

## PALEOECOLOGY OF EARLY–MIDDLE PERMIAN MARINE COMMUNITIES IN EASTERN AUSTRALIA: RESPONSE TO GLOBAL CLIMATE CHANGE IN THE AFTERMATH OF THE LATE PALEOZOIC ICE AGE

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### ABSTRACT

Climate change has exerted a major influence on the biosphere in historical times, altering the geographic range of many species and elevating the extinction risk in both marine and terrestrial realms. This study investigates marine community change during the major early Permian climatic transition from the late Paleozoic ice age to a largely ice-free greenhouse climate. Quantitative counts of fossil abundance from 71 field assemblages and 15 collections from the literature, spanning the early and middle Permian (Sakmariian–Capitanian) of the Tasmania, Sydney, and Bowen basins of eastern Australia document substantial changes in the composition of marine communities during Sakmariian–Kungurian postglacial warming. During the last stages of glaciation (Sakmariian), communities were dominated by the brachiopod *Trigonotreta* and the bivalve *Eurydesma*, whereas communities from the later greenhouse climate (Kungurian–Guadalupian) contained abundant productide brachiopods such as *Terrakea* and *Echinalosia*. The shift was broadly synchronous at all paleolatitudes within eastern Australia but appears to have occurred first in offshore habitats. Artinskian communities may also have been much more variable than either earlier or later communities. This variability may have been triggered by rapid climate fluctuations, similar to the changes observed in Artinskian tropical terrestrial ecosystems, but it may also stem from sampling a greater number of depositional environments and habitat types. The ultimate fate of the dominant glacial genera differed after they lost dominance, with *Eurydesma* becoming extinct during climate warming but *Trigonotreta* persisting at low abundance levels for a much longer time. These results support the theory that climate change most often causes extinctions through indirect paleoecological effects and underscore the important consequences that even gradual, long-term climate change can have in marine ecosystems.

### INTRODUCTION

Temperature is one of the fundamental controls on the geographic distribution of modern terrestrial and marine organisms, influencing their growth, reproduction, and ultimate survival (Clarke, 1993; Walther et al., 2002; Harley et al., 2006; Parmesan, 2006). Changes in temperature can have a direct physiological impact on gas diffusion, metabolic rates, and biochemistry, potentially killing mature organisms. Organisms, however, often have relatively robust physiological tolerances that exceed the typical range of temperature fluctuations (Clarke, 1993). It is instead more common, especially in the marine realm, for temperature changes to have more pronounced ecological consequences, influencing the distribution

and survival of species indirectly through changes in reproductive potential, relative abundance, and strength and nature of interspecific interactions (Clarke, 1993; Harley et al., 2006). The broad importance of these direct physiological and indirect ecological effects is demonstrated by poleward shifts in the latitudinal range of many species during the current warming trend (Root et al., 2003; Parmesan, 2006). Predictions of widespread extinction during global warming (Walther et al., 2002; Thomas et al., 2004; Parmesan, 2006) and the potential for ecosystem disruption stemming from biodiversity loss (Symstad et al., 1998; Petchey et al., 2004; Larsen et al., 2005) further highlight the critical relationship between climate fluctuations and faunal change.

The deep-time perspective provided by the fossil record implies that biotic change is a common phenomenon during climate fluctuations (Kitamura et al., 2000; Roy et al., 2001; Falcon-Lang, 2004; Angiolini et al., 2005; Montañez et al., 2007). Pleistocene molluscan communities underwent significant compositional shifts as a result of immigration by warm-water taxa and extinction of cold-adapted species during glacial-interglacial climate change (Kitamura et al., 2000). In addition, climate fluctuations triggered geographic range shifts among Pleistocene mollusc species (Roy et al., 2001). Similar changes in community composition and geographic range have also been observed in terrestrial plant communities during the Pleistocene (e.g., Harrison and Prentice, 2003). Although they are less well constrained, climate fluctuations during the late Paleozoic ice age, the last major glacial episode prior to Cenozoic glaciation, also had widespread biological effects. Latitudinal diversity gradients became steeper and the average latitudinal range increased during early Permian climate warming (Powell, 2007), while within-assemblage species richness and diversity also increased (Angiolini et al., 2005). Both glacial-interglacial cycles and postglacial warming caused substantial community change in North American tropical forest ecosystems (Falcon-Lang, 2004; Montañez et al., 2007). In particular, rapid climate fluctuations during final early Permian deglaciation and transition to the middle Permian greenhouse world were accompanied by substantial restructuring of North American vegetation communities and major short-term disruptions in tropical forest ecosystems (Montañez et al., 2007).

The late Paleozoic ice age was marked by the development of alpine glaciers and polar ice caps on the southern supercontinent of Gondwana between the Late Devonian and middle Permian (Isbell et al., 2003). The waxing and waning of these large ice sheets were accompanied by major eustatic sea-level changes and dramatic fluctuations in global climate. Ice cover was not continuously present throughout the entire late Paleozoic, however; a large polar ice cap developed only during the latest Carboniferous–early Permian Glacial III interval, whereas isolated alpine glaciers were present during the latest Devonian and mid-Carboniferous Glacial I and II episodes (Isbell et al., 2003). Melting of the large Glacial III ice cap took place during the early Permian, with maximum deglaciation occurring during the Sakmariian Stage (Dickins, 1996; dos Santos et al.,

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1996; Visser, 1996; Angiolini et al., 2003; Isbell et al., 2003), and ultimate establishment of a largely ice-free greenhouse climate by the Kungurian Stage at the end of the early Permian (Isbell et al., 2003; Montañez et al., 2007).

The geological and paleontological record of postglacial climate change is well exposed in eastern Australia, which was located at high southern latitudes during the Permian with its eastern continental margin aligned in a broadly north-south orientation so that the Tasmania Basin was within the paleo-Antarctic circle and the Bowen Basin was located at high temperate latitudes. Early–middle Permian successions in Tasmania (Clarke and Banks, 1975; Rogala et al., 2007), the Sydney Basin in New South Wales (Eyles et al., 1998; Fielding et al., 2006), and the Bowen Basin in Queensland (Draper, 1988; Jones and Fielding, 2004) contain high-latitude glacially influenced marine sediments with diamictite, ice-rafted debris, and glendonites. There were four discrete Permian glacial intervals in the Sydney-Bowen basin (Fielding et al., 2008). The first two in the Asselian–early Sakmarian and late Sakmarian–early Artinskian both included sizeable ice sheets, whereas the later Kungurian–early Roadian and late Guadalupian episodes had more limited alpine glaciers. Although cold conditions persisted in eastern Australia through the middle Permian (Jones and Fielding, 2004; Jones et al., 2006; Fielding et al., 2008), the majority of global climate change occurred between the start of widespread deglaciation in the Sakmarian and the onset of greenhouse conditions in the Kungurian (Montañez et al., 2007).

Late Paleozoic climate change also had pronounced effects on marine diversity, latitudinal diversity gradients, and invertebrate extinction and origination rates (Stanley and Powell, 2003; Angiolini et al., 2005; Powell, 2007), but it is not clear whether early Permian marine communities also exhibited major paleoecological changes in the relative abundance of dominant taxa, similar to the shift in tropical plant communities, during postglacial climate warming. This study uses quantitative counts of relative abundance to assess the paleoecology of early–middle Permian (Sakmarian–Capitanian) marine communities in a high-latitude, periglacial setting in eastern Australia in order to determine the relationship between global climate change and marine ecology in the aftermath of the late Paleozoic ice age. In addition to indicating possible paleoecological responses to the long-term warming trend, quantitative counts may reveal if there were rapid environmental fluctuations or short-term ecological disruptions in marine communities during deglaciation. Finally, this study will examine the links between postglacial climate warming, ecological change, and the fate of the glacial biota in order to ascertain whether climate change caused the extinction of cold-adapted taxa and, if so, the direct or indirect mechanisms through which temperature changes contributed to such extinction.

## MATERIALS AND METHODS

Biotic change during postglacial climate warming is assessed through quantitative field counts of 71 marine fossil assemblages from the early and middle Permian (Sakmarian–Capitanian) of eastern Australia (Supplementary Data 1<sup>1</sup>). Each count includes a minimum of 100 specimens, identified to species level and counted in the field, except for 12 small or sparsely fossiliferous outcrops from Tasmania and Queensland that yielded 60–100 specimens per sample; the overall mean sample size is 110 specimens. Rhynchonelliform brachiopods, bivalves, and gastropods are the most common constituents, but other organisms counted include rugose corals, rostroconchs, and conulariids. Bryozoan colonies are abundant and crinoid ossicles are also present in many samples but are not included in the counts because they are nearly always fragmented or disarticulated. Counts of bivalved taxa (brachiopods and bivalves) are based on the total number of articulated specimens and all disarticulated valves. Most genera can be confidently identified, although the brachiopod *Tomioopsis* was grouped with its allies (*Ingelarella*, *Homevalaria*, and

*Tabellina*) into a single operational taxonomic unit (*Tomioopsis*) because their classification scheme, which emphasizes differences in micro-ornament, is difficult to apply in the field when specimens are preserved as molds or casts. *Tomioopsis* is an accessory component in nearly all assemblages, so this grouping would not significantly impact the statistical analyses.

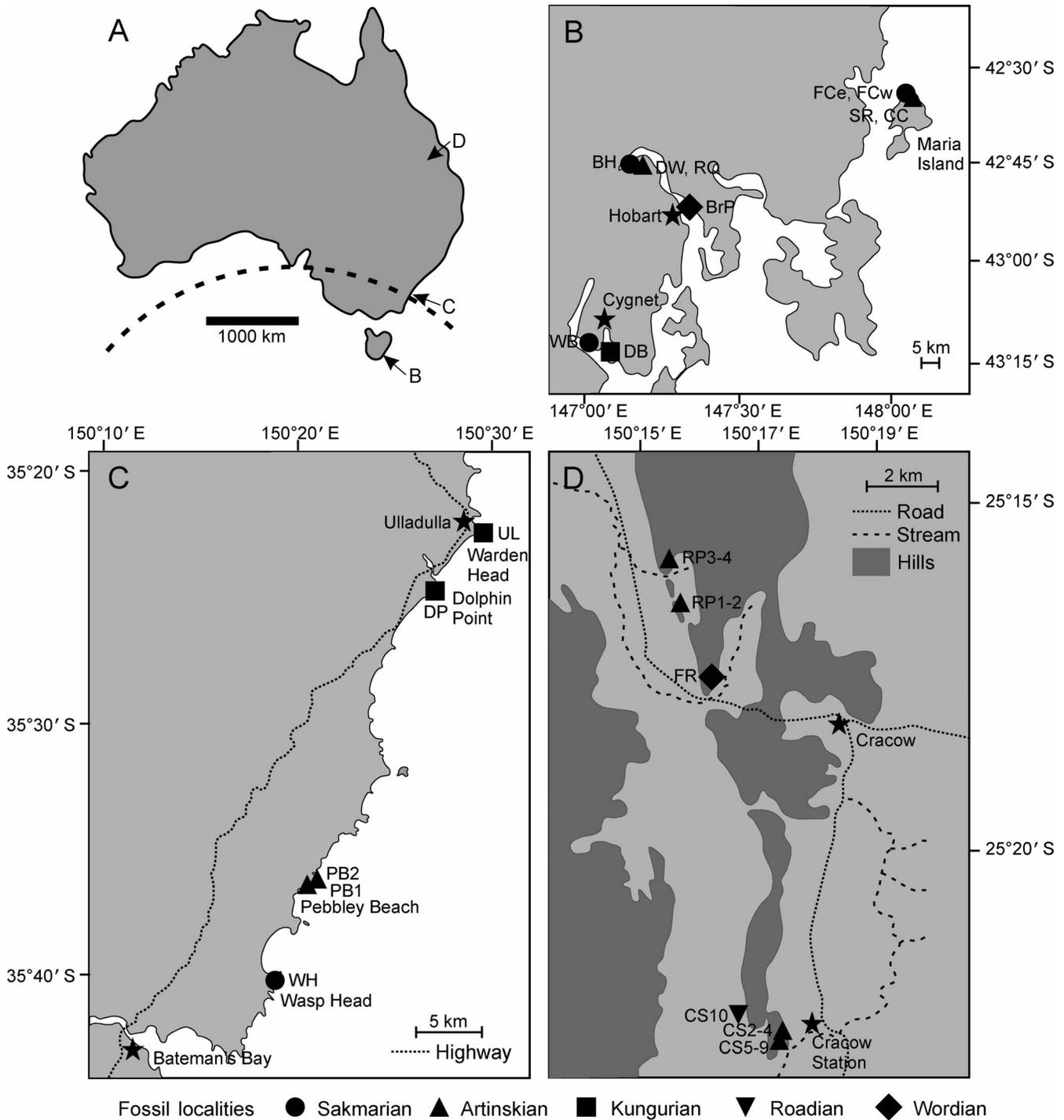
Each sample consists of counts obtained from a single bedding surface; a total of 36 bedding surfaces was counted from the Tasmania Basin, 20 from the Sydney Basin, and 15 from the Bowen Basin (Fig. 1). The complete count is based on pooled replicate samples taken along the length of the available outcrop, which varied in scale from <1 m to >100 m at Maria Island, where replicates of sample FC9 were obtained from both ends of the so-called Fossil Cliffs. These sampling localities span nearly 20° of paleolatitude, from the polar Tasmania Basin within the paleo-Antarctic Circle at close to 70° S, to the Bowen Basin in cold temperate regions at ~50° S (Isbell et al., 2003). The age of each sample is based on biostratigraphic determinations in Briggs (1998), Reid (2003), and Fielding et al. (2008), which allow reliable correlation among the eastern Australian basins (Fig. 2). Precise correlation to the global zonation, however, is hampered by the absence of biostratigraphically important conodonts and fusulinids and the rarity and endemic nature of ammonoids in eastern Australia. Within each basin, counts were obtained from paleoenvironments ranging from high-energy shoreface sands and gravels to low-energy offshore siltstones and mudstones. The depositional environment of each sample was assessed using standard sedimentological criteria in the field and data from previously published interpretations (e.g., Eyles et al., 1998; Fielding et al., 2006; Rogala et al., 2007).

In the Tasmania Basin, Sakmarian samples include 12 beds from the shallow-water Darlington Limestone Member at Maria Island and 5 additional samples from offshore beds of the Bundella Mudstone in the Cygnet and Hobart areas (Figs. 1, 2; Supplementary Data 1<sup>1</sup>). A total of seven Artinskian samples were counted, including four from the Berriedale Limestone, one from the Nassau Siltstone in the Hobart area, one from the Counsel Creek Formation (Berriedale equivalent), and one from the quiet-water siltstones of the Skipping Ridge Formation (Nassau Siltstone correlative) on Maria Island. The 11 Kungurian samples occur in siltstones of the Deep Bay Formation in the Cygnet area. One sample from the Wordian Ferntree Formation was counted at Bellerive Point, Hobart. The lower parts of the Sydney Basin succession are sparsely fossiliferous, and only three counts were made from the Sakmarian Wasp Head Formation and two from the Artinskian Pebble Beach Formation, both from high-energy, nearshore, coarse-to-granular sandstone. The Kungurian Wandrawandian Siltstone is richly fossiliferous in the Ulladulla area, and 15 beds from these slope mudstones and siltstones were counted. The early Permian succession in the Cracow area of the Bowen Basin does not contain Sakmarian deposits; instead the Artinskian and younger deposits rest unconformably on the Camboon Volcanics. A total of 12 Artinskian beds were counted: three from limited exposures of the Fairyland Member of the Buffel Formation near Cracow Homestead; five from finer siltstones of the Elvinia Member also near Cracow Homestead; and four from the Rose's Pride Member, a succession of coarse volcanoclastic sandstones developed near the basal unconformity near the old Rose's Pride Mine site. One count each was also made from the early Guadalupian (Roadian–Wordian) Brae and Otrack Formations.

Data from the new field collections are supplemented by quantitative counts of 15 Guadalupian fossil assemblages, each with at least 60 specimens, published by Waterhouse (1987) from the Brae, Otrack, and Flat Top Formations in the Bowen Basin. Those samples are indicated in the data analysis with four digit sample numbers corresponding to the numbers, locality, and stratigraphic information given in Waterhouse (1987). Although some of those collections may be pooled from multiple beds over a narrow stratigraphic interval (Waterhouse, 1987), they were counted in a similar manner and include the same faunal groups as this study.

Time averaging and post-mortem transportation were assessed in each bed based on standard taphonomic criteria, including sorting, orientation,

<sup>1</sup> www.paleo.ku.edu/palaios

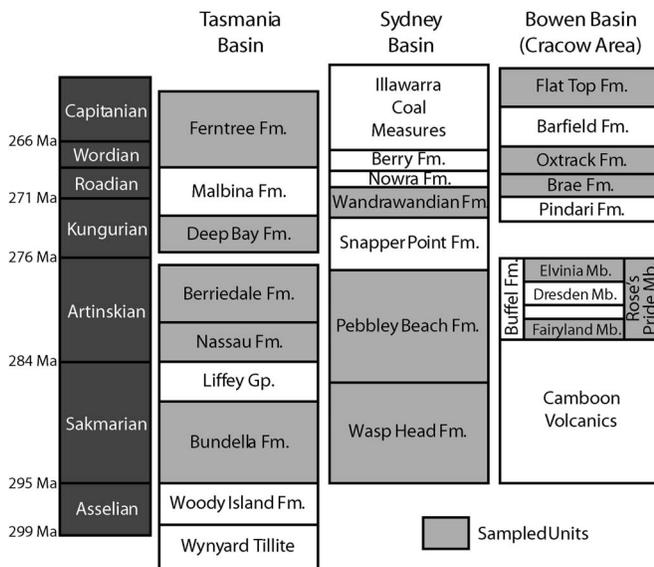


**FIGURE 1**—Location of the sampling sites in this study. Abbreviations for sample numbers are given in Supplementary Data 1<sup>1</sup>. A) Map of Australia showing the location of the Tasmania (B), Sydney (C), and Bowen Basin (D) sampling localities. Dashed line shows the Early Permian position of the Antarctic Circle (after Isbell et al., 2003). B) Map of southeastern Tasmania indicating the location of Early Permian collections. C) Map of the New South Wales coastline showing the location of sampling sites in the southern Sydney Basin. D) Map showing Artinskian and early Guadalupian localities the Cracow area; sample FT1, collected 12 km north of the town of Theodore, is not shown.

fragmentation, and abrasion (Kidwell and Holland, 1991). Nearly all samples exhibited little size sorting and no grading, suggesting that transport was minimal. Even the sampled beds deposited in outer-ramp settings are ungraded and contain an even mixture of fossil sizes. The only samples with conspicuous size sorting are from the vicinity of Rose's Pride Mine (Queensland samples RP3 and RP4), suggesting that they may have undergone some winnowing or transport. Counted fossil specimens are well

preserved as a whole and comprise unabraded shells or molds in most samples, except in beds of coarse-grained sediments in high-energy near-shore environments (particularly in the Wasp Head and Pebbley Beach Formations of the Sydney Basin), where abrasion and fragmentation were moderate to extreme, possibly contributing to a preservational bias favoring large or thick-shelled fossils.

The 71 samples, ranging in age from Sakmarian (likely middle to late



**FIGURE 2**—Correlation of Permian formations in the Tasmania Basin, Sydney Basin, and Cracow area of the Bowen Basin. Tasmania Basin formation names are mostly based on units in the Hobart-Cygnnet area; correlative units on Maria Island are described in the text.

Sakmarian, although correlation to the global zonation is difficult) to Wordian, postdate the major mid-Sakmarian pulse of deglaciation (Dickins, 1996; dos Santos et al., 1996; Visser, 1996; Angiolini et al., 2003; Isbell et al., 2003) but span the interval of most pronounced global climate change from the earliest Permian icehouse to the middle Permian greenhouse (Montañez et al., 2007). Sakmarian assemblages were deposited during the last part of major ice-sheet development and are termed icehouse samples, whereas Artinskian assemblages are transitional, and Kungurian and Guadalupian samples formed during initial stages of the greenhouse climate (Montañez et al., 2007). Fluctuating glacial and interglacial conditions persisted in eastern Australia even into the middle Permian (Fielding et al., 2008) and are superimposed on the overall global warming trend; however, most samples in this study were collected from interglacial units within eastern Australia. The temporal resolution of sampling in this study is also not sufficient to recognize subtler effects of the eastern Australian climate fluctuations.

Multivariate analyses (cluster analysis, detrended correspondence analysis [DCA], and non-metric multidimensional scaling [NMS]) were performed on the resulting matrix, containing the abundances of 84 genera from the 86 samples, using the PAST software package (Hammer et al., 2001). All cluster analyses were performed with unweighted pair-group mean averaging (UPGMA), using a variety of distance measures. Results from the Bray-Curtis (Sorensen) similarity coefficient are presented in the text as a representative example; dendrograms based on Jaccard and correlation coefficients are available (see Supplementary Data 2<sup>1</sup>). All cluster dendrograms recognize the same three primary clusters with minimal switching of group membership. Multivariate ordination through DCA and NMS has widely been used to recover gradients in paleoecology and ecological analysis (e.g., Shi, 1993). Although the use of detrending in DCA has been criticized, it is appropriate for studies such as this one where arching would otherwise result due to little compositional overlap between communities from opposite ends of the gradient (Holland, 2005). The detrending process, however, may emphasize the importance of axis 1 relative to secondary axes. Non-metric multidimensional scaling is an ordination technique based on a matrix of similarity coefficients for each pair of samples and is well suited to community ecological data because of its nonparametric nature (Clarke, 1993). NMS results based on Euclidian distance and the Sorensen (Bray-Curtis) coefficient are presented

in this study. The results of these multivariate techniques were then combined with independently derived stratigraphic, sedimentological, and paleogeographic data to assess temporal, environmental, and latitudinal controls on community change during early-middle Permian postglacial climate warming.

## FAUNAL COMPOSITION

### Tasmania Basin Assemblages

Sakmarian assemblages from the Bundella Formation (including the Darlington Limestone Member) are numerically dominated by the spiriferide brachiopod *Trigonotreta stokesi*, species of the bivalve *Eurydesma*, and *Deltopecten illawarrensis* (Table 1; for the complete data matrix, see Supplementary Data 3<sup>1</sup>). *Trigonotreta stokesi* is numerous in nearly all samples but is especially abundant in assemblages from the offshore Bundella Formation siltstones in the Cygnnet and Hobart areas. One sample from the Cygnnet area (WB1) contains abundant *Strophalosia concentrica* (productide brachiopod) in addition to *Trigonotreta stokesi*. In contrast, *Eurydesma* spp. and *Deltopecten illawarrensis* are very abundant in the Darlington Limestone at Maria Island but are rare in the other localities. Accessory components of the assemblages include the large gastropod *Keeneia* sp., the small gastropod *Peruwispira* sp., the spiriferinide brachiopod “*Pseudosyrinx*” *allandalensis* (possibly a *Cyrtella*, see Archbold and Gaetani, 1993), *Etheripecten subquiquelineatus*, and several species of the brachiopod “*Tomiopsis*.”

Most Artinskian samples from the Berriedale Limestone in the Hobart area and the correlative Counsel Creek Limestone on Maria Island are dominated by the spiriferide brachiopods *Sulcuplica* spp. (primarily *S. tasmaniensis*) and *Trigonotreta hobartensis*, although one is strongly dominated by the productide *Wyndhamia typica*. Many of the common accessory taxa from Sakmarian samples, at least at the generic level, are also present in the Berriedale Limestone, including *Deltopecten* sp., *Etheripecten* sp., and “*Tomiopsis*” spp. Other taxa, such as productide brachiopods *Terrakea pollex*, *Wyndhamia typica*, and terebratulide *Fletcherithyris* sp., also appear in the record for the first time. The underlying Nassau Siltstone contains a markedly different fauna, numerically dominated by the productide brachiopod *Echinalosia preovalis*. *Trigonotreta hobartensis*, *Sulcuplica tasmaniensis*, “*Tomiopsis*” sp., *Costatumulus farleyensis*, and *Fletcherithyris* sp. are also present at low to moderate abundance (5%–15% of the sample). Faunas from the Skipping Ridge Formation (Nassau equivalent) on Maria Island have a similar composition, with abundant *Echinalosia preovalis*, *Costatumulus farleyensis*, and *Sulcuplica tasmaniensis*. *Anidanthus springsurensis* (productide), “*Tomiopsis*” spp., *Streblopteria* sp. (pectinoid bivalve), and *Deltopecten* sp. are also present in lower numbers in the Skipping Ridge assemblages.

Kungurian assemblages from the Cygnnet area (Deep Bay section; DB) have a relatively consistent composition; the brachiopods *Cyrtella* sp. and *Echinalosia* cf. *discinia*, and the gastropod *Peruwispira* sp., are abundant in nearly all samples, whereas *Fletcherithyris* sp. is common in 5 of the 11 assemblages (DB4, 5, 6, 7, 8, 11). “*Tomiopsis*” spp. (DB2, DB6), *Stutchburia farleyensis* (DB2), and an orthotetide brachiopod similar to *Schuchertella* sp. (DB7, DB11) are accessory components, only reaching moderate to high abundance in 1 to 2 samples.

A single sample from the Wordian–Capitanian Fernree Formation (correlative of the Abels Bay Formation) was counted at Bellerive Point, Hobart. The assemblage was nearly exclusively composed of several species of the spiriferide “*Tomiopsis*.” The only other genus represented was the terebratulide *Fletcherithyris*, by a single specimen.

### Sydney Basin Assemblages

Sakmarian samples from the Wasp Head Formation are similar to those from the Tasmanian Darlington Limestone (Table 1), and are dominated by *Trigonotreta stokesi* with *Eurydesma* spp. also common. *Deltopecten illawarrensis* and “*Tomiopsis*” spp. are also present, while *Keeneia* sp.

**TABLE 1**—Geographic location, age, environment, and characteristic genera (three most abundant as measured by mean abundance of each collection) for each studied stratigraphic unit in eastern Australia.

Formation	Basin	Age	Environment	Abundant Genera (Overall Percent Abundance)
Darlington Lst.	Tasmania	Sakmarian	Onshore	<i>Trigonotreta</i> (39%), <i>Eurydesma</i> (36%), <i>Deltopecten</i> (15%)
Bundella	Tasmania	Sakmarian	Offshore	<i>Trigonotreta</i> (57%), <i>Strophalosia</i> (11%), <i>Tomiopsis</i> (8%)
Berriedale Lst.	Tasmania	Artinskian	Onshore	<i>Sulcifica</i> (36%), <i>Wyndhamia</i> (18%), <i>Trigonotreta</i> (14%)
Nassau	Tasmania	Artinskian	Offshore	<i>Echinalosia</i> (45%), <i>Costatumulus</i> (17%), <i>Trigonotreta</i> (9%)
Deep Bay	Tasmania	Kungurian	Offshore	<i>Cyrtella</i> (24%), <i>Peruvispira</i> (22%), <i>Echinalosia</i> (19%)
Abels Bay	Tasmania	Capitanian	Offshore	" <i>Tomiopsis</i> " {99%}
Wasp Head	Sydney	Sakmarian	Onshore	<i>Trigonotreta</i> (59%), <i>Eurydesma</i> (26%), " <i>Tomiopsis</i> " (6%)
Pebbley Beach	Sydney	Artinskian	Onshore	<i>Eurydesma</i> (76%), <i>Peruvispira</i> (12%), " <i>Tomiopsis</i> " (6%)
Wandrawandian	Sydney	Kungurian	Offshore	<i>Terrakea</i> (63%), <i>Echinalosia</i> (11%), <i>Neospirifer</i> (10%)
Fairyland	Bowen	Artinskian	Onshore	<i>Peruvispira</i> (54%), <i>Svalbardia</i> (12%), <i>Lipanteris</i> (9%)
Rose's Pride	Bowen	Artinskian	Onshore	<i>Megousia</i> (36%), <i>Eurydesma</i> (12%), <i>Trigonotreta</i> (11%)
Elvinia	Bowen	Artinskian	Offshore	<i>Echinalosia</i> (34%), <i>Costatumulus</i> (20%), <i>Rugosa</i> (14%)
Brae	Bowen	Roadian	Onshore	<i>Echinalosia</i> (39%), <i>Spinomartinia</i> (18%), <i>Neospirifer</i> (9%)
Oxtrack	Bowen	Wordian	Offshore	<i>Aperispirifer</i> (26%), <i>Echinalosia</i> (19%), " <i>Tomiopsis</i> " (15%)
Flat Top	Bowen	Capitanian	Onshore	<i>Terrakea</i> (33%), <i>Capillonia</i> (19%), " <i>Tomiopsis</i> " (10%)

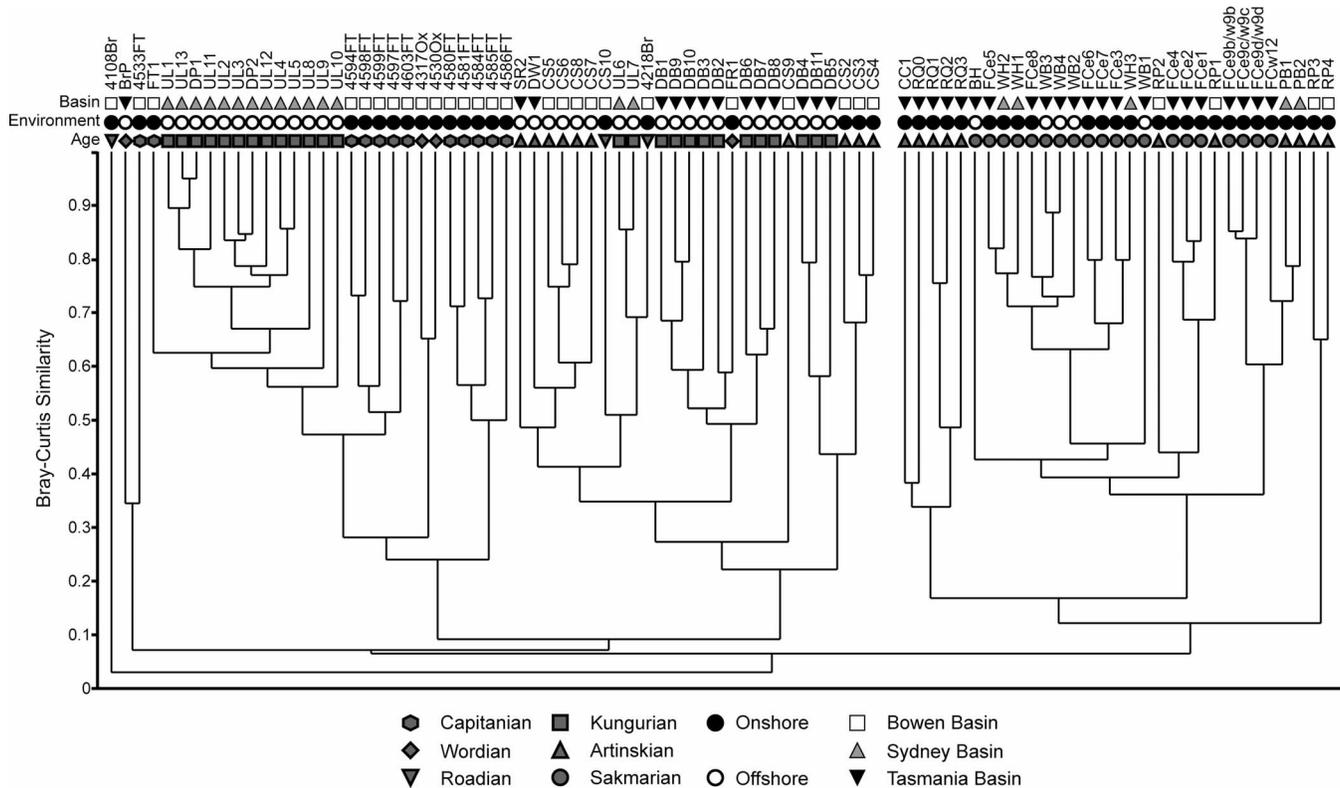
and "*Pseudosyrinx allandalensis*" are rare. In the Artinskian Pebbley Beach Formation, *Eurydesma* spp. are highly dominant, comprising more than 70%–85% of the two samples. *Peruvispira* sp. and "*Tomiopsis*" sp. are common in sample PB1, while *Trigonotreta* sp. and *Keeneia* sp. are present but less abundant. Those four genera also occur in sample PB2 but at an abundance of only 3%–4%.

Of the 15 Kungurian samples from the Wandrawandian Siltstone at Warden Head (WH) and Dolphin Point (DP) in the Ulladulla area, 13 are numerically dominated by *Terrakea concava*, whereas the two stratigraphically lowest beds counted (WH1 and WH2) contain abundant *Echinalosia maxwelli* and subordinate *Terrakea concava*. *Neospirifer* sp.

is moderately abundant in samples WH3, WH4, WH12, and DP1. "*Tomiopsis*" spp. and *Cyrtella* cf. *ulladullensis* are accessory components in sample WH8, while *Streblopteria* sp. and *Fletcherithyris* sp. are common in WH9. *Fletcherithyris* sp. is also abundant in sample WH10 (comprising nearly 50% of the assemblage) and WH11.

Bowen Basin Assemblages

The oldest Permian deposits in the Cracow area of the Bowen Basin are Artinskian in age. Three samples from the Fairyland Member, examined at Cracow Station, are dominated by the gastropod *Peruvispira*



**FIGURE 3**—Cluster dendrogram (Bray-Curtis similarity; UPGMA clustering) of the 86 early Permian fossil assemblages (collections are shown in Figure 1 and listed in Supplementary Data 1<sup>1</sup>). The temporal, geographic, and environmental contexts of each sample are indicated by symbols at the end of each dendrogram branch. Abbreviations for sample numbers are given in Supplementary Data 1<sup>1</sup>.

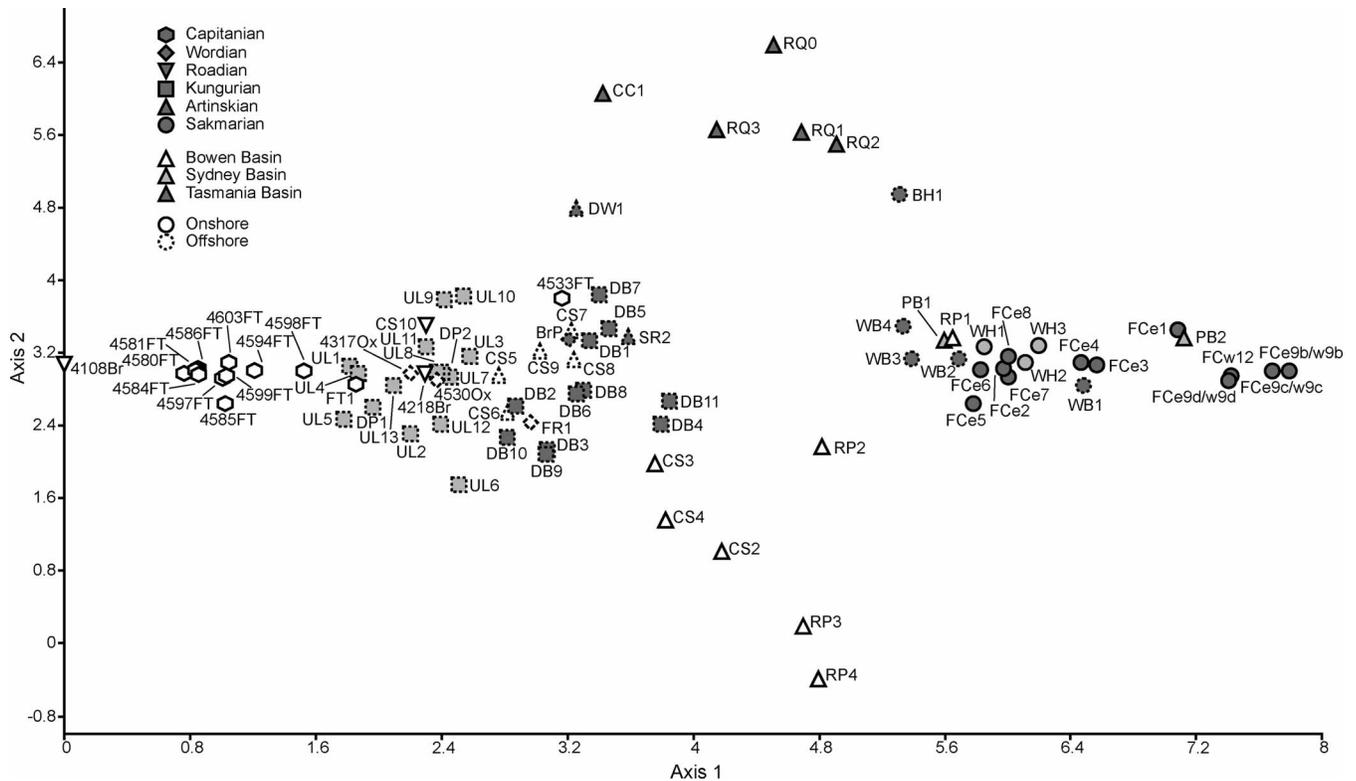


FIGURE 4—Detrended correspondence analysis (DCA) plot showing the relationship of all 86 eastern Australian fossil assemblages. Collections made by Waterhouse (1987) are labeled with four digit numbers and two letters to indicate the formation (e.g., 4108Br).

*promenata* (comprising >50% of the specimens) and also contain common specimens of *Lipanteris* spp. (an aulostegid brachiopod) and the chonetid *Svalbardia cracowensis* (Table 1). *Paraplatschisma rotunda* (a gastropod) and the brachiopods *Terrakea pollex* and *Echinalosia curtosa* are accessory components, either present at moderate abundance in a single sample or in lower numbers in all samples. *Eurydesma* is a notable component in the float on the hillside, but it is disproportionately preserved relative to more delicate taxa due to its robust shell and is not abundant in the sampled beds. Five assemblages were counted from the Elvinia Member, the stratigraphically highest unit in the Buffel Formation in the Cracow Station area. Of those, four are dominated by *Echinalosia preovalis* (CS4–CS7; Supplementary Data 3<sup>1</sup>) and one by *Costatumulus meritus* (CS8). *Echinalosia* is also common in the *Costatumulus*-dominated sample CS8 and *Costatumulus* is abundant in one of the *Echinalosia*-dominated samples (CS6). Other species that are common in some of the Elvinia Member collections include *Peruvispira* sp. (CS5, CS6), “*Tomiopsis*” spp. (CS6, CS7, CS8), *Trigonotreta australis* (CS7), and an unidentified solitary rugose coral (CS4, CS5, CS7). Assemblages from near Rose’s Pride Mine, the type area of the Rose’s Pride Member north of the town of Cracow, have a very different composition from either the Fairyland or Elvinia samples. Two of the Rose’s Pride samples contain a *Eurydesma*-*Trigonotreta* biota with abundant *Eurydesma sulcatum*, *Deltopecten illawarrensis*, and *Trigonotreta australis*. “*Tomiopsis*” spp., *Terrakea* cf. *dickinsi*, and *Acanthalosia domina* are also abundant in sample RP1, while *Paraplatschisma rotunda* (gastropod), *Lipanteris* sp. (productide brachiopod), and “*Tomiopsis*” spp. are common in RP2. The other two samples from the Rose’s Pride Formation contain few *Eurydesma* or *Trigonotreta*, and instead are dominated by the productide brachiopod *Megousia solita*. Sample RP3 is especially strongly dominated by *Megousia*, where it comprises 86% of the assemblage, while sample RP4 also contains moderately abundant *Trigonotreta australis* and *Cyrtella erecta*.

The Roadian Brae Formation, Wordian Oxtrack, and Capitanian Flat

Top Formations in the Cracow area are not as densely fossiliferous or well exposed as the underlying Artinskian units and, as a result, only two samples were counted from those units. The field counts, however, were also supplemented with counts previously made by Waterhouse (1987), which generally represent assemblages of similar composition. The Brae Formation sample, derived from a small outcrop northwest of Cracow Station near locality UQ4218 of Waterhouse and Briggs (1986), contains abundant *Echinalosia discinia* with common *Neospirifer concentricus* and *Terrakea paucispinosa*. Waterhouse sample (4218Br in Supplementary Data 2<sup>1</sup>) is similarly dominated by *Echinalosia*, but sample 4108Br instead contains abundant *Spinomartina* (spiriferide brachiopod). The Ox-track Formation sample, located at “Fossil Hill” just west of the town of Cracow, is numerically dominated by *Peruvispira* sp., *Echinalosia robusta*, and “*Tomiopsis*” spp. and contains numerous other species in low numbers, including *Cyrtella nobilis*, *Parallelodon capillatus*, and *Magniplicatina perfecta*, among others. *Peruvispira* and *Tomiopsis* are also common in two samples counted by Waterhouse, but the spiriferide *Aperispirifer* is dominant. In field sample FT1 from the Flat Top Formation, *Terrakea multispinosa* is highly abundant, while the chonetid *Capillonia semicircularis*, bivalve *Elimata prima*, and spiriferide *Aperispirifer lethamensis* are present but not common. *Terrakea multispinosa* also dominates many of the Waterhouse samples, although *Capillonia* is most abundant in 4580FT, 4581FT, 4584FT, and 4585FT. *Elimata* is common in samples 4594FT, 4597FT, and 4603FT, while *Aperispirifer* is common in 4598FT.

#### EARLY PERMIAN FAUNAL CHANGES

The 86 early and middle Permian samples from the Tasmania, Sydney, and Bowen basins display marked variations in faunal composition, as apparent from the clear separation of three major clusters in the cluster dendrogram (Fig. 3). One cluster contains all Sakmarian assemblages (as well as some shallow-water Artinskian samples from the Pebley Beach

Formation in the Sydney Basin and the Rose's Pride Member in the Bowen Basin), and is discriminated by the abundance of *Eurydesma*, *Trigonotreta*, and *Deltopecten*. The dominant genera in this cluster, especially *Eurydesma* and *Trigonotreta*, are typical of the cool-adapted biota that existed throughout Gondwana during the later stages of the late Paleozoic ice age (Runnegar, 1979; Shi and Archbold, 1993). The other two major clusters include all Kungurian and Guadalupian samples and the remaining Artinskian assemblages, and are distinguished by abundant productides, such as *Echinalosia* or *Terrakea*. *Eurydesma* is absent from these samples, and *Trigonotreta* and *Deltopecten* are rare. Similarly, dominant postglacial genera *Echinalosia* and *Terrakea* are not found in the Sakmarian samples. In the Bray-Curtis dendrogram (Fig. 3), the two postglacial clusters are grouped as more closely similar, with the glacial Sakmarian cluster separated. A similar pattern is observed with use of correlation coefficient (Supplementary Data 2<sup>1</sup>), but the Jaccard dendrogram groups the postglacial cluster containing Tasmania Basin Kungurian assemblages and all Artinskian samples as being more similar to Sakmarian assemblages than the cluster containing Sydney Basin Kungurian and Guadalupian samples.

Regardless of minor differences in topology, Artinskian samples are distributed across both major clusters in the dendrogram, occupying a transitional position between the icehouse Sakmarian and greenhouse Kungurian-Guadalupian. A few Artinskian samples, from the Pebley Beach Formation in the Sydney basin and the Rose's Pride Member in the Bowen Basin, contain an icehouse-style *Eurydesma-Trigonotreta* biota, whereas many other Artinskian samples (e.g., from Skipping Ridge and Nassau Formations in Tasmania and the Elvinia Member in the Bowen Basin) contain a typical postglacial, productide-dominated assemblage with abundant *Echinalosia* and some specimens of *Terrakea* and *Costatumulus*. The Artinskian record in eastern Australia also contains a number of assemblages that are unlike typical examples of either the icehouse or greenhouse communities. Samples from the Berriedale Limestone in the Tasmania Basin contain abundant *Sulciplica tasmaniensis* in addition to a mixture of typical glacial and postglacial genera, and one sample is dominated by *Wyndhamia typica*, a species that is occasionally present but usually rare in other samples. In the Bowen Basin, the Rose's Pride Member contains assemblages strongly dominated by the brachiopod *Megousia solita* (53% in RP3 and 86% in RP4), a genus that is found in only six samples outside of the Rose's Pride area and never comprises >3% of any other assemblage in this study. Assemblages from the Fairyland Member likewise contain several unusual genera that are abundant only in those samples, including *Lipanteris* spp. and the chonetid *Svalbardia cracowensis*, which is restricted to the Fairyland samples.

The distinct separation of Sakmarian icehouse communities from Kungurian and Guadalupian greenhouse assemblages is also apparent in the DCA plot (Fig. 4) and both NMS analyses (Fig. 5). The separation is not as distinct when Euclidian distance is used in the NMS analysis, but there still is no overlap between Sakmarian and Kungurian-Guadalupian samples (Fig. 5A). In all ordination techniques, however, Artinskian samples plot as a transitional group with some overlap of the Sakmarian cluster and some samples within the postglacial cluster; others are intermediate between the two groupings (Figs. 4, 5). Furthermore, the separation among Kungurian, Roadian, Wordian, and Capitanian assemblages is much less than that between those clusters and Sakmarian samples. This is especially true in the DCA plot (which emphasizes axis 1) and Euclidian NMS, in which there is noticeable overlap among Kungurian and Guadalupian clusters. Even in NMS ordination with the Sorensen coefficient (Fig. 5B), the Kungurian and Guadalupian samples are much more tightly clustered, and all are distinctly separated from Sakmarian assemblages.

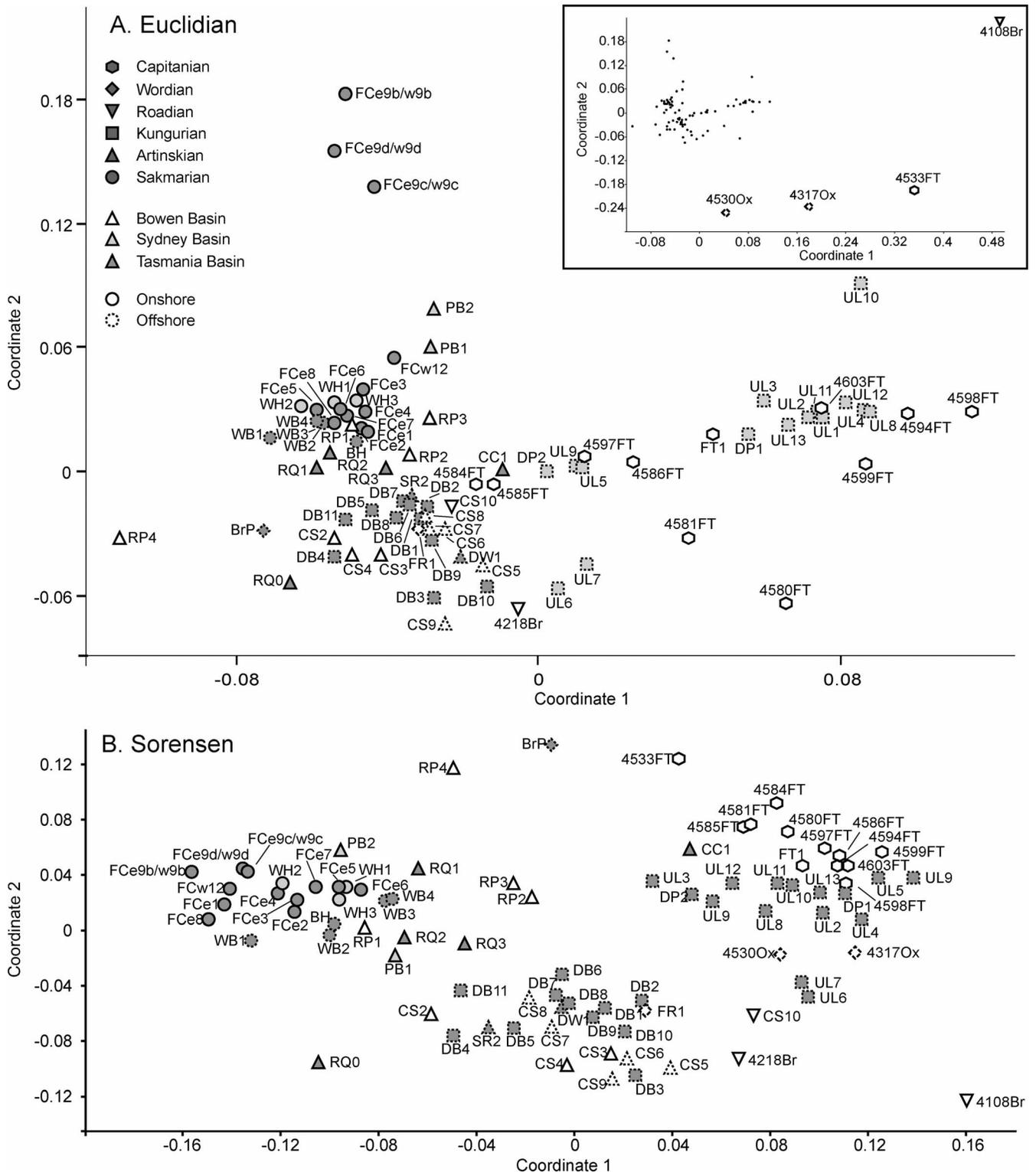
The results of the cluster analysis and ordination indicate that marine communities in eastern Australia underwent substantial changes in composition and dominance between the Sakmarian and Kungurian, coincident with the global transition from an icehouse to greenhouse climate (e.g., Montañez et al., 2007). Although this faunal transition occurred

over 10–15 myr, its concurrence with global climate change, combined with the small amount of faunal change in the succeeding 10-my Kungurian-Capitanian interval, is consistent with the idea that climate change played a major role in the shift in dominance. Continuing climate fluctuations in eastern Australia, such as the minor glacial resurgences in the Kungurian-early Roadian and late Guadalupian (Fielding et al., 2008), did not have a recognizable impact on the biota in this data set, but temporal resolution is limited and most samples were collected from interglacial formations, so additional data may reveal more subtle faunal changes. Sakmarian assemblages, during the last stages of the ice age, are dominated by *Eurydesma* and *Trigonotreta* but are replaced by assemblages dominated by *Echinalosia* and *Terrakea* during the transition to warmer postglacial climates of the Kungurian and Guadalupian. Artinskian samples appear transitional, with some more similar to glacial assemblages and others more similar to the postglacial biota; however, there is not sufficient biostratigraphic resolution in the cold-water Australian successions to determine whether the community shift was a gradual process or if it had a more complicated pattern.

### Geographic Variation

The age of the fossil assemblages and their position within the early-middle Permian icehouse-greenhouse transition (Montañez et al., 2007) appear to be the fundamental underlying control on their biotic composition, but the collection of quantitative data from a variety of depositional environments and a wide paleolatitudinal range allows the importance of geographic and environmental variations to be assessed. For example, did the eastern Australian faunal change occur first in polar latitudes in Tasmania or earlier in cold-temperate conditions in the Bowen Basin? If climate warming was an important factor, then community change might be expected to occur first at highest latitudes where organisms were most adapted for cold conditions. Superimposing the paleolatitudinal position of each Artinskian sample (Tasmania, Sydney, or Bowen basins) on the cluster dendrogram (Fig. 3), however, reveals that assemblages from the polar Tasmania Basin and the more temperate Bowen Basin are distributed in two of the three clusters and in both primary clusters on the dendrograms. This indicates that the Tasmania and Bowen basins each contained some samples with a *Eurydesma-Trigonotreta* icehouse biota and some with a typical *Echinalosia-Terrakea* greenhouse biota during the Artinskian. Results from NMS analyses are consistent with the patterns from cluster dendrograms, as there is nearly complete overlap between samples from all latitudinal zones within the Artinskian field (Fig. 5), with some samples plotting close to the Sakmarian assemblages and others arrayed within the Kungurian field. The DCA plot, however, separates Artinskian samples from the Tasmania and Bowen basins along axis 2 with only minimal overlap (Fig. 4). Samples from the Tasmania basin with high axis 2 scores are dominated by *Wyndhamia* or *Sulciplica* (both absent or rare in Queensland), whereas samples from the Bowen basin with low axis 2 scores are dominated by *Megousia*, *Peruvispira*, *Svalbardia*, or *Lipanteris*, of which only *Peruvispira* is present in the Artinskian of Tasmania. This suggests that although both basins contained representatives of typical icehouse and greenhouse aspect, they diverged significantly in the ecological composition of other assemblages.

Kungurian samples may exhibit more consistent latitudinal variation, with Tasmanian assemblages from the Deep Bay Formation grouping with Artinskian offshore samples and Sydney Basin assemblages of the Wandrawandian Formation grouping with most Guadalupian samples (Fig. 3). This pattern is observed in all dendrograms examined, and the cluster containing Deep Bay samples is grouped even more closely with the glacial Sakmarian cluster when the Jaccard coefficient is used (Supplementary Data 2<sup>1</sup>). The distinction is largely enforced by differences in the abundance of *Echinalosia* (more common in Tasmania) and *Terrakea* (highly dominant in the Sydney Basin). It is not clear, however, to what degree paleolatitude controlled the faunal changes relative to other

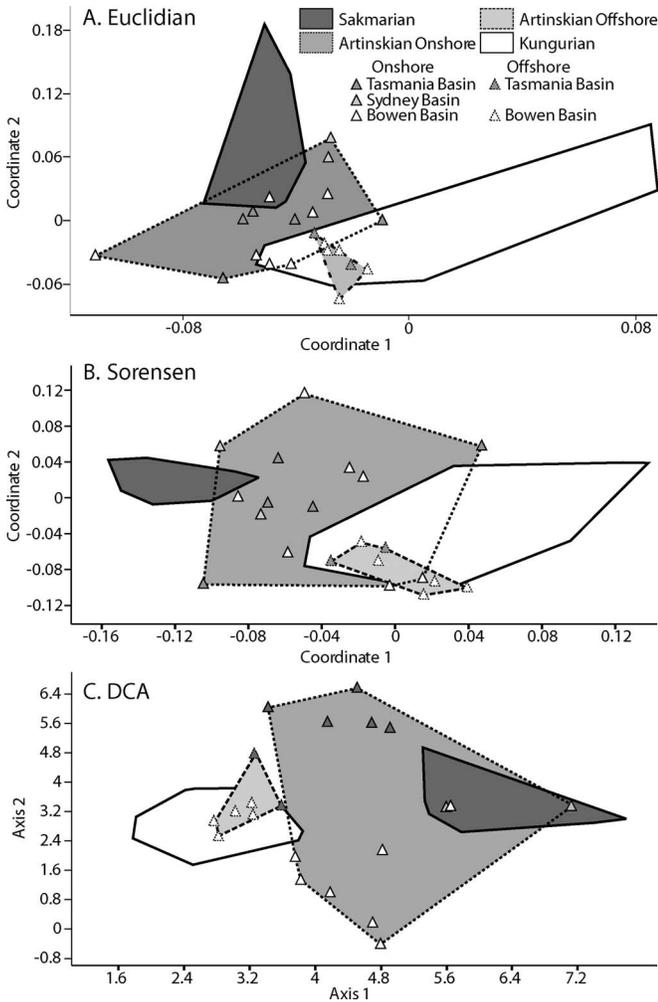


**FIGURE 5**—Non-metric multidimensional scaling (NMS) plots, using A) Euclidian distance and B) Sorensen distance. Stratigraphic, geographic, and environmental symbols are the same as in Figure 4. Inset in panel A shows the complete plot.

factors like paleoenvironment, as the samples from the Wandrawandian Formation are derived from deeper-slope mudstones compared to the outer-ramp siltstones and fine sandstones of the Deep Bay Formation. In addition, *Echinalosia*-rich samples also occur in two samples from the Kungurian of the Sydney Basin and occasionally in Guadalupian formations from the Bowen Basin (e.g., 4218Br from the Roadian Brae and FR1 from the Wordian Otrack Formations).

Environmental Variation

In contrast to the equivocal evidence for latitudinal variations, superimposing information about the depositional environment of each Artinskian sample onto the cluster dendrogram (Fig. 3) shows clear partitioning of assemblages from shallower and deeper habitats into different clusters. Each sample was coded as either onshore (i.e., higher-energy,



**FIGURE 6**—Environmental segregation of Artinskian samples, as shown on A) Euclidian NMS, B) Sorensen NMS, and C) DCA plots. Convex hulls for Sakmarian, Artinskian onshore, Artinskian offshore, and Kungurian samples are outlined.

shallow-water environments above wave base) or offshore (i.e., quiet-water deposition in deeper water below wave base), based on sedimentological criteria observed in the field. All Artinskian onshore samples, regardless of their paleolatitude, are grouped together with Sakmarian glacial samples in the cluster distinguished by the abundance of *Eurydesma* and *Trigonotreta*. Most Artinskian offshore samples, however, contain abundant specimens of the productide brachiopod *Echinalosia* and nearly all are grouped in the cluster with Kungurian postglacial assemblages. Similar environmental distinctions are not observed in Sakmarian data or in the Guadalupian samples, which consistently cluster together (Fig. 3); comparison with the Kungurian is not possible as all samples are from more distal settings. This pronounced differentiation between shallow-water and deeper-water samples during the Artinskian is also apparent on the DCA and both NMS plots (Figs. 4, 5), where offshore samples plot within the Kungurian field and onshore collections are distributed more widely and partially overlap the Sakmarian field (Fig. 6). Together, the results of the cluster analysis and ordination suggest that the faunal transition may have occurred first in offshore habitats before spreading into shallower environments.

The diachronous timing of faunal change in different depositional environments may have been caused by oceanographic changes along the eastern Australian margin. Upwelling of colder deep water was a pervasive feature along the continental margin during the early Permian (Jones et al., 2006), suggesting that changes in the upwelling regime or

the character of the deep-water mass may have influenced offshore communities to a greater degree than their onshore counterparts. If latitudinal temperature gradients, local prevailing wind strength, or thermohaline circulation weakened during the transition to the postglacial greenhouse climate, the extent or strength of upwelling along the eastern Australian margin may have decreased correspondingly. There is sedimentological and climate model evidence for episodic upwelling persisting in eastern Australia until the Wordian (Gibbs et al., 2002; Winguth et al., 2002; Jones et al., 2006). In addition, any putative shift to a weakened upwelling regime would have resulted in greater changes in onshore environments, not offshore communities that would still be influenced to some extent by cool deep waters. Instead, nearshore settings may have been affected by changes in the extent of glaciations and the magnitude of glacial runoff. Freshwater glacial runoff would have been at its maximum during the middle and late Sakmarian deglaciation, influencing a greater range of environments, perhaps including more offshore settings. Episodic glaciation persisted at low levels in eastern Australia into the Wordian and Capitanian, although Guadalupian glacial intervals were much less severe than widespread earliest Permian or moderate Artinskian events (Fielding et al., 2008). These continuing cold conditions raise the possibility of continued influence of glacial runoff, although it would likely have been less pervasive, affecting nearshore environments during the more moderate Artinskian glacial interval but having minimal impact in more offshore settings.

Recognition of early faunal change in offshore habitats, however, may not necessarily imply forcing by diachronous environmental change. Productide brachiopod-dominated communities in Artinskian offshore habitats may instead reflect establishment of a typical late Paleozoic onshore-offshore faunal gradient following amelioration of environmental conditions during postglacial warming. During the late Paleozoic, pedically attached brachiopods were the most abundant brachiopod groups in shallow settings while reclining productides were most abundant in quiet, mud-rich offshore habitats (Yancey and Stevens, 1981; Pérez-Huerta and Sheldon, 2006; Clapham and Bottjer, 2007). This pattern is also present in the eastern Australian Permian, where spiriferides (along with molluscs) tend to be abundant in higher-energy shallow habitats, while productides dominate offshore. The Sakmarian of the Tasmania Basin is a notable exception, and productides are absent or extremely rare in nearly all offshore beds, possibly excluded from the region because of harsh environmental conditions, such as low temperature. The only productide present is *Strophalosia* (e.g., Clarke and Banks, 1975; Leaman, 1976; Clarke and Baillie, 1984; Farmer, 1985; Clarke, 1990), and even it is present only in a few offshore beds. In contrast, more temperate areas of Gondwana, including Queensland and the northern Sydney Basin, contained a greater diversity and abundance of productides during the Asselian and Sakmarian (e.g., Waterhouse, 1982; Archbold, 1983, 1985, 1995; Archbold and Gaetani, 1993; Angiolini, 1995; Angiolini et al., 1997, 2005; Briggs, 1998; Archbold and Hogeboom, 2000; Shen et al., 2000; Cisterna et al., 2002). The fact that productides are more diverse, and almost certainly more abundant given their extreme rarity in Tasmania, in similar glacially influenced sediments elsewhere in Gondwana, such as the Lyons Group of Western Australia (e.g. Archbold, 1983; Archbold, 1995), suggests that proximity to ice sheets or magnitude of glacial runoff input were less important than other factors in controlling the Artinskian faunal transition. Instead, the exclusion of cool-adapted Gondwanan productides—especially members of the Linoproductidae and Monticuliferidae that are common in the more temperate Bowen or Western Australian basins—from the Tasmania basin may indicate that they were unable to inhabit the coldest polar regions of the supercontinent. Such latitudinal differentiation of community structure would be enhanced during glacial times by the stronger pole-equator temperature gradient, whereas reduction in the latitudinal temperature gradient during the shift to a greenhouse climate would tend to homogenize faunal gradients. Postglacial warming in the Artinskian may have resulted in overall warmer-water conditions both onshore and offshore in eastern Australia

in general and the Tasmania basin in particular, due to weakening of the latitudinal temperature gradient. These changes would have enabled more productives to colonize their preferred offshore habitats while spiriferides and *Eurydesma* persisted in their preferred onshore habitats, leading to the observed environmental segregation of community types.

Although major compositional variations among Sakmarian or Kungurian assemblages from different environments are not apparent from the cluster analysis, more subtle environmental gradients in the faunal assemblages can be recognized in the DCA and NMS ordination plots. In the DCA diagram (Fig. 4), the 86 fossil samples are distributed along axis 1 in general correspondence with their age within the deglaciation succession, from glacial Sakmarian assemblages at high values to post-glacial Capitanian assemblages at low values. Within the grouping of Sakmarian samples, there is also a transition from shallow-water, *Eurydesma*-dominated assemblages in the Darlington Limestone at higher values to offshore, *Trigonotreta*-dominated assemblages (containing no *Eurydesma*) from the Bundella Mudstone at lower values. Onshore and offshore Sakmarian assemblages are segregated on both NMS plots as well (Fig. 5), although they group quite closely to each other. Similarly, Kungurian samples are arrayed on the DCA diagram from *Echinalosia*-dominated assemblages from the offshore Deep Bay Formation at higher values to *Terrakea*-dominated assemblages from deeper-slope deposits of the Wandrawandian Siltstone at lower values. The two groups are separated on both NMS plots as well, although this may reflect a geographic gradient, as described above. Together, these results highlight the hierarchical importance of environmental controls on community composition, from the influence of small-scale changes in substrate and energy to the overarching impact of climate changes during early Permian deglaciation.

#### Variability in Community Composition

Results of the DCA ordination (Fig. 4) show that there are substantial differences in the degree of variability among assemblages of Sakmarian, Artinskian, Kungurian, and Capitanian age (Roadian and Wordian sample sizes being too small for comparison). Sakmarian, Kungurian, and Capitanian communities each plot in fairly tightly defined clusters, distributed along axis 1 in a broad environmental gradient (discussed above) but displaying little variability along axis 2. Only a single Sakmarian sample (BH1, containing abundant *Keeneia* in addition to *Trigonotreta*) deviates substantially on the secondary axis from the typical values for other assemblages of that age. Kungurian and Capitanian samples are both distributed in a similar narrow range along axis 2. In contrast, the variability exhibited by the suite of Artinskian samples is considerably larger than that of either Sakmarian, Kungurian, or Capitanian assemblages (Fig. 4). Artinskian assemblages are distributed considerably more widely along axis 2, including unusual samples with abundant *Sulcipleca* or *Wyndhamia* from the Berriedale Limestone; those with abundant *Peruvispira*, *Lipanteris*, and *Svalbardia* from the Fairyland Member; and those dominated by *Megousia* from the Rose's Pride Member. This broad range of dominant genera is also unique to the Artinskian in these samples. A similar pattern is revealed in the Sorensen coefficient NMS ordination, but to a much lesser degree, whereas the Artinskian is less variable than either Kungurian or any Guadalupian clusters when Euclidian distance is applied to the NMS analysis (Fig. 5).

The DCA ordination pattern of relatively consistent community structure during the Sakmarian, Kungurian, and Guadalupian, but a high degree of variability in the transitional Artinskian, is similar to that documented in North American tropical forest ecosystems during the same time interval by Montañez et al. (2007); however, confounding sampling, geographic, or environmental factors may have been an important influence on the observed pattern. The more limited Guadalupian sample set from the Bowen basin also contains a wider range of dominant genera, including *Spinomartinia* in sample 4108 from the Roadian Brae Formation and *Aperispirifer* in samples 4317 and 4530 from the Wordian Ox-track Formation (Waterhouse, 1987), suggesting that greater sampling

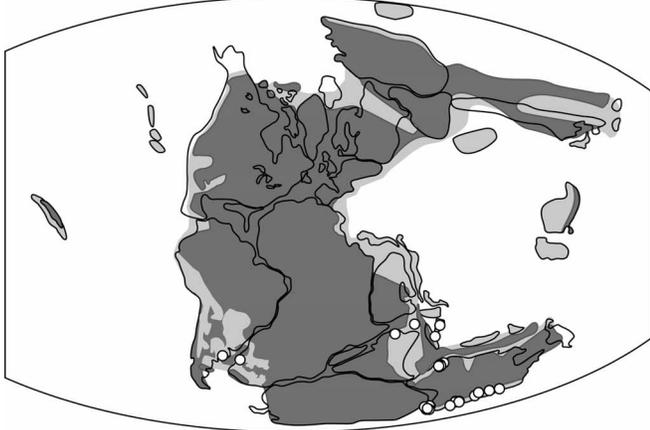
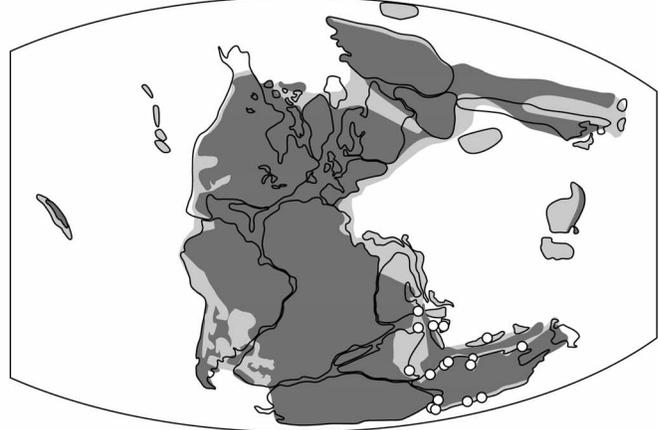
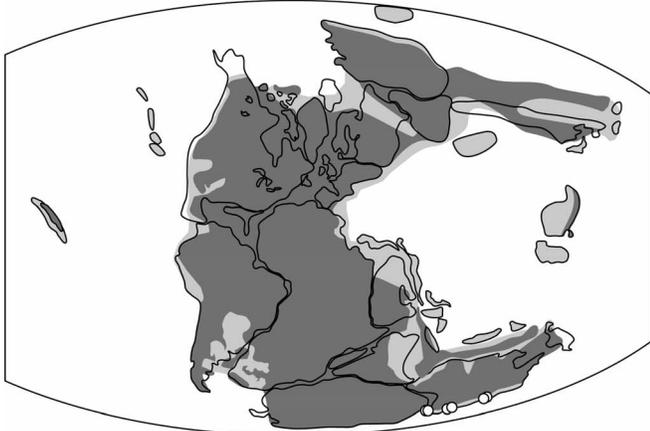
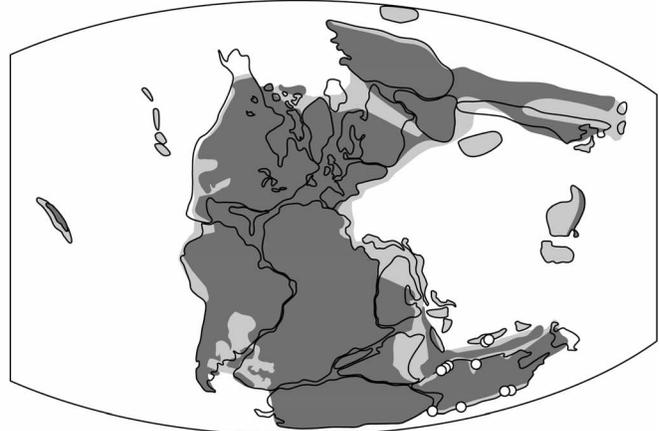
would likely reveal even greater variability. In addition, the geographic range covered by Artinskian samples in this dataset is greater than the Sakmarian, Kungurian, or Guadalupian, representing all three studied eastern Australian basins. Artinskian fossil assemblages were also sampled from a wider range of depositional environments, including shoreline volcanic conglomerate and volcanoclastic sandstones of the Rose's Pride and Fairyland Members, quiet-water offshore siltstones of the Elvinia Member, shallow marine limestones of the Berriedale Formation, and inner-ramp granular sandstones of the Pebley Beach Formation, recording more habitats and therefore probably a greater number of community types.

#### Fate of the Glacial Biota

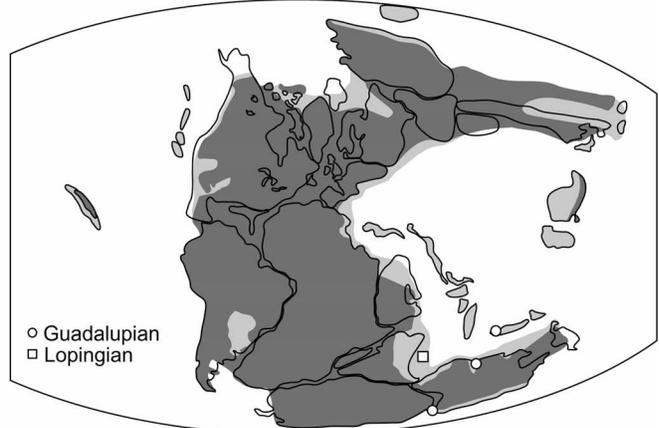
The dominant genera of the Sakmarian glacial biota in eastern Australia, *Eurydesma* and *Trigonotreta*, became much less abundant during the Artinskian and Kungurian, suggesting that those cold-tolerant organisms were unable to adapt to warming temperatures in the aftermath of the late Paleozoic ice age. In contrast, other taxa from the Sakmarian glacial assemblages, such as "*Tomiopsis*" and *Peruvispira*, either had broader environmental tolerances or were better able to adapt to the changing conditions and remained present in moderate abundance in the Kungurian samples. Do these represent regional ecological shifts reflective of more widespread changes in the geographic range of *Eurydesma* or *Trigonotreta*, and what is the ultimate fate of those genera during early and middle Permian global warming?

During the final stages of the late Paleozoic ice age (Asselian–Sakmarian), both *Eurydesma* and *Trigonotreta* enjoyed a wide distribution throughout much of Gondwana (Fig. 7A, B). The cold-water affinity of those genera is demonstrated by their narrow latitudinal distribution, restricted to relatively high southern latitudes even during the glacial interval. *Trigonotreta* did range into more temperate regions, such as Oman (Angiolini et al., 1997), Tajikistan and northern Pakistan (Grunt and Dmitriev, 1973; Angiolini, 1995), India (Singh and Archbold, 1993), and Yunnan (Shen et al., 2000), among others, during the Asselian and Sakmarian. *Eurydesma* was also found at somewhat lower latitudes during that time—for example, in Afghanistan (Termier et al., 1974), India (Srikantia et al., 1978; Waterhouse and Ranga Rao, 1989), and the Lhasa Block, Tibet (Liu and Cui, 1983). The geographic ranges of these two genera underwent quite dissimilar changes during Artinskian and Kungurian climate warming. Although their geographic patterns are in part influenced by the temporary or permanent disappearance of marine deposition from parts of Gondwana (such as Oman and the South American basins) during the Artinskian and Kungurian, marine fossil localities are known from throughout central and eastern Gondwana (e.g., central Afghanistan, Karakorum region, Tibet, Sibumasu terrane in Thailand, and Australia) during that time. *Trigonotreta* remained relatively widespread throughout central and eastern Gondwana (Fig. 7D) despite being significantly less abundant than at its peak during the glaciation. In contrast, *Eurydesma* became restricted to the coldest region of the supercontinent in eastern Australia (Fig. 7C), consistent with its dramatic reduction in ecological dominance during postglacial warming.

*Eurydesma* was ultimately a casualty of postglacial climate warming (Runnegar, 1979), and its last occurrences are in a few Kungurian localities from the Tasmania Basin (Fig. 7C). *Trigonotreta* survived early Permian climate change and persisted, but at extremely low numbers, until the close of the Permian (Fig. 7E). It has been reported from the Roadian in Tasmania (Clarke, 1971) and Western Australia (Archbold and Thomas, 1986) and from the early Guadalupian (Roadian–Wordian) in Thailand (Archbold, 1999), but it is only known from a single area after that, from the Wuchiapingian and Changhsingian (late Permian) in southern Tibet (Shen et al., 2001). These results highlight the fact that cold-adapted taxa can have differing responses to climate warming, with some surviving and maintaining their earlier levels of abundance (e.g., "*Tomiopsis*"), others surviving but losing their ecological dominance

A. *Eurydesma* - Asselian-SakmarianB. *Trigonotreta* - Asselian-SakmarianC. *Eurydesma* - Artinskian-KungurianD. *Trigonotreta* - Artinskian-Kungurian

— EXTINCT —

E. *Trigonotreta* - Guadalupian-Lopingian

**FIGURE 7**—Paleogeographic maps showing the distribution (open circles) of *Eurydesma* (A,C) and *Trigonotreta* (B,D,E) during the end of the late Paleozoic ice age in the Asselian and Sakmarian (A–B), the postglacial warming period during the Artinskian and Kungurian (C–D), and the greenhouse of the Guadalupian and Lopingian (middle and late Permian) (E).

(e.g., *Trigonotreta*), and still others becoming extinct during the warming phase (e.g., *Eurydesma*). The extinction of *Eurydesma* also postdated its substantial reduction in relative abundance within local communities, implying that the proximate effects of climate change were on the ecological relative-abundance structure of communities (Clarke, 1993), with extinction ultimately resulting from those ecological changes.

## CONCLUSIONS

The shift from the glacial *Eurydesma-Trigonotreta* biota to the post-glacial *Echinalosia-Terrakea* biota paralleled the global transition from icehouse climates in the Sakmarian to the initiation of greenhouse conditions in the Kungurian, implying that early Permian climate warming

caused substantial changes in the biotic composition and relative-abundance structure of eastern Australian benthic-marine communities. Most early–middle Permian faunal change occurred in the Artinskian icehouse-greenhouse transition, with only minor compositional changes between the Kungurian and Capitanian. Paleoeological change during the Artinskian was synchronous at all latitudes, at least at the level of temporal resolution available, although there was substantial geographic variability between the Tasmania and Bowen basins in unusual assemblages dominated by endemic or otherwise rare taxa such as *Svalbardia*. The primary shift from *Eurydesma-Trigonotreta* to *Echinalosia-Terrakea* assemblages appears to have occurred first in offshore habitats, and this diachronous appearance of productide-dominated assemblages is likely a result of the relaxation of environmental restrictions, such as cold temperature, due to climate warming in the Artinskian, rather than oceanographic changes in glacial runoff or the upwelling system. The large magnitude of these changes in relative abundance indicates that early Permian climate change triggered substantial long-term shifts in the composition of benthic marine communities. Variability in the Artinskian record is consistent with disruption of marine community structure over shorter timescales, similar to that observed in the terrestrial realm, but may have been influenced by geographic or environmental differences in sampling.

The relative timing of ecological change and the extinction of glacial taxa are also consistent with the idea that climate change most often causes extinctions indirectly, through its effects on ecological parameters such as abundance (Clarke, 1993; Harley et al., 2006). Dominant genera during the icehouse interval, such as *Eurydesma*, became less abundant within communities and became less geographically widespread before they ultimately disappeared from marine ecosystems. It was this reduction in population size and geographic range, combined with probable shifts in ecological interactions within communities, that likely contributed to their later extinction, rather than direct physiological stress from increasing temperatures.

Although the far-field paleoecological effects of postglacial climate warming on, for example, tropical marine communities during the early–middle Permian remain poorly understood, these results imply that even long-term gradual warming can trigger substantial ecological shifts in which dominant glacial taxa are nearly completely replaced by a new set of abundant genera. The ecological shifts caused by postglacial warming also led to extinction of some cold-adapted taxa, underscoring the important taxonomic and ecological consequences of climate change in the marine realm.

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