Climatic implications from the sequential changes in diversity and biogeographic affinities for brachiopods and bivalves in the Permian of eastern Australia and New Zealand

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ABSTRACT

Brachiopoda and Bivalvia of successive macro-invertebrate zones of eastern Australia and New Zealand are analysed to demonstrate a sequence of climatic change throughout the Permian Period, reflecting glacial episodes, separated by warmer intervals. Three such glacial intervals are indicated for the Early (Cisuralian) Permian (a long Asselian episode, a brief Artinskian episode and a substantial Kungurian interval), followed by a cold Roadian interval (Middle Permian–Guadalupian), and a very late Permian (Lopingian) episode. Markedly warmer intervals developed in the possibly late Asselian, Baigendzinian and much of the Lopingian. In addition, relatively long cool times allowed the flourishing and comparative diversification of eastern Australian faunas at several stages.

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1. Introduction

As in the Pleistocene and Recent, the Permian world endured episodic glaciation, centred on Gondwana, and in strong contrast to the climatic regime for the Permian palaeotropics. Permian glacial conditions are recorded by tillites, varves, and dropstones, and are further indicated by particular fossils and biotic assemblages found in association with these sediments, such as the bivalve *Eurydesma* and *Eurydesma* fauna (Waterhouse and Bonham-Carter, 1975; Runnegar, 1979; Dickins, 1985). Given that this genus is not known in palaeotropical sediments, even in the absence of glacigene sediments, *Eurydesma* points to cold conditions, and is psychrophilic. By contrast, many palaeotropical faunas of Permian age, such as fusulines and compound rugose corals, are never found either in glacigene sediments, or in regions deemed to have been high-latitude, but only where oceanic waters were uniformly warm (e.g., South China and parts of Japan during the Permian). There is added complexity. Climate changed throughout the Permian Period, and stratigraphic intervals in eastern Australia with tillites and dropstones are interspersed with marine intervals with different, warmer-water fossils, whilst on land, coal measures accumulated that demanded a warmer climate (Waterhouse, 1963, 1973, 1976; Loughnan, 1975). Marine faunas were strongly affected by such shifts in climate, so that even in the Permian high latitudes of eastern Australia and New Zealand, faunas associated with tillites and dropstones differ from those with links to lower latitudes.

The Permian faunas of eastern Australia and New Zealand, called the Austrazean Province by Archbold (1983), are broadly assessed in this paper to trace the sequential exchanges in diversity and biogeographic affinities. The faunas expand the data available from sediment type, because glacigene sediment is generally restricted to near-source deposits, and often readily cannibilised by tectonism and erosion, whereas off-shore marine shelves may still preserve some of the sedimentary record with cold-water faunas. Anyone familiar with glaciers and mountain terrains knows how variable and ephemeral conditions are for the deposition and preservation of tillite: the number of tillite bands can be counted, but may mean little in a Palaeozoic time-frame that is relatively coarse.

One question addressed by Stehli (1970) and Stehli and Grant (1971) has been the reliability of sampling for fossil assessment. A scheme was devised to assess reliability of sampling through the proportion of so-called cosmopolitan brachiopod families present in any collection (Stehli and Grant, 1971). But this approach was flawed in assuming that various palaeotropical brachiopod families were of world-wide extent—very few were. Waterhouse (1972, 1982) showed that the supposedly cosmopolitan families were far from ubiquitous,

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and consequently proposed a different standard for eastern Australian and New Zealand faunas. This, further elaborated by Waterhouse and Bonham-Carter (1975), was based on a world-wide and comprehensive brachiopod faunal assessment, to impose quality control on samples and estimates of palaeolatitudes and climate of these samples, and to indicate alliance of families to high latitudes (polar), low latitudes (tropical) and temperate latitudes. A scoring method was elaborated that encompassed a degree of flexibility. Even apart from mere numerical values, it was possible to gain high value from the occurrence of a single species or genus. Their emphasis on families remains justifiable, because there are a number of related genera that are similar in their palaeolatitudinal distribution, and may be clustered as families or subfamilies, or even superfamilies. But the calibration needs to be adjusted, because there have been significant changes to brachiopod family classification, as well as considerable expansion in described faunas and improved age control over the past three decades.

2. Diversity changes throughout marine Permian of eastern Australia and New Zealand

2.1. Eastern Australia–New Zealand Permian sequences and faunal successions

Permian rocks and marine macro-invertebrate faunas are common in eastern Australia and New Zealand and have attracted many palaeontological studies over the past 170 years (see Waterhouse, 2011 for a recent review). However, due to their endemism associated with their high southern latitude position and a lack of index fossils such as conodonts and fusulines that are widely used for global chronostratigraphic definitions, the faunas are generally difficult to be correlated precisely with those in the palaeotropical regions such as the Urals, South China, or the diverse Texas faunas in southwest USA. Although some of the faunas remain to be systematically described or updated, sufficient is known to permit the proposition of several general biostratigraphic schemes (e.g., Briggs, 1998; Waterhouse, 2008a, and earlier references therein cited). The discussions presented in this paper are based on a Permian zonal scheme recently proposed by Waterhouse (2008a), with minor updates in Waterhouse (2011). This scheme has been based on a series of detailed and systematic re-assessments and syntheses of the eastern Australia and New Zealand Permian faunas in the last decade (e.g., Waterhouse, 2001, 2002a,b, 2008a,b, 2010).

The combined eastern Australia–New Zealand succession of macro-invertebrate zones, as shown in Fig. 1, is integrated from the brachiopod and bivalve successions of eastern Australia and New Zealand. The integration across the Tasman is both possible and necessary because the sequences and faunas between the two sides appear to complement each other despite some local differences. The best-known rocks and faunas of Queensland and New South Wales show a number of stratigraphic and faunal gaps, so that faunas well developed in one area are feebly developed or absent from other sequences. The same arrangement pertains widely over eastern Australia, where packets of often fossiliferous Permian sediments are separated by chronologic and faunal gaps undetectable, or at least immeasurable in terms of duration, except through fossil correlation. The gaps are not visible in the field, so they have to be detected through close study of the fossils. The staggered nature of the marine fossil record, especially for the late Early Permian, Middle Permian and Late Permian, have been calibrated against the much more continuously marine sequences of New Zealand (Waterhouse, 2002a; Waterhouse and Shi, 2010), which at intervals share faunas with the Bowen Basin of central Queensland (Waterhouse and Sivell, 1988). But the lower Early Permian (Asselian, Sakmarian) fossil record of New Zealand is incomplete, and so the interpretation for eastern Australia must rely on internal evidence, buttressed by consideration of distant faunal sequences in Western Australia and south and southeast Asia, as discussed below under biogeographic affinities.

2.2. Standard cold-water faunas

Provisionally, first assessments presented herein are based on two approaches. An eastern Australian standard of cold-water Permian faunas is recognised, based on genera that occur in most eastern Australian and New Zealand Permian faunas, as enumerated below and also in part summarised in Waterhouse and Shi (2010). Various key genera have to be a flexible part of the standard (Table 1). Either *Terrakea*, *Paucispinauria*, or *Saetosina*, constitute eastern Australian representatives of Subfamily Paucispinaurinae. If any one of these three is not present, that is taken to indicate incomplete sampling. *Echinalosia*, *Wyndhamia*, *Pseudostrophalosia*, *Glabauria*, *Strophalosia* or *Marginalosia* are all taken as critical members of the Strophalosiidae, which is represented by one or other (or more) of these genera in a well sampled collection. The variation in permitted genera is based on extensive observation published in systematic and stratigraphic monographs and articles, and allows a degree of flexibility and reality in applying the method. If standard genera are missing, then the inferred (estimated) species diversity of a sample is, with reservations as explained shortly, regarded as incomplete and is adjusted by multiplying the number of species present in the sample by the number of dominant genera missing from the sample (Fig. 1).

Cold-water bivalves include *Etheripecten*, *Orbiculopecten*, *Striochondria*, *Eurydesma*, *Stutchburia*, *Merismoptera*, *Myonia*, *Pachymyonia* and *Vacunella*. These are more sporadic in samples: but one outstanding group, *Eurydesma* Morris and its descendent genus *Glendella* Runnegar, is widespread, and often form monospecific communities associated with tillite and often glacial-type sediment (Runnegar, 1970; Waterhouse and Gupta, 1978). They are recognised as an index of cold-water, pointing to conditions probably even more severe than endured by any brachiopod assemblage.

Judged from the fossil record, there are six intervals of very low faunal diversity in the eastern Australian–New Zealand Permian (Fig. 1): two in the basal Permian of eastern Australia, one brief interval in the Artinskian, and another near the top of the Early Permian (middle Kungurian) (*Glendella dickinsi* Zone); the Middle Permian includes a basal Wordian or upper Roadian interval, and the Late Permian one interval in the Changhsingian. This assessment is close to the depiction of the Permian climatic regimes in Waterhouse (1976, fig. 10, p. 38).

2.3. High diversity faunas

Between the faunal intervals governed by cold-water taxa occur a number of intervals in which the eastern Australian dominants are few, or entirely missing. Given the nature of genera present, the absence of eastern Australian dominants implies different all-pervasive conditions—not substrate or water-depth because such may be comparable, and different substrates have been sampled—but different climate and temperature. Such faunal intervals are dominated by genera that are comparatively rare, or even missing, from faunas that have a substantial number of the eastern Australian dominants (Table 1). Such genera include taeniothaerids (i.e., *Taeniothaerus*), *Waagenoconcha*, *Stenoscisma* or allies such as *Bicamella* and *Coledium*. *Ambikella* or *Ingelarella*, two cold-water genera, may be replaced by *Martiniopsis* which is found in warmer waters of south Asia and Russia etc., or by *Tigillumia*, its ally; *Attenuatella* and *Biconvexiella* may be present in abundance, yet are absent from the low diversity faunas, and the same is true for martiniids, including *Spinomartinia*; *Neospirifer* or *Simplicisulcus* replaces *Aperispirifer*; and spiriferellids *Arcullina* and *Alispiriferella* enter the faunas. Such genera are typical of Permian faunas in warmer or warm-temperate water regions of south-east Asia, Timor, and Himalaya; and some of these even appeared in the Changhsingian tropical waters of South China and northern Thailand (e.g., *Attenuatella* and *Spinomartinia*) (Waterhouse, 1983; He et al., 2007). The Late Permian includes two such intervals, both in Changhsingian, above a suspected early Wuchiapingian warm-water interval not based directly on diversity data. There are two