

A review of Australian mosasaur occurrences

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Abstract

Mosasaur are rare in Australia with fragmentary specimens known only from the Cenomanian-lower Turonian Molecap Greensand (Perth Basin), Campanian - lower Maastrichtian Korojon Calcarenite (Carnarvon Basin), and upper Maastrichtian Miria Formation (Carnarvon Basin), Western Australia. These units were laid down during a near-continuous marine inundation of the western margin of the Australian landmass (which followed separation from India in the Valanginian and genesis of the Indian Ocean) in the Early-Late Cretaceous. The Australian mosasaur record incorporates evidence of derived mosasaurids (mainly plioplatecarpines); however, as yet no specimen can be conclusively diagnosed to genus or species level. The fragmentary nature of the remains provides little basis for direct palaeobiogeographic comparisons. However, correlation with existing data on associated vertebrates, macroinvertebrates and microfossils suggests that the Western Australian mosasaur fauna might have been transitional in nature (particularly following palaeobiogeographic separation of the northern and southern Indian Oceans during the mid-Campanian), potentially sharing elements with both northern Tethyan and austral high-latitude regions.

Keywords: Mosasaurs, Late Cretaceous, Australia, palaeobiogeography

Introduction

Australian Cretaceous marine reptile fossils are plentiful although currently poorly documented. At present, most of the described material (comprising mainly ichthyosaurs, plesiosaurs and chelonioid turtles) is derived from extensive lower Cretaceous epicontinental marine deposits in central and northeastern Australia (see Kear, 2003 for summary). In contrast, Late Cretaceous marine reptiles, particularly mosasaurs, are extremely rare. To date, Australian mosasaur remains have been recovered exclusively from continental-margin marine units in Western Australia, specifically the Cenomanian - lower Turonian Molecap Greensand (Perth

Basin), Campanian - lower Maastrichtian Korojon Calcarenite (Carnarvon Basin) and upper Maastrichtian Miria Formation (Carnarvon Basin).

Several previous reports have dealt with Australian mosasaurs (e.g., Lundelius & Warne, 1960; Molnar, 1991; Long, 1998, 1999; Kear, 2003, 2004), although few specimens have been thoroughly described. It is, therefore, the purpose of this article to present an up-to-date summary of the Australian mosasaur record and assess its potential palaeobiogeographic relationships. This is intended to provide a platform for more detailed future studies, including a descriptive analysis of Australian mosasaur specimens currently in preparation by JEM and JAL (see Martin & Long, 2002).

Abbreviations and terminology

Repository abbreviations: UWA, University of Western Australia, Perth; WAM, Western Australian Museum, Perth. Lithostratigraphic nomenclature for Australian mosasaur-bearing deposits follows Playford et al. (1976) and Shafik (1990) for the Perth Basin, and Hocking et al. (1987) for Carnarvon Basin units. Informal systematic terminology for Mosasauridae follows the phylogenetic analyses of Bell (1997) with 'russellosaurine' referring to a clade containing Tylosaurinae + Plioplatecarpini, 'plioplatecarpine' referring to the lineage comprising species of *Ectenosaurus*, *Platecarpus* and *Plioplatecarpus*, and 'mosasaurine' referring to the diverse clade incorporating *Clidastes*, *Globidensini*, *Mosasaurus* and *Plotosaurus*.

Geological setting

Previous accounts of regional geology (some including maps) and depositional environments for mosasaur-bearing units in Western Australia have been given by Belford (1958), McWae et al. (1958), Playford et al. (1976), Hocking et al. (1987) and Shafik (1990). The geographic distribution of known localities is given in Fig. 1.

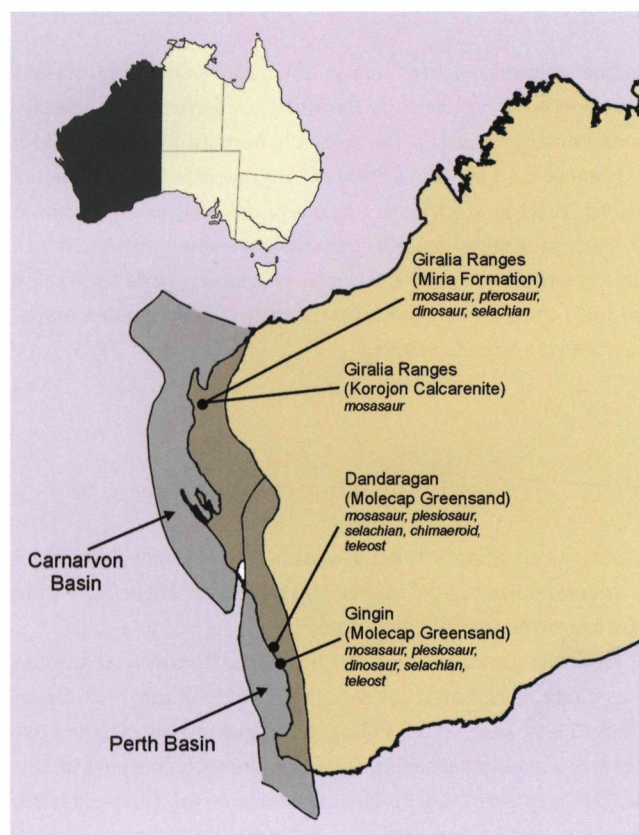


Fig. 1. Map of Western Australia (with Perth and Carnarvon basins shaded) showing localities and units that have produced mosasaur and other associated vertebrate fossils.

At present, Australian mosasaur remains are known solely from the Molecap Greensand, Korojon Calcarenite and Miria Formation. The Molecap Greensand is a continuous sequence of weathered shallow-marine strata that crops out extensively in the southern coastal areas of the Perth Basin in south-western Western Australia. The unit comprises mainly glauconitic sandstones with a basal phosphatic lag deposit; this may represent either reworked material, or a basal conglomeratic sequence distinct from the overlying sandy sediments. Playford et al. (1976) suggested that the Molecap Greensand was laid down in a transgressive coastal shallow-marine environment, over irregular topography, and with unfavourable, potentially poorly oxygenated bottom-water conditions.

The age of the Molecap Greensand is contentious. Rich palynomorph assemblages have been used to determine a Cenomanian-early Turonian range (Shafik, 1990). This contrasts with some earlier estimates, which favour a much younger late Coniacian-early Santonian age for the deposit (Belford, 1958; McWae et al., 1958). Macrofossils are sporadic throughout the Molecap Greensand but include fragmentary remains of mosasaurs, plesiosaurs, selachians, chimaeroids, teleost fish and dinosaurs. Isolated, probably reworked ichthyosaur material is also known from the basal part of the sequence. Invertebrates are uncommon (an artifact of poor preservation), and only a handful of benthic molluscan taxa have been identified (see Etheridge, 1913; Feldtmann, 1951, 1963; Henderson et al., 2000).

The Korojon Calcarenite together with the overlying Miria Formation comprise a thin sequence of condensed, uncemented chalk (foraminiferal calcarenite) with abundant phosphatic grains and nodules. Both units were laid down under predominantly low-energy, shallow-marine shelf conditions, established during a latest Cretaceous transgressive episode in the Carnarvon Basin of northwestern Western Australia (Apthorpe, 1979; Hocking et al., 1987). A distinct series of winnowed sediments rich in nodular phosphorite forms the uppermost portion of the Korojon Calcarenite and marks the boundary with the Miria Formation. This corresponds to a probable mid-Maastrichtian regressive event, recognised by a widespread disconformity in strata of that age all along the Western Australian continental margin (McNamara et al., 1988).

Both the Korojon Calcarenite and Miria Formation are typically poorly exposed but can be recognised in outcrop by phosphatic steinkerns, which occur within the weathering residuum (Henderson & McNamara, 1985a). These are conspicuous in the type sections in the Giralia Ranges (Giralia and Marilla Anticlines), south of Exmouth Gulf.

The Korojon Calcarenite is generally very poor in macrofossils, although has produced calcitic bivalves (mainly *Inoceramus*, a characteristic taxon serving to distinguish the Korojon Calcarenite from overlying Miria Formation), rare ammonites and an isolated mosasaur vertebra. Henderson & McNamara (1985a) considered the paucity of cephalopods and other

aragonitic shells to be a diagenetic phenomenon, non-indicative of fossil content at the time of deposition. Identification of key heteromorph ammonite taxa including *Nostoceras*, and early species of *Eubaculites* have been used to establish an early Maastrichtian age for the upper phosphorite-rich portion of the Korojon Calcarenite (Henderson et al., 1992). Underlying sediments within the sequence are considered largely Campanian in age on the basis of foraminiferal evidence (Edgell, 1957).

Late Cretaceous vertebrate fossils from the Miria Formation include both mosasaurs and selachians. Isolated dinosaur and pterosaur bones suggest deposition in close proximity to land. Macroinvertebrate assemblages are extremely rich comprising a diverse range of pelagic cephalopods (Glenister et al., 1956; Henderson & McNamara, 1985b; Henderson et al., 1992, 2000) and benthic molluscs (Darragh & Kendrick, 1991, 1994; Henderson et al., 2000). These have been used in conjunction with microfossil data (see Henderson et al., 2000) to indicate temperate to warm temperate sea surface temperatures at the time of deposition (Darragh & Kendrick, 1994). Species of the planispiral *Pachydiscus* (*Pachydiscus*), and distinctive heteromorph ammonite taxa including *Baculites*, *Eubaculites*, *Glyptoxoceras* and *Diplomoceras* specify a late Maastrichtian age for the unit (Henderson & McNamara, 1985b; Henderson et al., 1992).

A review of Australian mosasaur discoveries

Australian mosasaur remains were first documented by Lundelius & Warne (1960), who described a fragmentary forelimb (UWA 37092) with abraded ulna and phalanx (Fig. 2A - D), from the upper section of the Molecap Greensand (top of McIntyre Gully section) of McIntyre Gully, near the township of Gingin, on the southwestern coast of Western Australia. The poor condition of the material did not permit assignment to a specific taxon, although general morphology of the ulna and slender proportions of the associated phalanx (see Lundelius & Warne, 1960 for discussion of characters), are sufficient to warrant possible affinity with *Platecarpus* (Lundelius & Warne, 1960; Long, 1998). Long (1990, 1993) provided additional illustrations of this specimen and calculated an estimated length of 2.6 m for the complete animal based on comparison with *Platecarpus*.

Long (1998) reported three associated trunk/caudal vertebrae (WAM 91.8.16) from the Miria Formation of Cardabia Station in the Giralia Ranges, south of Exmouth Gulf, central-western Western Australia. The specimens (Fig. 2E, F) were well preserved with complete neural arches present on two of the centra, and appear to represent a large (around 6 - 8 m) mosasaurid of uncertain affinity. The Miria Formation has also

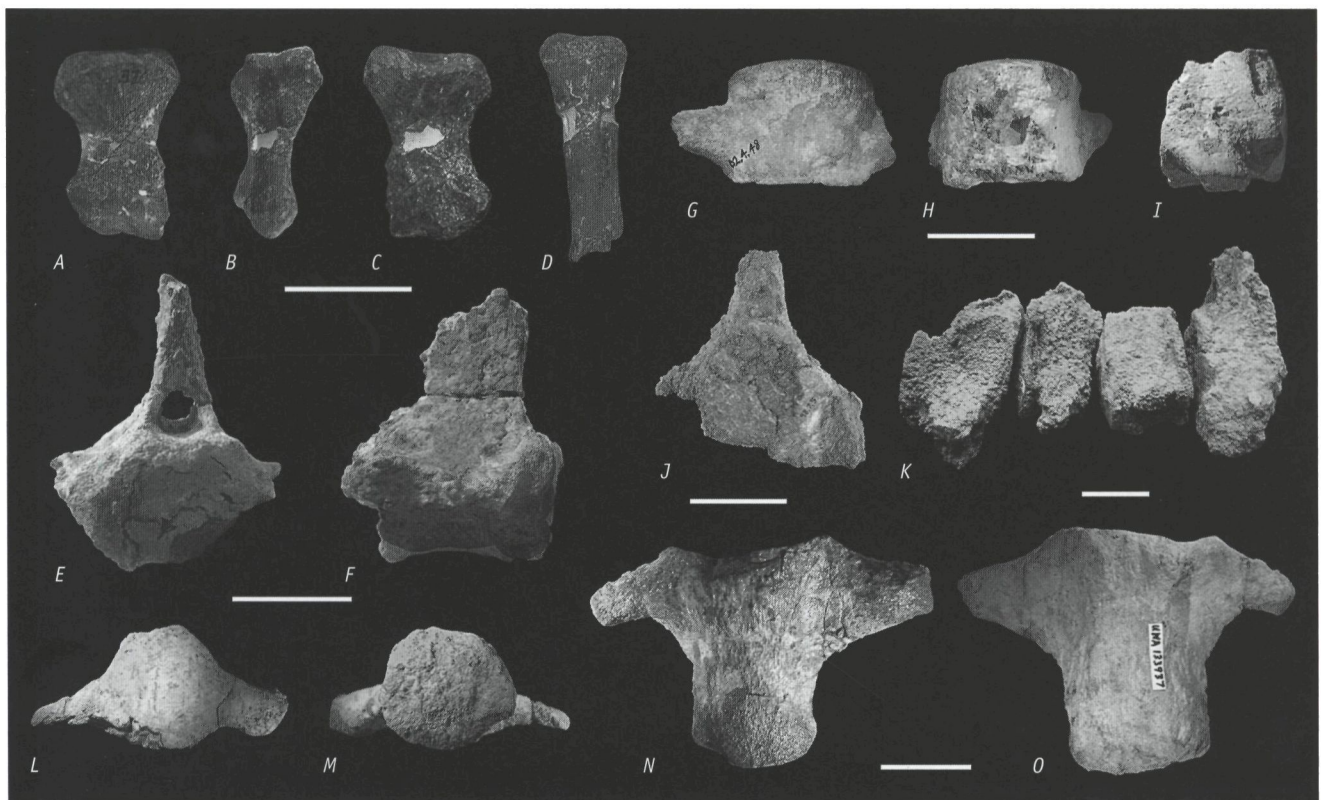


Fig. 2. Mosasaur remains from the Late Cretaceous deposits of Western Australia. cf. *Platecarpus* ulna (UWA 37092) in A - dorsal; B - posterior; and C - ventral views; D - cf. *Platecarpus* phalanx (UWA 37092) in dorsal view. Scale bar is 30 mm. WAM 91.8.16-B, mosasaurid anterior caudal vertebra (Miria Formation) in E - anterior; and F - lateral views. Scale bar is 40 mm. WAM 02.2.48, probable plioplatecarpine caudal vertebra (from Miria Formation locality south of West Tank, Giralia Station, Giralia Ranges) in G - ventral; H - dorsal; and I - lateral views. Scale bar is 40 mm. J - probable plioplatecarpine caudal vertebra (WAM 98.7.5, Molecap Greensand) in anterior view; K - caudal series in lateral view. Scale bar is 40 mm. Korojon Calcarenite mosasaurid ?pygal vertebra (UWA 133937) in L - anterior; M - posterior; N - ventral; and O - dorsal views. Scale bar is 40 mm.

subsequently produced other fragmentary mosasaur vertebrae (Fig. 2G - I). These are all taxonomically indeterminate but suggest the presence of a small-bodied probable plioplacarpine (identified on the basis of small size and rounded centra) in the deposit.

Recently, the Molecap Greensand has yielded additional mosasaur remains including a series of ten trunk/caudal vertebrae with articulating haemal arches (WAM 98.7.1-10) from a locality north of the township of Dandaragan, southwestern Western Australia (Long, 1999). This material (Fig. 2J, K) is currently under study by JEM and JAL, but appears to belong to a moderately sized plioplacarpine.

In 2003, a field party from the University of Western Australia recovered an isolated mosasaur pygal vertebra (UWA 133937, Fig. 2L - O) from deposits of the Korojon Calcarenite in the area of C-Y Creek, Giralia Ranges. This specimen has yet to be described, but nevertheless represents the first discovery of vertebrate remains from this unit, and also a new stratigraphic occurrence for Mosasauridae in Australia.

Palaeobiogeographic implications of Australian mosasaurs

As presently understood, the Australian mosasaur record is dominated by plioplacarpines. Members of this group are known from marine strata in North America, Europe, North Africa, the Middle East and northern South America (e.g., Russell, 1967; Lingham-Soliar, 1991, 1994a - c; Mulder, 1999; Bardet et al., 2000; Bardet & Pereda Suberbiola, 2002; Kiernan, 2002), indicating a wide distribution throughout the Northern Hemisphere. Remains attributed to the plioplacarpine genus *Platycarpus* have also been reported from Upper Cretaceous (Campanian-Maastrichtian) deposits in the Southern Hemisphere, and in particular New Zealand (Lydekker, 1888; Welles & Gregg, 1971; Lingham-Soliar, 1994b). Subsequent reassessment, however, indicates that the taxonomic assignment of this material is untenable (Welles & Gregg, 1971; Bell et al., 1999). As a result, the recent definitive recognition of plioplacarpines in Western Australia (Martin & Long, 2002), in conjunction with other 'russellosaurine' taxa (*Plioplacarpus*, *Lakumasaurus*, *Tylosaurus*, *Taniwhasaurus* and possibly *Hainosaurus*) in New Zealand (Welles & Gregg, 1971; Bell et al., 1999) and Antarctica (Martin, 2002; Martin et al., 2002; Novas et al., 2002), is highly significant as it firmly re-establishes the presence of this lineage in the southern oceans by at least Coniacian times.

Mosasaurs achieved a near-global radiation during the Late Cretaceous. However, many taxa appear to have been regionally restricted, probably in response to localised controlling factors such as habitat preference, prey productivity and prevailing water temperatures. Evidence for this has been found in the well-documented mosasaur assemblages of North America, which show marked palaeoenvironmental (e.g., Kiernan, 2002)

and latitudinally influenced (e.g., Nicholls & Russell, 1990) taxonomic segregation. Interestingly, latitude in particular and its relationship to prevailing water temperature, is thought to have been a major constraint on the taxonomic composition of North American mosasaur faunas. For example, Russell (1966) and Nicholls & Russell (1990) noted that plioplacarpines, and specifically the genus *Platycarpus*, seem to have dominated Campanian high-latitude environments (e.g., Anderson River, Canadian North West Territories placed at $\sim 70^\circ$ N), in contrast to contemporaneous lower-latitude regions (e.g. Niobrara Formation, Kansas, Mooreville Chalk, Alabama, ranging from $\sim 30^\circ$ - 40° N), which exhibited a more partitioned fauna of plioplacarpines, mosasaurines, tylosaurines and basal mosasaurids (*Halisaurus*). Interestingly, this distribution pattern is reversed in the Southern Hemisphere where Campanian-Maastrichtian high-latitude localities (e.g., New Zealand and Antarctica) support a taxonomically diverse assemblage of not only plioplacarpines, but also tylosaurines and predominantly mosasaurines (Wiffen, 1990; Bell et al., 1999; Martin et al., 2002; Novas et al., 2002). The reasons for this contrasting distributional pattern are unknown, although clearly several mosasaurian clades appear to have successfully radiated into high-latitude cooler-water environments during the Late Cretaceous.

All of the currently documented high-latitude mosasaur localities in the Southern Hemisphere (namely Seymour and Vega Islands, Antarctica and North and South Islands, New Zealand) are thought to have lain at around 80° S throughout much of the mid-Late Cretaceous. Conversely, the Western Australian deposits occupied a lower-latitude region between 40° S (Carnarvon Basin) and 50° S (Perth Basin; Embleton, 1984). This is comparable to some of the lower latitude localities in North America (e.g. Niobrara Formation), as well as the southern mid-latitude deposits of northern Patagonia (which lay at $\sim 50^\circ$ S). In the latter, fragmentary mosasaurine remains occur within a Late Cretaceous (Campanian-Maastrichtian) Austral Transitional province (situated above 46° S) characterised by marine reptile (plesiosaur), macroinvertebrate and microfossil assemblages exhibiting a mixture of Tethyan and Weddellian influences (see Gasparini et al., 2001 for discussion). Transitional assemblages also occur in the Upper Cretaceous of Western Australia (see below), perhaps suggesting that mosasaur faunas from this region might similarly have incorporated taxa from both low- and high-latitude areas.

Correlations with sympatric vertebrate fossil records

Direct correlation of the Western Australian mosasaur remains with those known from other transitional mid-latitude faunas is impossible given the fragmentary nature of the current material. Nevertheless, assessment of associated non-mosasaurian vertebrate fossils does provide a basis for

preliminary palaeobiogeographic comparisons. To date, several important taxa have been identified (especially from the Molecap Greensand), mainly representing widely distributed non latitude-specific forms. Importantly however, some characteristic high-latitude taxa are present including potentially the elasmosaurid plesiosaur *Mauisaurus* (Long & Cruickshank, 1998), a taxon known elsewhere from austral high-latitude localities in New Zealand (Welles & Gregg, 1971; Wiffen & Moisle, 1986), the Antarctic Peninsula (Fostowicz-Frelick & Gaździcki, 2001) and Patagonia (Gasparini et al., 2003). Examples of cosmopolitan vertebrates include the Cretaceous teleost *Protosphyraena* sp. (McNamara et al., 1993) and the widespread, long-ranging selachians *Notorynchus*, *Squatina*, *Paraorthacodus* and *Cretalamna*. These are common in the Molecap Greensand, together with other selachian taxa such as *Centrophoroides*, *Protosqualus*, *Anomotodon* and *Protolamna*, all of which have good records from the Cretaceous of Europe and North America (Cappetta, 1987; Williamson et al., 1993). Chimaeroid material from the Molecap Greensand has yet to be described but appears to be related to the cosmopolitan genera *Ischyodus* and *Edaphodon* (Kemp, 1991; McNamara et al., 1993).

Very few of the Molecap Greensand chondrichthyans have been diagnosed to species level. The only confidently identified taxa are the lamnids *Cretalamna appendiculata*, a well-known Cretaceous pelagic form with near-worldwide distribution (Cappetta, 1987; Williamson et al., 1993), *Cretalamna gunsoni* (M. Siverson, pers. comm. 2004), an endemic species known elsewhere from the upper Albian-Cenomanian Alinga Formation, Western Australia (Siverson, 1996); and *Squalicorax kaupi*, a cosmopolitan anacoracid (Cappetta, 1987; Siverson, 1996). This pattern, characterised by a minimum degree of endemism, is common to Cenomanian-Turonian selachian faunas from elsewhere in the world, which also tend to exhibit regionalised species-level differentiation, accounting for most of the geographic variation between what are otherwise remarkably homogeneous generic-level faunas (Williamson et al., 1993).

Chondrichthyan remains from the Miria Formation are poorly known, but may include the wide-ranging anacoracid *Squalicorax*. This taxon has a near-worldwide distribution throughout much of the Late Cretaceous, although the group does not persist past the end of the Mesozoic (Cappetta, 1987).

Correlations with existing macroinvertebrate/microfossil data

The generally cosmopolitan palaeobiogeographic affinities of marine vertebrates found in the Western Australian mosasaur-bearing units are coherent with those of the invertebrates and microfossils. For example, in the Molecap Greensand (and overlying Gingin Chalk), macroinvertebrates (primarily ammonites) have a pandemic character, sharing representatives with contemporary assemblages in northern Australia and New Zealand (Wright, 1963; Henderson, 1973). Similarly, micro-

invertebrates, particularly foraminifera, exhibit a low degree of faunal endemism (a common phenomenon throughout the Late Cretaceous of Australia), and a distinctly transitional faunal composition including taxa from both austral cool water and northern Tethyan warm water regions (Henderson et al., 2000). Studies of calcareous nannofossils from the Perth and Carnarvon basins indicate a distinct austral influence prior to the early Campanian (Shafik, 1990). By the Maastrichtian, however, marked faunal segregation had occurred with the more northerly Carnarvon Basin forming part of an extratropical nannoprovince dominated by warm-water conditions and a cosmopolitan Tethyan-influenced fauna. In contrast, the southern Perth Basin comprised a distinct austral nannoprovince, characterised by cooler waters and an almost exclusively southern-influenced nannofossil assemblage. Support for this observation has been found in the sympatric macroinvertebrate record, which shows that benthic molluscs, especially in the Miria Formation (Carnarvon Basin), were highly cosmopolitan, reflecting the warmer-water conditions and close proximity of the austral margin of the Indian Ocean to the Tethyan Realm (Darragh & Kendrick, 1994). Ammonites also are represented by a mixed fauna that includes some distinctive austral elements (e.g., kossmaticeratids) but is otherwise dominated by cosmopolitan immigrant taxa probably derived from contemporary assemblages in southeastern Africa, and particularly southern India (Henderson & Heron, 1977; Henderson & McNamara, 1985b; Henderson et al., 1992, 2000).

Conclusions

Australian mosasaur fossils are very poorly known but nevertheless provide an interesting addition to the group's global record. The fragmentary nature of the material hampers their utility for definitive palaeobiogeographic comparisons. However, when placed in context with other associated fossils some preliminary hypotheses can be put forward. For example, the Western Australian mosasaur fauna (presently comprising mainly plioplacarpines and perhaps the genus *Platycarpus*) may well have been cosmopolitan in composition (similar to other well-documented austral mosasaur assemblages; see Novas et al., 2002), with generic-level representatives from both northern Tethyan and austral high-latitude regions. This conclusion is supported by the pandemic character of sympatric vertebrate taxa (particularly chondrichthyans) and the transitional nature of macroinvertebrate/microfossil assemblages, which show marked regional differentiation between the Carnarvon and Perth Basin units. This to a large part reflects the recognised palaeobiogeographic separation of the northern and southern Indian Oceans during the mid-Campanian (see Huber & Watkins, 1992), and the subsequent development of distinct northern tropical and southern cool-water marine faunal provinces in the Australian region (Shafik, 1990).

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