum width	60.47
	Maximum length	124.25
Intermedium	Maximum height	31.48
	Maximum width	55.49
	Maximum length	76.22
Largest complete phalanx	Maximum height	27.86
	Maximum width	97.88
	Maximum length	42.91
	Width across waist	34.92
Smallest complete phalanx	Maximum height	19.38
	Maximum width	58.41
	Maximum length	27.59
	Width across waist	17.54



proximal margin is anteroposteriorly elongate and tapers distally to give a somewhat trapezoidal outline. The ulna (also broken into two sections) has a similar shape although the proximal margin is shorter anteroposteriorly. The carpal elements (Text-fig. 3A, C; Table 2) are all large and polygonal with raised well-formed borders. The largest centrally positioned bone of the carpus, probably representing the intermedium (see Caldwell 1997), is weakly pentagonal in shape and bordered anteriorly and posteriorly by the subequally sized, rhomboidal radiale and ulnare. Two incomplete bones adhering to the posteroventral margin of the ulnare could be part of the pisiform and a supernumerary element. Alternatively, the 'contact' between them might represent a break, making the supernumerary the ventral section of a proximodistally elongate pisiform that could have contacted the posterodistal margin of the humerus. Similar supernumerary ossifications are present along the anterior margin of the carpus between the radiale and C1, and possibly also the radiale and anteroventral margin of the radius. The phalanges cannot be arranged with precision because of disarticulation during the early stages of preparation. All are cylindrical and rather elongate with constricted mid-sections. Proximal phalanges are large and more elongate than distal; all are dorsoventrally compressed.

The femur (Text-fig. 3D; Table 2) is slightly shorter than the humerus and differs in being asymmetrical in dorsal view, with the posterior margin of the shaft being slightly concave. The distal extremity is incomplete but suggests marked anterior and posterior expansions. The ventral surface of the shaft bears a large rugosity marking the insertion of the *m. puboischiofemoralis externus*. The femoral head is massive, and like the humerus, poorly ossified, suggesting the presence of a cartilage cap covering both the dorsal trochanter and the articular surface.

*Gastroliths.* At least 107 round to ellipsoidal smooth stones were recovered scattered around the anterior torso (posterior to the coracoids) of SAM P24560. The maximum diameter of these stones ranges from 7.05 to 129.55 mm, with an average of 28.02 and total weight of 2.762 kg. The stones are of diverse lithologies although quartzite predominates. Rounded pebbles do occur in the surrounding Bulldog Shale sediments of Andamooka but rarely occur in aggregations as they do here. The stones are therefore interpreted as gastroliths, either used for ballast (*sensu* Taylor 1994) or for the mechanical breakdown of ingested food (*sensu* Cicimurri and Everhart 2001).

### Relationships

SAM P24560 is an enigmatic specimen, which shares diagnostic features with several taxa traditionally allied with the Cryptoclididae. This is significant because it represents the first potential record of this 'group' from the Lower Cretaceous. The family Cryptoclididae was first established by Williston (1925) and later emended by Brown (1981, 1993) and Brown and Cruickshank (1994) who included the taxa *Tricleidus* Andrews, 1909, *Cryptocleidus* Phillips, 1871, *Kimmerosaurus* Brown, 1981, *Col-*

*ymbosaurus* Seeley, 1874 (possibly congeneric with *Kimmerosaurus*; Brown *et al.* 1986), *Aristonectes* Cabrera, 1941 and *Morturneria* Chatterjee and Creisler, 1994 (a replacement for the preoccupied *Turneria* Chatterjee and Small 1989; considered a junior synonym of *Aristonectes*; see Gasparini *et al.* 2003b). Other potentially related taxa include *Vinialesaurus* Gasparini, Bardet and Iturralde-Vinent, 2002, *Pantosarus* Marsh, 1893 (see O'Keefe and Wahl 2003a) and *Tatenectes* O'Keefe and Wahl, 2003b. The Cryptoclididae was initially diagnosed on the basis of cranial and dental characters, including a trend towards homodont dentition, increase in the number of premaxillary teeth, increase in the number of dentary teeth, a trend towards reduction or loss of the tooth ornamentation, a relatively large orbit, subvertical jugal separating the orbital and infratemporal fossae margins (and short contact with the postorbital), occipital condyle formed by the basioccipital or more commonly the basioccipital and exoccipital, and loss of the prearticular and coronoid. Postcranial characters (where discernible) were considered mostly to be plesiomorphic but included cervical vertebrae count ranging from around 30 to 42 (< 40 *sensu* Bardet *et al.* 1999), anteroposteriorly compressed vertebral centra throughout the cervical series, cervical centra generally lacking a lateral longitudinal crest, cervical ribs single-headed, ventral rami of the scapulae relatively broad and meeting in the ventral midline, lack of an intercoracoid foramen, and humerus with a marked distal expansion. Recently, O'Keefe (2001) drastically revised the cryptoclidid clade, adding the Jurassic 'elasmosaurid' *Muraenosaurus* Seeley, 1874, removing *Tricleidus*, which was placed in an unresolved sister taxon relationship with *Kimmerosaurus*, *Morturneria* and polycotyliids, and reassigning *Kimmerosaurus* and *Morturneria* to the controversial (see Welles 1962; Kear 2002b) family Cimoliasauridae (re-diagnosed on the basis of homodont dentition and reduction or loss of the tooth ornament). This classification was not used in the subsequent study of Cruickshank and Fordyce (2002), who retained the traditional family-level grouping, and described a new genus, *Kaiwhekia*, from the uppermost Cretaceous of New Zealand. This taxon was considered to be only distantly related to the other Late Cretaceous forms *Morturneria* and *Aristonectes*, but rather indicated multiple radiations of 'cryptoclidid' plesiosaurs in the southern oceans during the latter part of the Mesozoic. In contrast, a subsequent examination of Cretaceous 'cryptoclidid' taxa by Gasparini *et al.* (2003b) recognised *Morturneria* to be a junior synonym of *Aristonectes* and allied the taxon with Elasmosauridae. This not only restricted the known stratigraphic range of Cryptoclididae to the middle-Late Jurassic, but also brought into question the status of both Cryptoclididae (*sensu* Brown 1981; Brown *et al.* 1986) and Cimoliasauridae (*sensu*

O'Keefe 2001) as viable clades, and left the affinities of taxa such as *Kimmerosaurus* in doubt. In response, O'Keefe and Wahl (2003b) provided a revised phylogeny, which placed both traditional cryptoclidid and revised cimoliasaurid taxa (including *Aristonectes*) under a new taxonomic designation, 'Cryptocleidoidea'. However, they stressed that much of the generic-level taxonomy within this group was unstable and thus in critical need of revision. As a result, the present study restricts provisional referral of *Opallionectes* to Family indet., in anticipation of future work on the interrelationships of 'cryptoclidid/cimoliasaurid' taxa and the establishment of a viable consensus on their higher-level taxonomic affinity.

The lack of adequate cranial remains for *Opallionectes andamookaensis* precludes the use of existing data sets (e.g. Bardet *et al.* 1999; O'Keefe 2001, 2004; Gasparini *et al.* 2003b) to determine relationships. This is because trees generated from these cranio-mandibular-reliant analyses fail to produce adequately resolved placements for taxa based on dental and postcranial characters alone. Nevertheless, the holotype specimen of *Opallionectes andamookaensis* displays a unique combination of diagnostic features that support both its affinities with other 'cryptoclidid/cimoliasaurid' plesiosaurs and its recognition as a new genus and species. These include (1) the presence of needle-like, labiolingually compressed (ovoid) teeth that lack any surface ornamentation. This feature has previously been considered an autapomorphy for *Kimmerosaurus*, and differs markedly from *Tricleidus*, *Cryptocleidus*, *Vinialesaurus*, *Tatenectes*, *Aristonectes* (= *Morturneria*) and *Kaiwhekia* in which the teeth are typically more circular in cross-section and show distinct surface ornamentation (albeit reduced in some taxa); tooth morphology is unknown in *Colymbosaurus* and *Pantosaurus*. (2) The presence of cervical centra, which are anteroposteriorly short relative to their height and transversely expanded (ovoid), typically with platycoelous articular surfaces. This resembles the condition in the Cretaceous *Aristonectes* (= *Morturneria*) and *Kaiwhekia*, although in these taxa the cervical centra have a more binocular shape (unlike the cervicals of *Opallionectes*, which are ovoid) resulting from the development of a deep ventral groove (also present in derived elasmosaurids; Bardet *et al.* 1999). The cervical centra of *Aristonectes* (= *Morturneria*) also show distinct longitudinal ridges on the lateral centrum surfaces. This feature occurs in elasmosaurids (Welles 1962; Brown 1993; Bardet *et al.* 1999) and was considered (along with the binocular centrum shape and platycoelous articular surfaces) by Gasparini *et al.* (2003b) to be a key synapomorphy allying *Aristonectes* (= *Morturneria*) with Elasmosauridae. Morphology of the cervical vertebrae in typical Jurassic 'cryptoclidids/cimoliasaurids' (e.g. *Cryptocleidus*, *Kimmerosaurus*) differs markedly from any of the Cretaceous taxa in exhibiting a subcircular centrum shape

and deeply amphicoelous articular surfaces (Brown 1981, 1993; Brown *et al.* 1986; Chatterjee and Small 1989; O'Keefe 2001). (3) Coracoids meet along their entire midline (intercoracoid embayment absent). This condition is traditionally regarded as a characteristic of plesiomorphic plesiosauroids and occurs in all 'cryptoclidids/cimoliasaurids' in which the pectoral girdle is known (Brown 1981; Bardet *et al.* 1999). (4) The presence of supernumerary ossifications along the anterior margin of the epipodial row. Caldwell (1997) recorded supernumerary elements associated with the radiale and distal radius of *Cryptocleidus*. Similar ossifications adhering to the anterior margin of the radiale are present in the distal forelimb of *Opallionectes*. (5) Elongate humerus with straight, narrow shaft and expanded distal extremity. The elongate, distally expanded humerus of *Opallionectes* is comparable in form with those of some Jurassic 'cryptoclidid/cimoliasaurid' taxa, particularly *Colymbosaurus*, *Pantosaurus* and *Tatenectes*, all of which share a characteristic straight, proportionately narrow shaft. However, the humeri of these taxa are distinctive in their possession of an additional posterodistal facet (also occurring in *Tricleidus*) for articulation with the pisiform (Andrews 1910; Brown 1981; O'Keefe and Wahl 2003a, b). Although the distal humerus in the holotype specimen of *Opallionectes* is incomplete, the likely presence of a proximodistally elongate pisiform in the proximal epipodial row might indicate that a similar contact occurred on the posterodistal margin of the humerus in this taxon.

## OTHER ASSOCIATED MARINE REPTILES

### *Elasmosauridae*

The remains of elasmosaurids (Text-fig. 4A–D) occur in both the Bulldog Shale and the Oodnadatta Formation. Almost all of the material to date has been fragmentary, consisting of isolated vertebrae, teeth and other elements. Several incomplete skeletons (all lacking cranial material, e.g. SAM P14539; SMM P71.1.1) have been recovered from the opal-bearing deposits of the Bulldog Shale at Andamooka. These are very similar in morphology and probably represent a single taxon.

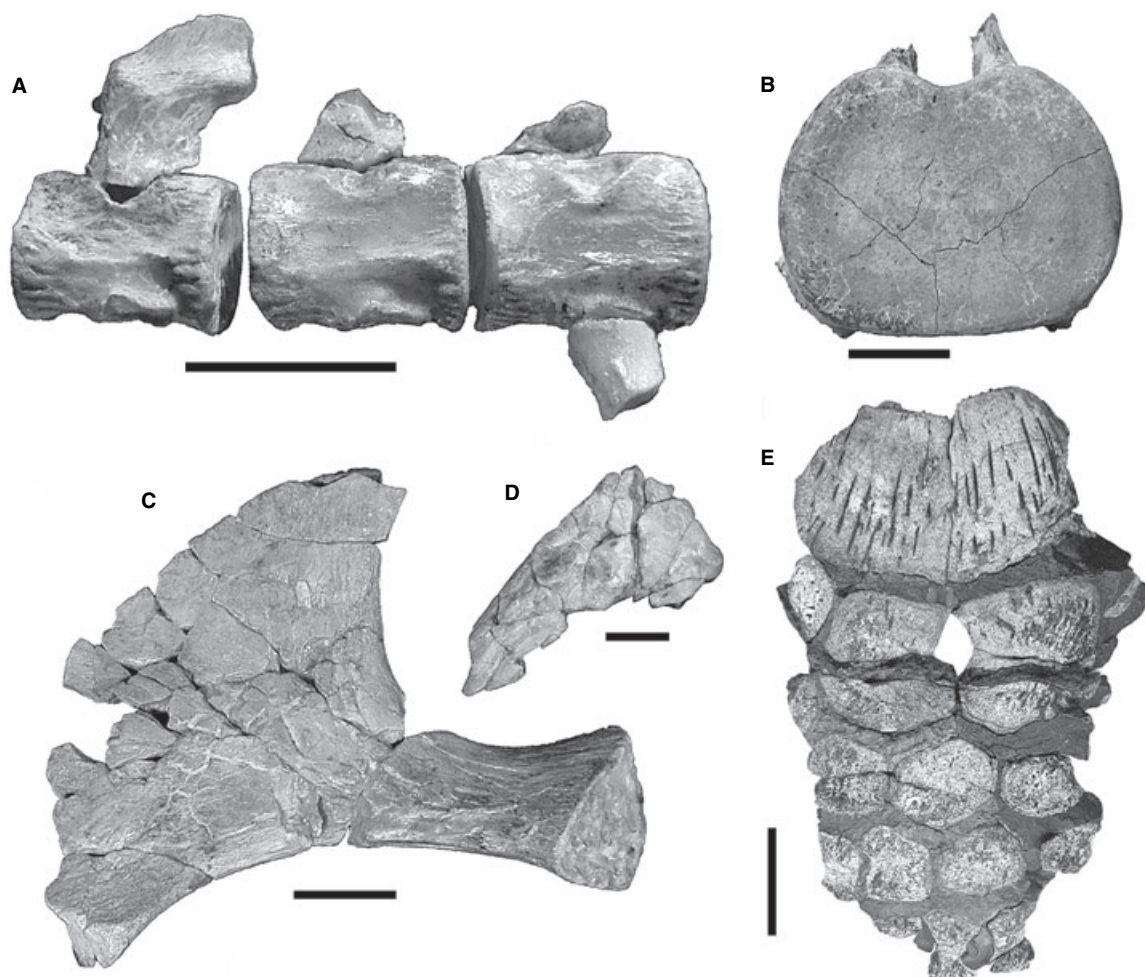
The elasmosaurid remains in the Bulldog Shale and Oodnadatta Formation exhibit several diagnostic features supporting attribution to the family. These include anterior/middle cervical vertebrae that are always longer than high, platycoelous and have prominent longitudinal ridges on the lateral centrum surfaces, development of a wide intercoracoid foramen, and the presence of short, stout propodials that are massively built and have a marked expansion of the distal extremity. Currently no characters

serve conclusively to diagnose the specimens beyond Elasmosauridae gen. et sp. indet. This is a common phenomenon with Australian elasmosaurid fossils, most of which require extensive taxonomic and phylogenetic revision (Kear 2003a).

Nearly all of the elasmosaurid remains recovered from both the Bulldog Shale and the Oodnadatta Formation display features consistent with derivation from osteologically immature individuals (including lack of fusion between the vertebral centra, neural arches and ribs, and incompletely ossified articular surfaces on the girdle elements, and propodials *sensu* Brown 1981). Despite this, most specimens are still reasonably large [approximately 6–7 m based on comparative estimates of vertebral column length and centra proportions with *Hydrotherosaurus alexandrae* Welles, 1943 and *Callawayasaurus columbiensis* (Welles, 1962)] and probably represent young adults.

#### *Polycotylidae*

A fragmentary plesiosaur specimen (SAM P36356) from Hermit Hill, Lake Eyre South, is tentatively allied with the Polycotylidae on the basis of its anteroposteriorly compressed, amphicoelous centra and supernumerary ossifications in both the epipodial and the propodial rows of the limb (see Text-fig. 4E). O’Keefe (2001) recorded the presence of supernumerary ossifications in both the epipodial and the propodial rows as a key postcranial character distinguishing the family Polycotylidae (although it also occurs in some other plesiosaur taxa including *Rhomaleosaurus*). Carpenter (1996), however, noted that the number of articulatory facets on the distal propodial of polycotylids is highly variable and cannot be used confidently for taxonomic determination within the group. Despite this, the distinctive limb morphology of SAM P36356 (along with the vertebral structure) is



**TEXT-FIG. 4.** Plesiosauroid remains from South Australia. A, elasmosaurid cervical series (SAM P14539). B, elasmosaurid posterior cervical vertebra (SAM P39618) in anterior view. C, elasmosaurid clavicular arch (SAM P34156) in ventral view. D, elasmosaurid scapula (SAM P14539) in medial view. E, polycotylid partial limb. Scale bars represent 50 mm in A, 20 mm in B and C, and 40 mm in D and E.

sufficient to distinguish it from all other currently recognised Bulldog Shale plesiosaurs.

Polycotyloid remains have been recovered from several Cretaceous deposits in Australia, most notably the Aptian Wallumbilla Formation (Doncaster Member) of White Cliffs in north-western New South Wales (Kear 2003a, 2005). Material from this unit currently represents the oldest example of the group from anywhere in the world (Sato and Storrs 2000). Interestingly, the Wallumbilla Formation is laterally equivalent to the Bulldog Shale (Krieg and Rodgers 1995), which suggests that early polycotyloids might have been widely distributed throughout at least the southern parts of the Australian epicontinental seaway during the Early Cretaceous.

#### *Rhomaleosauridae*

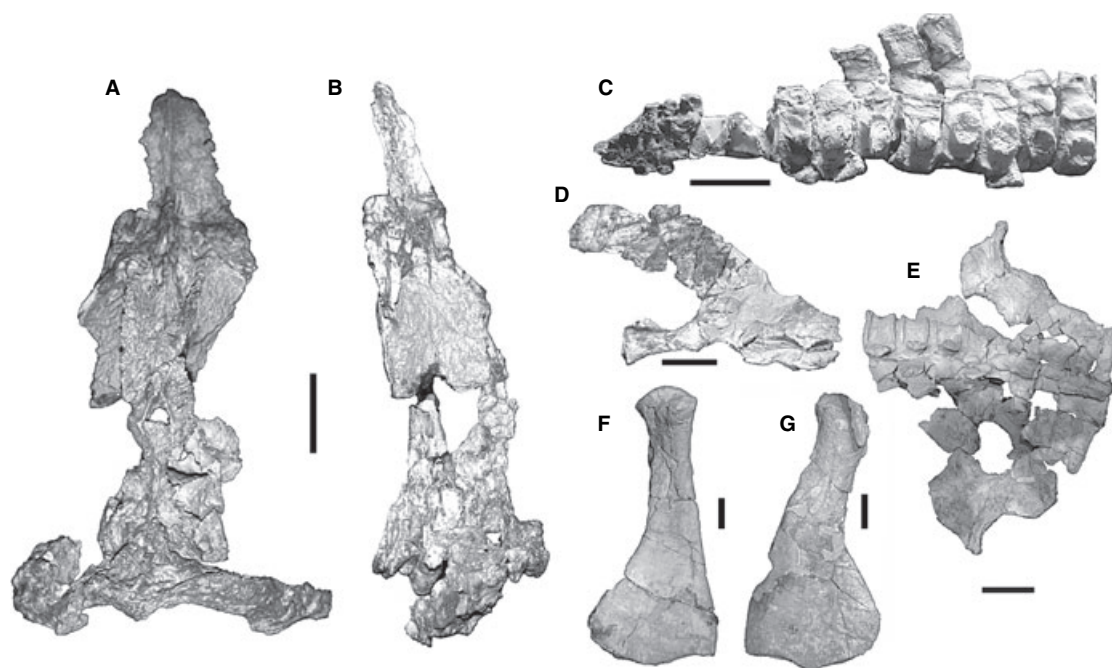
The South Australian rhomaleosaurids are represented by the single genus *Leptocleidus*. This is currently the most widely distributed generic-level plesiosaur taxon known from Australia and the most common marine reptile in the Bulldog Shale deposits (Cruickshank *et al.* 1999; Alley and Pledge 2000; Kear 2003a). The taxonomic interrelationships of the Australian *Leptocleidus* specimens are currently unclear, but at least two distinct species appear to be present. Remains from the Upper Hauterivian–Barremian Birdrong Sandstone of Western Australia have been assigned to the large-bodied *Leptocleidus clemai* Cruickshank and Long, 1997 (Cruickshank and Long 1997). Material from the Bulldog Shale (Text-fig. 5) is morphologically distinct (see below) but does share a range of derived features common to other members of the genus. These include the presence of a triangular skull outline; prominent mid-nasal ridge that merges with the sagittal crest; sagittal crest flanked by deep depressions that delineate protruding orbital rims; prominent expansion on the squamosal mid-line present at the rear of the sagittal; snout bearing a rosette of procumbent teeth (possibly up to six), which are conical and circular in section with striae reduced or absent on the buccal surface; dorsomedially directed trough on the articular; weakly anteroposteriorly compressed (spool-shaped) cervical centra with centrum lengths consistently less than heights (O’Keefe 2001); cervical neural arches with large prezygapophyses orientated approximately 45 degrees to the horizontal axis; cervical vertebra count high, consisting of as many as 20 centra not including the atlas-axis; cervical ribs single-headed; humerus nearly as large as femur with symmetrical distal end; and interclavicle and clavicle large in comparison with the scapula (see Kear 2003b for summary). Characters that indicate probable species-level distinction (to be examined in more detail elsewhere) include: (1) the presence of prominent crests along the

midline of the skull and medial orbital rims. These are not developed on the skulls of either *L. superstes* (Andrews 1922) or *L. capensis* (Andrews 1911; Cruickshank 1997), although a strong sagittal crest and deep depressions delineating the orbital rims (‘well marked channels’ *sensu* Andrews 1922) are present in both taxa; the skull is unknown in *L. clemai* (Cruickshank and Long 1997). (2) Orientation of the post-temporal bar and posteroventral rami of the squamosals. The post-temporal bar and posteroventral rami of the only complete skull (AM F99374; Text-fig. 5A) are nearly vertically orientated, giving the back of the skull a short, high, ‘squared-off’ profile. This is unlike the condition in *L. superstes* and *L. capensis*, in which the posteroventral rami are notably posteroventrally sloped and the back of the skull comparatively lower and more elongate (see Andrews 1922; Cruickshank 1997). (3) Proportionately large, slender pterygoid process on the basioccipital. This feature is most conspicuous in a small juvenile specimen from Andamooka (SAM P15980), and contrasts with the common condition in other pliosauroid taxa in which the pterygoid processes tend to be short and stocky (see Andrews 1913; White 1935; Cruickshank 1994). (4) Tooth morphology. Teeth recovered with the *Leptocleidus* sp. material from the Bulldog Shale conspicuously lack the mesodistal carinae present on the teeth of *L. capensis* (Cruickshank 1997). Other features, however, including the slightly recurved tooth shape and an absence of striations from the buccal surface of the crown, are shared by both forms. The teeth are unknown in *L. superstes* and *L. clemai* (see Andrews 1922; Cruickshank and Long 1997).

Like the elasmosaurids, the South Australian rhomaleosaurid material comprises mainly immature individuals (showing important features such as lack of fusion between the vertebral centra, neural arches and ribs, and incompletely ossified articular surfaces on the girdle elements, humerus and femur, *sensu* Brown 1981), ranging in size from about 700 mm to 2.1 m in length (based on estimates from the most complete skeletons AM F99374, SAM P15980 and SAM P39915). Surprisingly, other isolated elements (vertebral centra and propodials) suggest the presence of even smaller animals, perhaps around 500 mm, based on comparison of individual bones relative to the smallest, most complete individual SAM P15980.

#### *Pliosauridae*

Alley and Pledge (2000) and later Kear (2002a) attributed the existing South Australian pliosaurid material (then represented by a single tooth, SAM P22525) to the genus *Kronosaurus* Longman, 1924. This assignment is followed



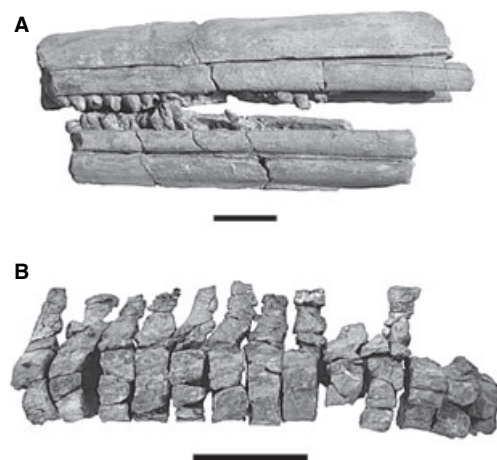
**TEXT-FIG. 5.** *Leptocleidus* sp. remains from South Australia. Partial skull (AM F99374) in A, dorsal and B, lateral views. C, articulated caudal series (AM F99374) showing fused terminal 'pygostyle-like' structure. D, scapula (AM F99374) in lateral view. E, pelvic region (AM F99374) in dorsal view. F, humerus (AM F99374). G, femur (AM F99374). Scale bars represent 50 mm in A–E and 20 mm in F–G.

herein, with the conical shape of the crown and absence of distinct carinae serving conclusively to diagnose the specimens as cf. *Kronosaurus* sp. This is in accordance with Massare (1997), who suggested that both 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 SAM P22525 (together with a second tooth SAM P40022) to cf. *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 known from Australia (Kear 2003a).

#### *Ichthyosauria*

Ichthyosaur fossils are regularly encountered in the Bulldog Shale. However, they are much less common than those of plesiosaurs, which show both a numerical and a taxonomic dominance at most localities. Most, if not

all, Australian Cretaceous ichthyosaur material can be assigned to the ophthalmosaurid *Platypterygius*, currently the most widespread valid genus of Cretaceous ichthyosaur (see McGowan and Motani 2003). Not surprisingly, therefore, the Bulldog Shale remains (Text-fig. 6A–B) also exhibit at least three key diagnostic characters suggesting affinity with this taxon (as yet no potentially unique spe-



**TEXT-FIG. 6.** Ichthyosaur remains from South Australia. A, snout and mandible sections (SAM P14508). B, vertebral series (SAM P39255). Scale bars represent 50 mm in A and 200 mm in B.

cies-level features can be identified). These include (1) robust dentition with tooth roots quadrangular in cross-section (considered a synapomorphy for all species of *Platypterygius*; Bardet 1990), (2) angular with extensive external exposure, reaching as far anteriorly as surangular (a feature common to all ophthalmosaurids; see Motani 1999), and (3) a well-developed distal facet (in addition to those for the tibia and fibula) on the femur for articulation with an anterior zeugopodial element. This last feature appears to be restricted to *Platypterygius hercynicus* (Kuhn 1946), *P. longmani* (B. Kear, unpublished data) and the questionable genus *Yasykovia* (Upper Jurassic, Volga region, Russia; Efimov 1999, considered a junior subjective synonym of *Ophthalmosaurus* by Maisch and Matzke 2000) among post-Triassic ichthyosaurs, and differs from the typical condition in *P. americanus* (Nace 1939, 1941), other ophthalmosaurids (e.g. Andrews 1910; Bardet and Fernandez 2000), post-Triassic (e.g. Maisch 1998) and Triassic (e.g. Camp 1980; McGowan 1995; McGowan and Motani 1999) ichthyosaur taxa (for which the element is described) in which the femur commonly bears two facets for the tibia and fibula only.

## PALAEOECOLOGICAL IMPLICATIONS OF THE ASSEMBLAGE

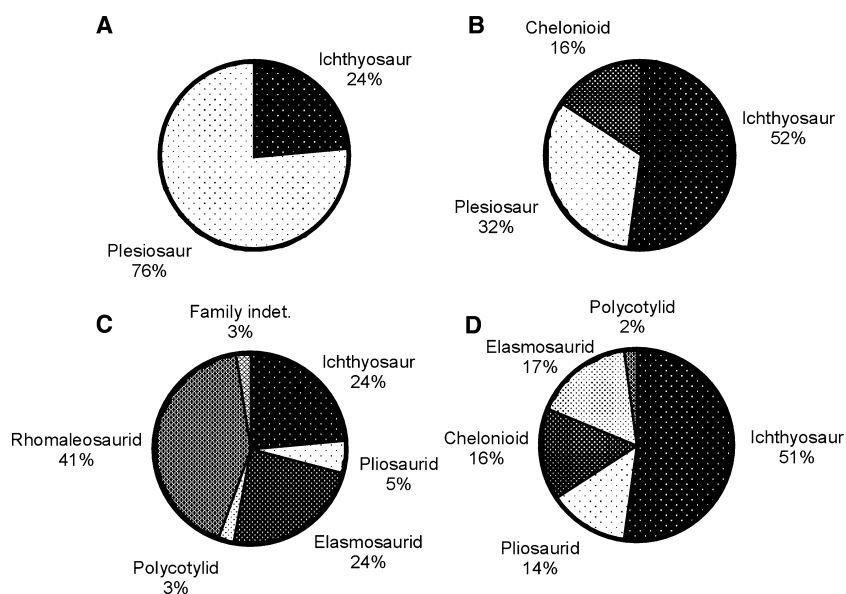
The fossil marine reptiles of the Bulldog Shale and Oodnadatta Formation constitute two examples from a range of assemblages known from Cretaceous southern high-latitude deposits. Occurrences from elsewhere include ichthyosaurs and plesiosaurs from the Aptian Wallumbilla Formation (Doncaster Member) of White Cliffs, New South Wales, Australia (Kear 2003a, 2005), isolated plesiosaur teeth and rare bones from the Aptian–Albian Wonthaggi and Eumeralla formations of Victoria (Rich *et al.* 1988; Vickers-Rich 1996), and Griman Creek Formation of northern New South Wales/southern Queensland, Australia (Kear 2003a), numerous plesiosaur and mosasaur skeletons from Maastrichtian deposits in Patagonia (see Gasparini *et al.* 2003a for summary) and Antarctica (Martin *et al.* 2002; Novas *et al.* 2002), particularly the Lopez de Bertodano Formation of Seymour Island (Chatterjee *et al.* 1984; Chatterjee and Small 1989; Martin 2002) and Vega Island (Case *et al.* 2000), excellently preserved plesiosaur and mosasaur specimens from units including the Campanian–Maastrichtian Katiki Formation and Maastrichtian Conway Formation of New Zealand (Welles and Gregg 1971; Wiffen and Molesley 1986; Bell *et al.* 1998; Cruickshank and Fordyce 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 Creta-

ceous high-latitude sediments 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 documented assemblages, the marine reptile fauna of the Bulldog Shale is particularly unusual because it occurs in association with palaeoclimatic indicators (e.g. glacial erratics, glendonites and growth-banded wood), denoting seasonally very cold to near freezing conditions (see Frakes and Francis 1988, 1990; Sheard 1990; Dettmann *et al.* 1992; Frakes *et al.* 1995; De Lurio and Frakes 1999). This contrasts markedly with climate regimes typically tolerated by modern aquatic reptiles, but suggests that some Mesozoic taxa (including both ichthyosaurs and plesiosaurs) were able to cope with extremely low average water temperatures. Indeed, the material recovered to date even includes large numbers of small-bodied juvenile and subadult specimens (representing mainly plesiosaurs), indicating that a range of age groups were capable of surviving in the Bulldog Shale's cold-water depositional environment. A high proportion of juvenile plesiosaur fossils also occurs in some other Cretaceous high-latitude marine deposits (see Wiffen *et al.* 1995; Case *et al.* 2000), and could reflect a tendency towards age-related habitat partitioning (with juveniles inhabiting inshore marine/estuarine–freshwater depositional environments; Wiffen *et al.* 1995) and/or preferential utilization of nutrient-rich cooler water ecosystems by younger individuals (in an effort to facilitate rapid growth and development during short-lived seasonal increases in available food resources). Exactly what adaptations (if any) allowed these diverse taxa and age groups to survive is unknown. However, various physiological mechanisms (perhaps including rapid growth coupled with metabolic or mass-dependent endothermy in adults; the latter documented in the living leatherback turtle, *Dermochelys coriacea*; Paladino *et al.* 1990) and/or behavioural strategies (such as seasonal migration or short-term hibernation in smaller freshwater/coastal forms, vis-à-vis the American alligator, *Alligator mississippiensis*; Brisbin *et al.* 1982) might have facilitated their successful exploitation of cold-water habitats along the southern coastal margins of the Australian Cretaceous epicontinental seaway.

Of the marine reptile clades currently recorded from the South Australian deposits, plesiosaurs are by far the most diverse (including up to five families) and most numerous (see Text-fig. 7A, C; Table 3). Plesiosaurs also form the dominant element in marine reptile faunas from Upper Cretaceous high-latitude deposits in the Northern Hemisphere (Nicholls and Russell 1990), Antarctica (Martin 2002), and the Lower Cretaceous Wallumbilla Formation of White Cliffs, New South Wales (in which as many as three families may be present including Polycotyliidae;

**TEXT-FIG. 7.** Relative abundance (in %) of marine reptile taxa in both the high-latitude (c. 70°S) Lower Aptian–Lower Albian deposits of the Bulldog Shale of South Australia (A, C), and lower latitude (c. 45°S) Upper Albian Toolebuc Formation of Queensland (B, D). C and D show breakdown per cent of various plesiosaur clades. Numbers of individual specimens are listed in Table 3.



see Kear 2003a, 2005). This latter unit is a lateral equivalent of the Bulldog Shale, and shares a similar macro-invertebrate fauna (see Ludbrook 1966; Johns 1968; Day 1969), as well as palaeoclimatic indicators including ice-rafted erratic boulders, glendonites and growth-banded fossil wood (Burton and Mason 1998). This characteristic faunal composition contrasts markedly with typical lower latitude Cretaceous marine reptile assemblages. For example, in Australia the Upper Albian Toolebuc Formation of north-eastern Queensland (which lay at approximately 45°S palaeolatitude at that time) preserves plesiosaurs in far fewer numbers (and with reduced taxonomic diversity, although as many as three family-level clades are still present; see Text-fig. 7B, D; Table 3) relative to ichthyosaurs, and includes chelonioids as a new element in the fauna (Kear 2003a, 2004). The reasons for this difference 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–near freezing conditions in at least the southern reaches of the Australian Cretaceous epicontinental seaway during the late Neocomian–Early Albian (Frakes and Francis 1988) may have provided an effective barrier to the successful dispersal of groups such as chelonioids, which do not appear in the Australian Cretaceous record prior to the uppermost Albian (Kear 2002a, 2003a, 2004). 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 chelonioids, 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 in some taxa (see Mrosovsky 1980).

The taxonomic composition of the South Australian marine reptile fauna highlights its cosmopolitan nature and relationships with taxa from elsewhere. For example, the ophthalmosaurid ichthyosaur *Platypterygius* recorded in the Bulldog Shale is known from many Cretaceous deposits around the world (McGowan 1972). Similarly, the rhomaleosaurid *Leptocleidus*-like remains have been reported from the Lower Cretaceous (Valanginian–Upper Aptian/Lower Albian) freshwater and near-shore marine deposits of England (Andrews 1922), South Africa (Andrews 1911; Strömer 1935; Cruickshank 1997), Western Australia (Cruickshank and Long 1997; Long 1998;

**TABLE 3.** Numbers of specimens recorded for the various marine reptile groups present in both the Bulldog Shale of South Australia and the Toolebuc Formation of Queensland.

Taxonomic group	Bulldog Shale	Toolebuc Formation
Ichthyosauria	9	196
Rhomaleosauridae	16	–
Pliosauridae	2	51
Plesiosauroidea Family indet	1	–
Elasmosauridae	9	62
Polycotylidae	1	8
Chelonioida	–	59
Total	38	376

Cruickshank *et al.* 1999; Kear 2002a, 2003a, 2004), the Northern Territory (Kear 2002a, 2003a) and Canada (P. Druckenmiller, pers. comm. 2003; see also Druckenmiller 2002). Lastly, the large pliosaurid *Kronosaurus* is recorded from Aptian–Albian strata in New South Wales (Kear 2003a, 2005), Queensland (Longman 1924; White 1935; Molnar 1991; Long 1998; Kear 2003a, 2004) and South America (Hampe 1992).

Interestingly, the Bulldog Shale also preserves some potentially endemic forms, including the enigmatic *Opal-ionectes andamookaensis*, a probable new species of *Leptocleidus*, and possibly one of the earliest known polycotylids. This suggests that isolating barriers (perhaps including climate) were in effect, and that these may have prompted the evolution of new taxa and clades, such as the Polycotylidae, which appears to have had its origins (or at least early evolution) in the high-latitude epicontinental seas of eastern Gondwana sometime in the Neocomian–Early Gallic (Kear 2003a, 2004).

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