Ostracoda from the Miocene, Riversleigh World Heritage deposits, Queensland, including Progomphocyrhere n. gen., with discussion of palaeoenvironments and age

† Kenneth Glencoe MCKENZIE
School of Science & Technology
Charles Sturt University, Wagga Wagga, Australia

Michael ARCHER
School of Biological, Earth & Environmental Science
University of New South Wales, Sydney, Australia

Michael ENGELBRETSEN
Center for Ecostratigraphy & Palaeobiology
School of Earth and Planetary Sciences
Macquarie University, NSW, Australia

Elizabeth PRICE

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ABSTRACT - Examination of residues from the acid dissolution of Miocene freshwater limestones from Riversleigh, northwestern Queensland, Australia led to the recovery of three species of Ostracoda: Progomphocyrhere McKenzie n. gen. (type spec. Progomphocyrhere mawsontalenti n. sp.) represented by many specimens of both sexes; and Cypridopsis sp. and Cypretta sp. by single individuals only. The palaeoenvironment is likely to have been a shallow lake with swampy and/or grassy margins in which Progomphocyrhere lived endobenthically or grazed the sediment surface but cypridopines and cytherellines swam actively in shallows near the lake’s edge. Since the Gomphocythere group taxa have an African-Australian distribution, their evolution post-dates separation of these landmasses from Antarctica. Within continental areas, given their poor vagility, they were probably dispersed passively via birds. We discuss the implications of such considerations for the age of the Riversleigh deposits involved and their diverse faunal assemblages.

INTRODUCTION

Riversleigh is situated in northwestern Queensland, Australia, at about 19°S Lat. and 138°45’E Long., not far from the state border with the Northern Territory. The Tertiary deposits were discovered in the late 1890’s but a sustained programme of research by palaeontologists from the Queensland Museum, later the University of New South Wales did not commence until 1976. Fossil deposits from the Riversleigh World Heritage property have become widely known primarily because of their rich Oligocene, Miocene and Pliocene vertebrate faunas (Archer et al., 1994, 1995, 2000). Well preserved invertebrates are also known (Duncan & Briggs, 1996) but most of these have yet to be studied in detail. In the course of examining hand samples of Riversleigh limestone collected by one of us (EP), valves of ostracodes were found. The material comes from two late Early to early Middle Miocene localities: Ringtail Site and Gag Site. The slightly older fauna from Gag Site is dominated by terrestrial animals but has some aquatic components. The fauna from Ringtail Site is less diverse and dominated by aquatic animals but also contains some terrestrial taxa. SEM micrographs of freshwater Ostracoda from these localities have confirmed the presence of three species. Although the collection consists of single valves only, it includes both sexes and a juvenile of a new limno-cytherid genus. The other two ostracode species are represented by singleton adult females of well known genera.

METHODS

Uncrushed samples of freshwater limestone were dissolved in 10% acetic acid, using the buffering method developed by Jeppsson et al. (1985): 1255 g were processed from Ringtail Site and 950 g from Gag Site. Bones and teeth are seemingly unaffected by
such treatment but the fossils of some other groups could be lost by this process. Most purely calcitic ostracode valves were probably lost by dissolution whereas the corneous-chitinous limnocytherid valves were preserved.

In the systematic section, several conventions: RV = right valve, LV = left valve, L = length, H = height and B = breadth are used throughout.

The entire collection of Ostracoda is stored in the fossil collections of the Queensland Museum, Brisbane under numbers QMF 42706-42737.

SYSTEMATICS

Superfamily Cytheroidea Baird, 1850
Family Limnocytheridae Klie, 1938
Subfamily Timirasevinae McKenzie, 1960
Tribe Gomphocytherini Coli & Danielopol, 1978

**Progomphocythere** McKenzie & Archer n. gen.

Diagnosis - A gomphocytherine genus with a corneous-chitinous carapace characterized by a large brood pouch in females, presenting a swollen appearance posteriorly in dorsal view, with an elaborately developed frill along the entire conspicuously flattened ventral region, and a pitted ornament on the female valves which is differentiated in different areas of the valves; males slightly swollen posteroventrally, with a weaker but undifferentiated ornament. Hinge inverse lophodont. There is no eye tubercle.

Discussion - With respect to the two most closely related genera, the elaborate ventral frill in females is quite distinct from the typical ventral rim of Gomphocythere (Sars, 1924, pl. 17); and in Gomphodella even a weak ventral rim is scarcely developed. (Hussainy, 1969; De Deckker, 1981). There is another alate species in this group of ostracodes, all occurring in Lake Tanganyika (Park & Martens, 2001) but the alae are relatively incomplete, never developing into a continuous ventral frill as in females of Progomphocythere. They include Gomphocythere alata Rome, 1962, a small form (L = 0.46 mm) in which the ala is simple, extending to little beyond the midlength (Rome, 1962, fig. 77). Nor is its surface ornament differentiated over each valve as in females of Progomphocythere. Interestingly, Rome (1962, p. 279) reports that one female of G. alata carried 5 eggs and 3 juveniles in the brood pouch; one of these latter was precociously developed with both antennae and mandibles, a mouth, and anlagen of the maxilla and all three walking legs. The male of G. alata is not known.

Type Species - Progomphocythere mawsontalentini McKenzie, Engelbretsen & Price n. sp. The holotype is a mature female LV – QMF 42706.

**Etymology** - For Profs Ruth Mawson and John A. Talent, School of Earth and Planetary Sciences, Macquarie University, Sydney, who encouraged throughout the development and completion of this project.

**Progomphocythere mawsontalentini** McKenzie, Engelbretsen & Price n. sp.
Pl. 1, figs 1-12; Pl. 2, figs 1-8, Text-fig. 1 A-D

Material - The Queensland Museum, Brisbane, material (QMF 42706-42735) includes adult female and male RVs and LVs, plus a single A-2 juvenile RV. Total number of mature valves recovered is 34, comprising 10RV and 12LV females and 3RV and 4LV males. The sex of the A-2 juvenile valve is not determinable.

Localities - Specimens of Progomphocythere mawsontalentini n. sp. have been recovered from two Riversleigh localities: Ringtail Site and Gag Site.

Description - Shell corneous-chitinous, as indicated in the nature of the crushing exhibited by some valves (Pl. 1, figs 6, 11) and also by a general partial dissolution over the entire valve surface (Pl. 3, figs 1-4), equivalved, and notably sex-dimorphic.

Female shell medium-sized (L = 0.56-0.67 mm), with a large brood pouch, thus swollen posteriorly in dorsal view; breadth distinctly greater than the height; greatest breadth at about 3/4 the length from the anterior edge. In lateral view, height greater than half the length; dorsal margin straight or weakly inflexed above the well developed medial sulcus (also visible internally); ventral margin inflexed anteroventrally in the oral region; anterior margin rounded; posterior margin broadly rounded to accommodate the brood pouch; dominated by a prominent ventral frill extending along the entire flattened ventral margin, transversely-ribbed both above and below and broadest posterovertrally; ornament differentiated in different areas of the valves, distinctly pitted posteriorly and weakly pitted anteriorly of the median sulcus, but pitted in an approximately concentrical alignment below the ventral ala; marginal belt flattened and smooth along the anterior margin, also flattened to minor extent posterodorsally; normal pores include at least two types, a set of equally-spaced conuli immediately behind the anterior margin, representing the exits of 10-15 marginal pore canals (Text-fig. 1 B) and numerous simple pore conuli sited in the nodes between pits over the entire remaining surface (Text-fig. 1 C) apart from the ventral ala; four central adductor muscle scars in a vertical series, sited in a depression medially on the median sulcus; no eye tubercle. Internally, there is a distinct marginal selvage and well developed flange, but the inner lamella is very narrow around the entire periphery; the median sulcus, which is convex towards the anterior, divides...
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Text-fig. 1 - *Progomphoc'ythere mawsontalenti* n. sp. Riversleigh, Queensland, Gag Site. A) detail of ornament below ala (Pl. 1, fig. 10), x 309; B) detail of anteroventral margin (Pl. 1, fig. 1), x 332; C) detail of mid-posterior female (Pl. 1, fig. 1), x 281; D) detail of mid-posterior male (Pl. 1, fig. 2), x 330.

A-2 juvenile RV (L = 0.37 mm, H = 0.19 mm) similar in ornament to the male but more broadly rounded anteriorly than posteriorly and with only a weak posteroventral swelling, pore conuli not as evident as in adults, but certainly simple; hinge adont.

The sex of this juvenile cannot be determined with any certainty (Pl. 2, fig. 7).

Dimensions (in mm) -
- Mature females: L = 0.57-0.67; H = 0.33-0.35; B = about 0.40.
- Mature males: L = 0.55-0.59; H = 0.30-0.31; B = about 0.30.

The valves into approximately equal compartments; hinge inverse lophodont, consisting of terminal loculi separated by a smooth intervening ridge in the RV, with complementary terminal lobes and an accommodation groove in the LV.

Male shell medium-sized (L = 0.55-0.59 mm) also coneous-chitinious but not conspicuously flattened ventrally as in the female and without a brood pouch although slightly swollen posteroventrally (Pl. 2, fig. 5), to accommodate the evidently large hemipenes, making it broader posteriorly than anteriorly in dorsal view; breadth about equal to the height; greatest breadth rather less than 3/4 of the length from the anterior edge. In lateral view, height equal to or slightly greater than half the length, greatest height in the anterior forward of the ventral flexure; dorsal margin straight; ventral margin weakly inflected anteroventrally in the oral region; anterior and posterior margins both broadly rounded, the former higher; median sulcus present, less convex towards the anterior than in the female and placed towards the anterior half of the shell, rather than medially, so that the posterior compartment (when a valve is viewed internally) is larger than the anterior compartment, allowing for large hemipenes. Ornament comprising a more weakly expressed pitting than in females over the entire valve surface, anterior margin smooth, also with concentrically-aligned riblets in the somewhat swollen posteroventral area; numerous simple normal pore canals, but the exits of the marginal pore canals are not as obvious as in females although their number in the anterior of each valve is likely to be similar; four central adductor muscle scars, disposed as in the female; no eye tubercle. Internally, there is a distinct marginal selvage, and narrow flange and inner lamella; hinge inverse lophodont, organized as in the female.
Superfamily Cypridoidea Baird, 1845  
Family Cyprididae Baird, 1845  
Subfamily Cypridoidea Bronstein, 1947  
Genus Cypridopsis Brady, 1868

Cypridopsis sp.  
Pl. 2, fig. 9

Material - Mature female LV (QMF 42736).

Locality - The lone specimen was recovered from Gag Site, Riversleigh.

Description - Singleton mature medium-sized (L = 0.67 mm) female LV; greatest height medial and more than half but less than 2/3 the length; greatest breadth slightly behind the midlength, estimated at a little more than the height; subelliptical in dorsal view. In lateral view, dorsal margin convex; ventral margin weakly inflexed medially; anterior more narrowly rounded than the posterior margin; shell surface smooth; normal pore canals simple. Internally, inner lamella distinct, moderately broad anteriorly, damaged posteriorly; marginal pore canals and radial septa, since they lie within this lamella cannot be discerned; no definition of a cypretine central scar pattern; hinge adont, comprising an arcuate ridge in the RV which would be complemented by a groove in the LV; RV certainly overlaps the LV anterodorsally; no ventromarginal denticulations.

Dimensions (in mm) – L = 0.69; H = 0.50; B = about 0.43.

PALAEOENVIRONMENT

Our identifications of the living ostracode genera Cypridopsis and Cypretta, although based on singletons, are important for interpreting the likely palaeoenvironment of the deposits at Gag Site; they apparently do not occur in the material from Ringtail Site. Both genera have several natatory setae on their antennae that reach or even overlap the lengths of the terminal antennal claws. Thus, they are excellent and active swimmers. Progomphocythere, on the other hand, by analogy with living Gomphocythere group genera, had no natatory antennal setae and thereby was not a swimmer but likely grazed the water-sediment interface. It may also have lived endobenthically, as has been described for the Australian species Gomphodella australica by Hussainy (1969, p. 303).

The association of these three taxa at Gag Site is useful because it is similar to that at Lake Purrumbete, a volcanic maar in the Western District of Victo-
ria, where Hussainy (1969, p. 300) collected his material. Other associated small crustaceans at Lake Purrumbete include the ostracodes Candonocypria novozelandiae (Baird, 1843), Neunhamia fenestrata King, 1855, and Dacycylops sp., all Australian taxa, plus the copepod Microcylops and the cladoceran Macrotbrix (Hussainy, 1969; Chaplin, 1992). These animals live in shallow water near the lake margins among weeds and grasses with patches of clear water (in which the Neunhamia skates upside down over the lower water meniscus). Like Gomphodella, the Candonocypria also has an endobenthic habit of life. The environment is well oxygenated and fresh-oligohaline. Hussainy (1969) reports a TDS (Total Dissolved Solids) of 425 ppm. A small body of water with similar characteristics was the likely palaeoenvironment at Gag Site.

As Ringtail Site, where only Progymphocyt here valves have been recovered, a more permanent and deeper habitat might be expected. The ecological data reported by De Deckker (1981) confirm that Gomphodella can only occur in permanent freshwater because it lacks desiccation-resistant eggs (McKenzie & Hussainy, 1968) and that it can tolerate weakly brackish conditions - he cites a salinity of 2.3% at Fresh Dip Lake, near Robe, South Australia. His distribution records include recoveries from a short core at Blue Lake, Mount Gambier, South Australia and from two fossil sites in northwestern Tasmania (De Deckker, 1981). More recently, Maddocks & Iliffe (1993) found it in the Benara Sinkhole, near Mount Gambier. De Deckker (1981) also notes the possibility of an endobenthic habit of life that is amplified by the record of Gomphocythere sp. occurring interstitially in waters of the Rot6rua lakis, New Zealand.

Sars (1924) illustrates small eye tubercles on the shells of his Gomphocythere species from South Africa. No such tubercles are illustrated for the Lake Tanganyika species (Rome, 1962) and eye tubercles are neither reported nor illustrated for Gomphodella (Hussainy, 1969; De Deckker, 1981), nor is an eye tubercle evident in Progymphocyt here. Nevertheless, as far as it is known, all living species in the group possess eyes with fused eye cups. Another important aspect of the biology of these interesting animals is the fact that females use the brood pouch to carry not only fertilized eggs but young up to at least the second growth stage. The main reason for this is that non-marine cytheracean eggs lack the protective lipid coating that makes the eggs of many cypridoids desiccation-resistant and enables the dispersion of these tiny entities by winds and often by man thus transferring species even intercontinentally (McKenzie & Moroni, 1986). Different vectors are invoked to disperse non-marine cytheroids within continental areas as we discuss below.

Since all specimens were recovered as single valves only, it is likely that the palaeoenvironment was periodically agitated. This factor precluded the recovery of complete carapaces, which in the case of living mature females regularly carry some brooded young instars (Hussainy, 1969). De Deckker (1981) also found brooded young in some complete female carapaces from the Tasmanian fossil sites where females make up a high percentage of finds. Based on 30 valves, the sex ratio of Progymphocyt here at Riversleigh was about 2.5:1, favouring females; but it was almost 1:1 at Lake Purrumbete in a count of more than 4500 adults (Hussainy, 1969).

Most Riversleigh limestones formed in freshwater pools, cave deposits or open fissures. Palaeoecosystems are currently interpreted (Archer et al., 1995) ranged from complex closed forests (i.e. rainforest) in the Early and Middle Miocene, to more open forests by the Late Miocene and Pliocene. The presence of environmentally-demanding animals in the Early and Middle Miocene such as Hypsiprymnodon (musky rat kangaroos), dactylopsine petaurids (striped possums), Pseudochirops (green ringtail possums); Menura (lyebirds) and Orthonyx (log runners) (Boles, 1997), which today have representatives only in the rainforests of Australia and New Guinea, supports the interpretation of closed forest palaeocommunities. Changes in the abundance of Lechriodus frogs upwards through the Riversleigh sequences and the abundance of tiny

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**EXPLANATION OF PLATE 2**

Figs 1-8 - *Progymphocyt here majorisnensi* n. sp. Riversleigh, Queensland.
1. female LV internal oblique, 0.60 mm, x 107.
2. male RV internal, 0.56 mm, x 102.
3. male RV internal, 0.55 mm, x 107.
4. male RV internal, 0.55 mm, x 110.
5. male LV internal oblique, 0.55 mm, x 111.
6. male RV, 0.57 mm, x 111.
7. A-2 juvenile RV, 0.37 mm, x 166.
8. female LV, 0.57 mm, x 104.

Fig. 9 - *Cyprilopsis sp.* - female LV internal, 0.67 mm, x 90.

Fig. 10 - *Cypretta sp.* - female RV internal, 0.69 mm, x 84.

Fig. 1 is from Ringtail Site, the rest are from Gag Site.
bubble-nesting species further indicates that the Early and Middle Miocene forest communities were continually moist and warm (Tyler et al., 1990). In general terms, they existed under ‘greenhouse’ conditions of high (monsoonal) rainfall, warm temperatures and considerable biodiversity (Frakes et al., 1987). The drying and progressive opening of these rainforests began in the late Middle Miocene about 15 Ma ago but accelerated into the Late Miocene between 11.2 and 5.32 Ma ago when drier sclerophyll forests and woodlands began to dominate the region.

**DISTRIBUTION AND EVOLUTION**

Through the early Mesozoic, Cytheroidea remained a major component of non-marine ostracode faunas and limnoctyrids were represented mostly by the subfamily Tintiriasiavinae Mandelstam, 1960 with a worldwide distribution in the Neoocoman (Colin & Daniellopol, 1979); but these had declined sharply by the Upper Cretaceous, and Timiriasevia Mandelstam, 1947 itself was extinct by the Palaeocene. We interpolate here that the numerous records (often cited as questionable) of Gomphocythere from the Mesozoic (Kempf, 1980) are all of species with carbonate valves and thus correctly determined. Further, records from the Eocene of Libya (N. Kretic, personal communication, February 2003) have been determined as Elpidium and Kovalevskyia and do not have gomphocytherine characters (Zolnay, 1979, figs. 6-8); also a species described recently from the Late Cretaceous-Palaeocene Inter-Trappean Beds of the Deccan, India is a calcareous form referable to Cytheridella Daday, 1905 (D.J. Horne & D.L. Daniellopol, personal communications, February 2003). The general Late Mesozoic pattern is well expressed by non-marine ostracode faunas of Mongolia (Khand, 2000, fig. 1). Recent Tintiriasiavinae are represented by 4 genera and 30 or so species in Africa, South and Central America, Europe and Turkey, plus Gomphocythere and Gomphodella (Martens et al., 1998). This sharp decline in the late Mesozoic is explained as due to the narrow ecological tolerance limits and poor dispersion abilities (vagility) of tintiriasiavines. These limitations likely made them more vulnerable to major environmental disruptions than Cypridoidea which as a result expanded as the tintiriasiavines declined (Colin & Daniellopol, 1979). Modern non-marine ostracode assemblages are dominated usually by Cyprididae and populations often consist entirely of parthenogenetic females, with clones being common and the occasional co-existence of different morphotypes (Bellavere et al., 2002). Riversleigh is unusual in that so few cypridids have been recovered; but this poverty of record is likely an effect of the acetic acid digestion method used primarily to recover vertebrate bone fossils - on carbonate shells: fossils of small freshwater molluscs are also rare at Gag Site (see Methods).

The list provided by Hussainy (1969, Table 1) records 14 Gomphocythere species of which two (Gomphocythere australica Hussainy, 1969, and Gomphocythere sp. McKenzie, 1966) were put in Gomphodella by De Deckker (1981) who added the species Gomphodella maia De Deckker, 1981. Of these 15 species, Gomphocythere arrogensis (Ferguson, 1967 belongs in the genus Cytheridella Daday, 1905 since the shell is calcareous and lacks the typical gomphocytherine ornament, and the hirsute lappets in the genital area that also typify Gomphocythere are not recorded by Ferguson (1967). To these must be added a new species from Israel (Martens, 1993), 4 new species from Lake Tanganyika (Park & Martens, 2001) and 5 new species from Lake Nyassa (K. Martens, personal communication, February 2003) all belonging in Gomphocythere, as well as new Late Quaternary records for Gomphocythere angulata Lowndes, 1932 from the Ziway-Shala basin, Ethiopia (see Atafu & Russo, this volume). Thus, distribution of Gomphocythere and Gomphodella extends to Africa, Israel, Australia and New Zealand – the latter including Gomphocythere problematica (Brehm, 1932) from Waimate Gorge, South Island (Brehm, 1939) and Gomphocythere difff Hornibrook, 1955 from the Pyramid Valley Swamp, New Zealand. Clearly, Gomphocythereini evolved after the separation of South America from Africa that initiated in the mid-Cretaceous (Reyment & Dingle, 1987). India – which has few limnoctyrids (Battish, 2000) – was well removed from the other Gondwana blocks by the Late Cretaceous (McKenzie, 1999) but there remained a connection between South Africa and Australia via Antarctica, and New Zealand was also accessible at this time (Veevers, 1991, fig. 3C).

Martens (1995) notes several ‘soft parts’ affinities between Cytheridella and gomphocytherines (antennule, antenna, maxillule) as well as some differences (mandible palp, detail of the posterior body, hemipenis). Thus cytheridellines, which have calcareous shells and advent hinges, might well represent an ancestral linkage to the genera of our interest. The simplest evolutionary pathway for gomphocytherines, however, following the crucial development of a more chitinous carapace, likely proceeded from late Progomphocythere with an inverse lophodont hinge (Australia) to Gomphodella with a lophodont hinge in Australia and to Gomphocythere with an inverse lophodont hinge in Africa. The New Zealand species ascribed to Gomphocythere exhibits several differences in details of its soft anatomy from that genus sensu stricto (Brehm, 1939, p. 192) and await modern reevaluation. Nevertheless, the scenario summarized above suggests that gomphocytherines likely initiated in the Palaeogene but there is insufficient fossil evidence to test this hypothesis. Since the greatest diversity of Tintiriasiavinae is in Africa, including many species of Gomphocythere, the hypothetical ancestor may have evolved there. Despite being confined within relatively narrow ecological limits, poorly vagile and without desiccation-resistant eggs, resulting in restricted dispersion
opportunities, \textit{Gomphocycthere} has dispersed widely in South and East Africa from the Cape to Abyssinia. The most likely vectors for this dispersal are birds. It seems less plausible that large animals, such as wildebeest, buffalo, elephant and hippopotamus or early hominids, passively ferried fertilized or broodly females in moist mud plastered to their bodies as they roamed the African thorn scrubs and savannahs.

In Australia, the distribution of \textit{Gomphocycthere} is restricted to the southeastern part of the continent, including Tasmania. The hinge reversal that took place in its development from \textit{Progomphocycthere} is not regarded as requiring a long passage of time geologically; indeed, Martens et al. (1998, p. 45) synonymize \textit{Gomphocycthere} and \textit{Gomphocycthere}. But \textit{Progomphocycthere} is restricted to the Riversleigh deposits in Queensland. Ambient temperatures were certainly greater there throughout the Tertiary than in the southern states. Giving consideration to eustatic and climatic cycles as indicated by Cenozoic palaeogeography (Piccoli, 2002, fig. 4), dispersal southwards would be most favoured during the warm epochs of the Late Eocene and Early and Middle Miocene. The evolution to \textit{Gomphocycthere} probably occurred after the Miocene warmings, which followed on from a pronounced Oligocene cooling. The Newer Volcanics of Victoria in which many maar lakes occur are Pliocene in age (Abele et al., 1976, p. 217) and Quaternary fossils of the genus have been found in Tasmania. Again, the most likely dispersal vectors were birds. By the Miocene, the avian fauna of Australia was diverse and migration pathways already well established (Vickers-Rich & van Tets, 1982). Birds such as waders and ducks can carry ostracodes in moist muds attached to their feathers and in their crops (see McKenzie, 1971). Dispersal by birds via short flights from lake to lake or swamp readily accounts for the distribution of \textit{Gomphocycthere} from Robe and Mount Gambier in South Australia, through the Western District of Victoria (where Lake Purrumbete is located), to the swamps of northwestern Tasmania. Cooler Quaternary climates in southeastern Australia may have favoured development of a relatively weaker ornament. In any case, the hinge in \textit{Gomphocycthere} switched to lophodont. Meanwhile, \textit{Progomphocycthere} was unable to withstand the major environmental disturbances that terminated the existence of the Riversleigh fauna (Archer et al., 1989) and there are no other records of Timitriasevinai from Queensland.

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† Kenneth Glencoe McKenzie
School of Science & Technology,
Charles Sturt University, Wagga Wagga, Australia

Michael ENGELBREITSEN
Center for Ecostratigraphy & Palaeobiology,
School of Earth and Planetary Sciences
Macquarie University, NSW, Australia

Michael ARCHER
Elizabeth PRICE
School of Biological, Earth & Environmental Science
University of New South Wales, Sydney, Australia