

Faunal evidence for a cool boundary current and decoupled regional climate cooling in the Permian of western Laurentia

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ABSTRACT

Deglaciation following the late Paleozoic ice age was a complex climate transition marked by smaller glacial–interglacial transitions superimposed on an overall Permian warming trend. In contrast to this growing recognition of a dynamic climate system, few studies have investigated geographic variations in postglacial climate changes, which may have been as dynamic as the temporal variations. Because temperature and ocean circulation are important controls on the biogeography of marine invertebrates, many Permian taxa were characteristic of either paleotropical or high-latitude faunal realms. This study takes advantage of that temperature sensitivity, using a database of more than 5000 Permian fossil collections from northwestern Pangea to reconstruct spatial variations in Permian climate changes throughout the region. Cluster analysis demonstrates that localities in the Phosphoria basin (Nevada/Idaho/Wyoming) were taxonomically distinct from coeval faunas in Texas and occupied the transitional zone between Paleoequatorial and Boreal realms. Quantitative scoring of the faunal affinity of all taxa in 1 by 1° paleolatitudinal bins suggests that the western margin of Laurentia was affected by a persistent southward-flowing cool boundary current, and that the effects of the current became more pronounced throughout the Permian in conjunction with cooling in the Boreal ocean. The increasingly cool-water nature of Phosphoria basin faunas contrasted with warming in Texas and implies that northern and northwest Pangea were decoupled from the broader global warming trend following the late Paleozoic ice age.

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1. Introduction

The Permian was characterized by major fluctuations in global climate, from the peak extent of late Paleozoic ice sheets at the beginning of the period to an ice-free greenhouse climate by the end (Fielding et al., 2008; Isbell et al., 2003). The shift between these two climate states was not a smooth trend; rather, it was punctuated by several subsequent glacial intervals (Fielding et al., 2008; Korte et al., 2008; Montañez et al., 2007). Furthermore, climate changes were not uniform or synchronous in all regions. Whereas climate generally warmed in the tropics and Gondwana (Korte et al., 2008; Montañez et al., 2007), the Boreal region progressively cooled during the Middle and Late Permian, due in large part to oceanographic changes following closure of an oceanic gateway and connection to Tethys in the southern Uralian Seaway (Beauchamp and Baud, 2002; Reid et al., 2007).

Glacial ice was widespread throughout Gondwana during the earliest Permian (Asselian–early Sakmarian), the peak of the late Paleozoic ice age (Fielding et al., 2008; Isbell et al., 2003). Following rapid deglaciation in the Sakmarian (dos Santos et al., 1996; Fielding et al., 2008; Visser, 1996), climate warmed dramatically in the

Artinskian (Fig. 1), although with a short-lived cooling in the early Artinskian, both in the tropics and at high southern latitudes (Korte et al., 2008; Montañez et al., 2007). The late Artinskian may have been the warmest interval of the Early/Middle Permian as climate cooled slightly in the Kungurian and Middle Permian, particularly in Gondwana with the expansion of glaciers in eastern Australia (Fielding et al., 2008; Korte et al., 2008; Montañez et al., 2007). In contrast to the stable or slightly cooler temperatures in the Middle Permian of equatorial Laurentia (Montañez et al., 2007), there was pronounced regional cooling throughout the Permian in Boreal regions of Pangea, due in large part to oceanographic changes stemming from the closure of the oceanic gateway at the southern Uralian seaway (Beauchamp and Baud, 2002; Reid et al., 2007). Given the markedly different temperature trends in the two regions, it is important to document spatial variations in Permian temperature changes to fully understand the nature of climate fluctuations in the Permian icehouse–greenhouse transition in northwestern Pangea.

These temperature fluctuations have been reconstructed from a variety of proxy measurements, including oxygen isotopes (Grossman et al., 2008; Korte et al., 2008; Montañez et al., 2007) and climate-sensitive sediments such as coal, phosphorites, evaporite minerals, or glendonite (Gibbs et al., 2002; Jones et al., 2006). Despite potential complications from aridification (due to evaporation/precipitation balance in partially restricted epeiric seas) and changing seawater

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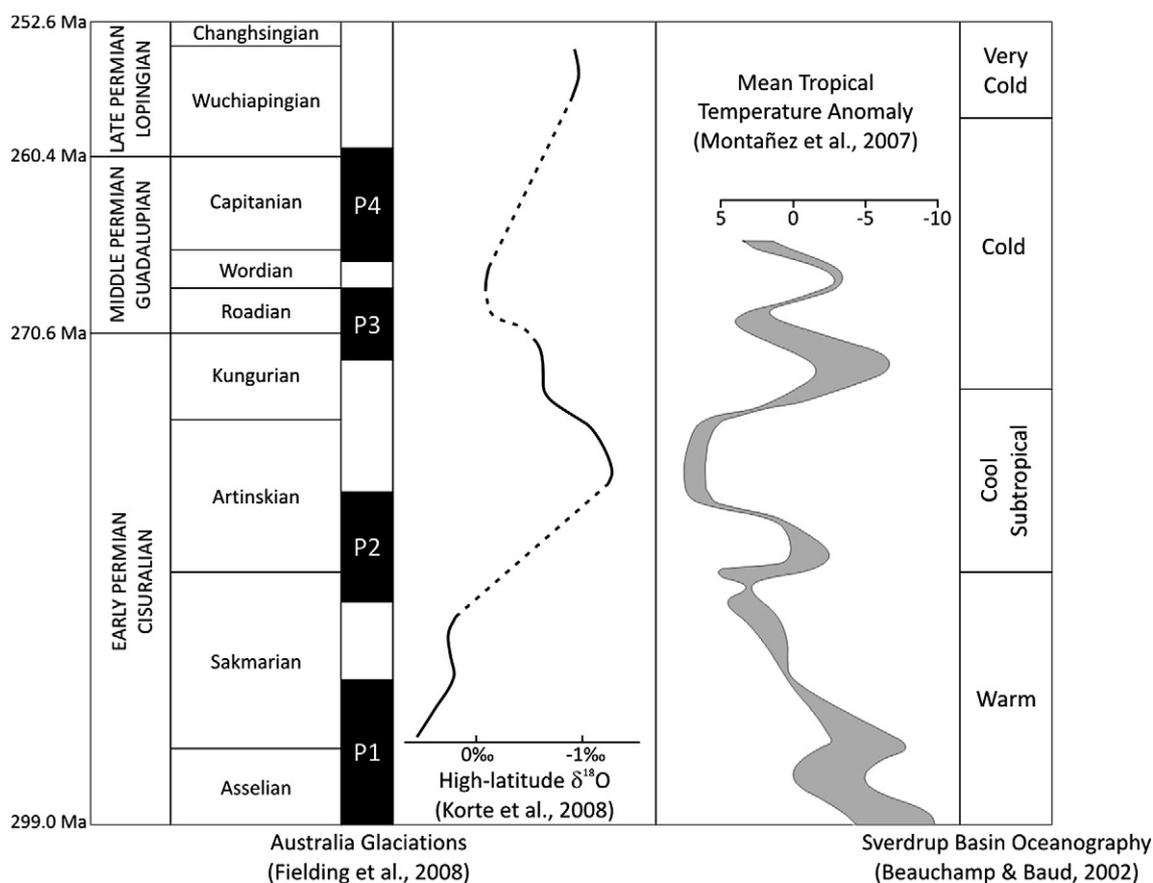


Fig. 1. Summary of Permian climate changes at high southern, tropical, and northern latitudes. Timing of eastern Australian glacial episodes (P1–P4) from Fielding et al. (2008) and eastern Australian oxygen isotope curve from Korte et al. (2008). Tropical ocean temperatures are based on brachiopod oxygen isotopes from western North America (Montañez et al., 2007) and are reported relative to 17.5 °C because of the potential local and regional variations environment or diagenesis. Sverdrup Basin ocean temperature changes are based on sedimentological proxies from Beauchamp and Baud (2002).

$\delta^{18}\text{O}$ (due to ice volume changes) (Grossman et al., 2008), oxygen isotope proxies provide the most refined temporal trends in paleotemperature. However, oxygen isotope proxy records are usually restricted to a few regions and do not provide fine-scale spatial coverage due to the time-intensive nature of the analyses and need for adequately preserved (i.e., minimally diagenetically-altered) material. In contrast, climate-sensitive sediments often provide excellent spatial and temporal coverage but in many cases (e.g., coal or phosphate) are not precise records of paleotemperature.

The distribution of marine invertebrate taxa provides a different approach that may combine the best aspects of the other proxies. Fossils are widespread and common, allowing reconstruction of environmental change at relatively fine spatial scales such as bivalve geographic ranges shifts during Pleistocene glacial–interglacial transitions (Kitamura et al., 2000; Roy et al., 2001). Although ocean circulation and dispersal patterns are also important, the distribution of marine invertebrates is more closely linked to temperature (at least compared to many types of climate-sensitive sediments) and it has long been known that certain late Paleozoic taxa had strongly tropical affinities whereas others were characteristic of polar regions (Stehli, 1957; Ustritskiy, 1974). Paleobiogeographic provinces were clearly demarcated during the Permian (e.g., Shen et al., 2009) and faunal composition has successfully been used as a paleoclimate proxy in other regional studies (Reid et al., 2007; Shi, 2000). This study creates a quantitative measure of the climate affinity of more than 2500 Permian marine invertebrate genera and applies that proxy to reconstruct regional climatic and oceanographic changes in the Early and Middle Permian of western Pangea. In particular, the proxy can constrain the geographic and temporal extent of regional climate

cooling in western Pangea and its relationship to warming of tropical regions in order to document the climate evolution of western Pangea during and after the late Paleozoic ice age.

2. Methods

The climatic affinities of marine invertebrates were quantified in two different ways. First, collections from a particularly well-sampled time slice (the Roadian–Wordian interval, early Guadalupian) were grouped into stations and analyzed using cluster analysis. The Roadian–Wordian was chosen because it is a short interval, approximately 5 Myr long, that contains widely distributed and abundant faunas, and because there is a robust, pre-existing paleobiogeographic scheme for the interval (Shen et al., 2009). This allows the faunal composition in localities of interest (Texas, the Phosphoria basin in Nevada/Idaho/Wyoming, Alaska/Yukon, and the Sverdrup basin in arctic Canada) to be placed in pre-defined biogeographic provinces (Shen et al., 2009) for comparison with other Paleoequatorial or Boreal localities. Roadian–Wordian brachiopods were grouped into 17 stations based on 5652 occurrences of 272 genera from 653 fossil collections in northern Pangea. A collection is a single faunal list from one place and can range in scope from a single bed at one outcrop to an entire stratigraphic unit in a basin, depending on the precision of reporting in the primary literature. An occurrence is the record of a single taxon in a collection. Bryozoans were grouped into 27 stations (1481 occurrences of 103 genera from 370 collections worldwide) and bivalves were grouped into 22 stations (1065 occurrences of 120 genera from 368 collections worldwide). Cluster analysis used average linkage agglomeration with similarity quantified by correlation

coefficient (Pearson's product-moment coefficient r). Although use of the correlation coefficient as a similarity measure takes shared absences into account (a property that can be disadvantageous) and is not traditionally used for biogeographic data, this methodology provides the clearest separation of faunal provinces and allows direct comparison with the Shen et al. (2009) dendrograms. All analyses were performed with R version 2.8.1 (R Development Core Team, 2008).

Second, 5334 fossil collections from northwestern Pangea (including 29,951 occurrences) were grouped into 1 by 1° paleogeographic bins and the mean paleolatitude of all recorded marine invertebrate genera occurring within each bin was calculated. This allows finer spatial and temporal resolution of changing faunal affinity and climate and includes groups such as corals, trilobites, sponges, and ammonoids that are too sparse for cluster analysis. The climate affinity of each genus must first be estimated by assigning a paleolatitude score calculated from the mean paleolatitude of all of its occurrences in the complete dataset (11,515 collections), then allowing the mean paleolatitude score of all genera reported in the chosen area (in this case, the 5334 collections from northwestern Pangea grouped into 1 by 1° bins) to be used as a climate proxy for that area. The absolute values of recorded paleolatitudes were used to avoid errors when calculating the mean for taxa that span the equator and all values are based on a 280 Ma paleogeographic reconstruction (Scotese, 2001). Paleolatitudes of localities in the Wrangellia/Alexander terrane were adjusted using published paleomagnetic data for late Paleozoic strata (Butler et al., 1997; Haeussler et al., 1992). The nature of the Permian fossil record, with substantially more localities recorded in paleotropical regions (especially the western United States and south China), will tend to bias the absolute mean values towards lower latitudes, reducing the power of the proxy in higher-latitude regions, but will still preserve relative differences in paleolatitude score among taxa. The mean value was calculated from all occurrences, rather than calculating a different value for each time interval, in order to increase the sample size and reduce the effect of noise arising from incomplete sampling and other biases.

Pooling data from multiple time intervals may obscure meaningful trends if there was significant directional bias in mean paleolatitudinal position from one stage to the next; thus, it is important to assess the effects of noise (resulting from incomplete sampling) on the data. Stage-to-stage changes in mean paleolatitude are symmetrically distributed with a mean of -0.05° , indicating no overall directionality in mean paleolatitude (Fig. 2A). The large variance in stage-to-stage changes is caused primarily by a combination of shifts in the geographic distribution of fossil collections and random fluctuations due to the extremely limited number of occurrences in a given interval (the median number of genus occurrences per stage is one). Some of the range shifts may reflect an actual biological signal but they cannot be distinguished from the overprint of sampling noise. Comparison at the stage level also reveals no significant bias in the direction of paleolatitudinal changes, ranging from a mean poleward shift of 6.8° from the Asselian to Sakmarian to an equatorward shift of 3.5° from the Artinskian to Kungurian (Fig. 2B). Although some of these shifts differ significantly from zero, they also correspond closely to changes in the geographic distribution of collections (e.g., from a mean collection paleolatitude of 16.5° in the Asselian to 32.7° in the Sakmarian, or from 32.9° in the Artinskian to 12.9° in the Kungurian), suggesting that variations in the locus of sampling are the primary driver of observed changes in taxon range. The randomness of noise present in stage-to-stage genus changes and the lack of a secular trend in this bias indicate that calculating a genus's mean paleolatitude from all of its occurrences is a reasonable approximation, on aggregate, of its climate tolerance.

The spatial and taxonomic resolution of analyses are limited by these sampling biases in the data. Single collections cannot be

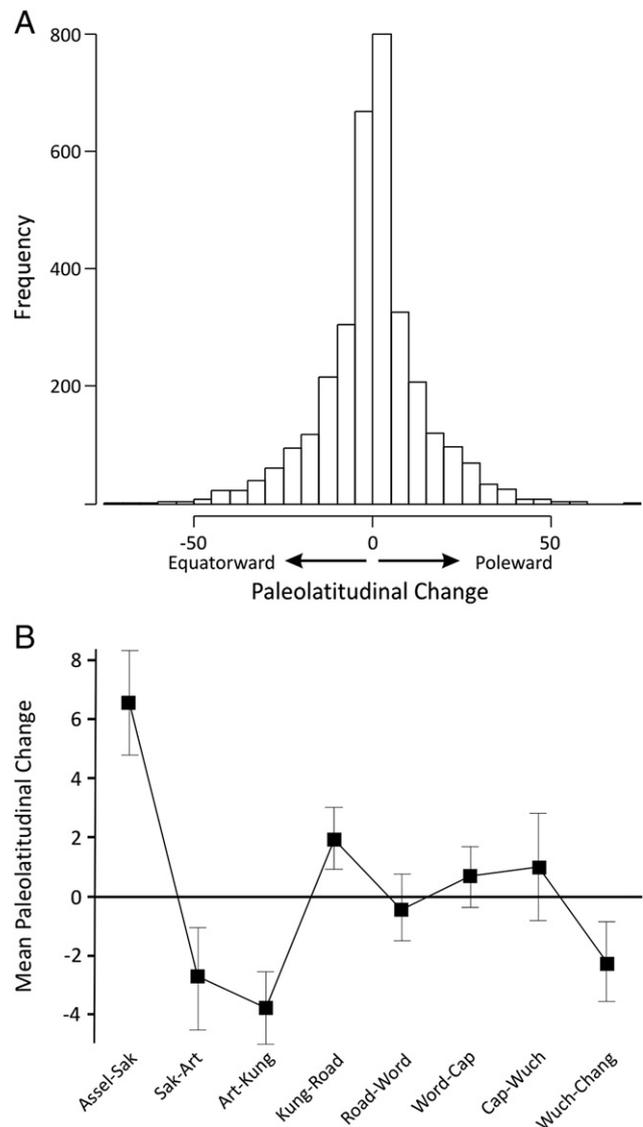


Fig. 2. A. Histogram of stage-to-stage changes in the mean paleolatitude of marine invertebrate changes. Although considerable apparent shifts due to random chance are possible (usually for poorly sampled taxa), the vast majority of taxa have stable mean paleolatitudes through time and there is no overall bias in the directionality of shifts. B. Mean change in the mean paleolatitude of all genera from one stage to the succeeding time interval (e.g., Ass-Sak is change from Asselian to Sakmarian). Error bars are 95% confidence intervals. Despite fluctuations due to temporal changes in the distribution of collections, there is no pervasive directionality to the shifts, suggesting that grouping all occurrences of a genus to calculate its overall mean paleolatitude is a reasonable assumption.

compared because they are almost never complete or even random samples of the local fauna. The majority of collections derive from papers analyzing single taxonomic groups (e.g., only ammonoids or athyridid brachiopods) and lists of the whole fauna are virtually non-existent. As a result, the median number of occurrences per collection is two genera (42% of collections contain only a single genus); this small sample size makes results from individual collections highly susceptible to random noise. For these reasons, collections must be pooled into larger geographic areas (such as 1 by 1° bins, sedimentary basins, or other pre-determined biogeographic regions) to smooth the noise and extract signals, although the magnitude of signal resolvable by the data is similarly attenuated. Likewise, it is not possible to analyze single taxa (for example, to determine if a genus is eurythermal or stenothermal, or to evaluate stage-to-stage changes in latitudinal range) due to the sparse geographic and temporal occurrences of individual taxa. The median number of occurrences for

a genus over its entire stratigraphic range is only six and the modal number of occurrences is one (Fig. 3A). When the data are subdivided at the stage level, the median number of occurrences for a genus per stage is only one (Fig. 3B) and 27% of genera, on average, were Lazarus taxa in a given interval (i.e., they were recorded before the interval in question and after but were not sampled in the selected time interval). Sparse occurrences necessitate pooling data from multiple collections and multiple time intervals to reduce noise from sampling effects, although this places constraints on the spatial, temporal, and taxonomic precision of analyses.

3. Faunal affinity of western Laurentian taxa

3.1. Brachiopods

The differentiation of Paleoequatorial and Boreal brachiopod faunas has long been used to demarcate the paleobiogeographic boundary between tropical and temperate climate zones in the Permian (Stehli, 1957). In North America, Stehli (1957) placed that boundary between 50° and 60° N (present-day latitude), separating tropical faunas with fusulinids and lyttoniid or richthofeniid brachiopods in the western United States Arctic faunas from Boreal faunas lacking those groups in the Canadian Arctic and Greenland. Stehli (1971) later revisited the Boreal–Tethyan boundary using a quantitative cluster analysis of brachiopod, fusulinid, and selected coral families. In this analysis, which pooled assemblages spanning much of the Permian, western North American localities in Oregon and

southeastern Alaska (Wrangellia terrane) grouped in the Tethyan cluster, although that cluster also included high-latitude localities in Novaya Zemlya and the Ural Mountains (Stehli, 1971). Waterhouse and Bonham-Carter (1975) used the same approach, but at the stage level rather than treating the entire Permian as one unit, to recognize three major clusters representing Gondwanan, Boreal, and Paleoequatorial faunas. With the exception of west Texas, nearly all other Cordilleran localities (e.g., Sonora, Oregon, Phosphoria, and Vancouver Island) clustered with Boreal faunas (Waterhouse and Bonham-Carter, 1975). Other analyses have reached different conclusions, instead grouping central Cordilleran localities such as the Phosphoria Basin with tropical brachiopod fauna in Texas, while localities in accreted terranes were more similar to Boreal regions such as the Canadian Arctic (Belasky et al., 2002; Wardlaw, 1977). These analyses are complicated by mixing faunas of different ages, but the primary reason for inconsistent clustering of localities in the western North America arises from the transitional character (sensu Shi et al., 1995) of those localities, combining Boreal and Paleoequatorial components, similar to transitional regions in northeast Asia and the Cimmerian blocks.

The paleobiogeographic affinity of western North American brachiopod faunas can be refined by examining only Roadian–Wordian (early Guadalupian) localities. A reconstruction of Roadian–Wordian brachiopod paleobiogeography has also recently been published (Shen et al., 2009), providing a global framework for comparison. The new analysis here incorporates regions such as the Phosphoria basin, Sverdrup basin, and Taimyr that were not included in the Shen et al. (2009) study. The resulting Q-mode dendrogram has three primary clusters (Fig. 4), corresponding to the Paleoequatorial realm, Boreal realm, and Northern Transitional Zone localities documented by Shen et al. (2009). The Paleoequatorial cluster contains two subgroupings representing the Panthalassan province (Chichibu and Mino-Tamba belts from Japan) and the Grandian province (Texas and Coahuila). The Boreal cluster also is consistent with Shen et al. (2009)'s differentiation of the Northeast European province (Russian Platform) and the Verkolyma Province (Verkhoyan and Kolyma-Omolon).

Localities in the Phosphoria Basin and Sonora both plot within the cluster containing Northern Transitional Zone faunas, rather than with Paleoequatorial realm localities in Texas and Coahuila (Fig. 4). Some typical Paleoequatorial genera were present in the Phosphoria basin, including *Composita* (Wardlaw, 1977) and *Paraspiriferina* (Cooper and Grant, 1976), but the Roadian–Wordian fauna was dominated by Boreal or bipolar taxa such as *Anidanthus*, *Bathymyonia*, *Costatumulus*, *Komiella*, *Rhynoleichus*, *Thamnusia*, and *Yakovlevia* (Cooper and Grant, 1975; Girty, 1910; Wardlaw, 1977; Weldon and Shi, 2000; Weldon and Shi, 2003). The Sonora fauna at El Antimonio had a more mixed character with many Paleoequatorial genera (e.g., *Hustedia*, *Spiriferellina*, *Glossothyropsis*) but still contained a substantial number of more typical Boreal genera (e.g., *Anidanthus*, *Bathymyonia*, *Costatumulus*, *Liosotella*, *Thamnusia*, *Yakovlevia*) (Cooper et al., 1953).

Wordian faunas were also present in the Pybus Formation of the Alexander terrane (Alaska) but only one brachiopod genus, the Boreal rhynchonellid genus *Septacamera*, has been published (Grant, 1971). Nevertheless, older Asselian and Artinskian faunas from Wrangellia also demonstrate a strong Boreal affinity, containing genera such as *Callaiapsida*, *Bruntonia*, *Septacamera*, and *Yakovlevia* (Grant, 1971; Yole, 1963), similar to faunas from the Jungle Creek Formation in the Yukon (Shi and Waterhouse, 1996). These results suggest that the paleobiogeographic boundary between Boreal and Paleoequatorial realms occurred at a lower latitude on the western margin of Pangea, as low as 15° N compared to its position at 30° N in east Asia (Mongolia, Primorye, and Japan).

3.2. Bryozoans

Similarities between the bryozoan fauna from the western United States and faunas from localities in Russia have been noted by

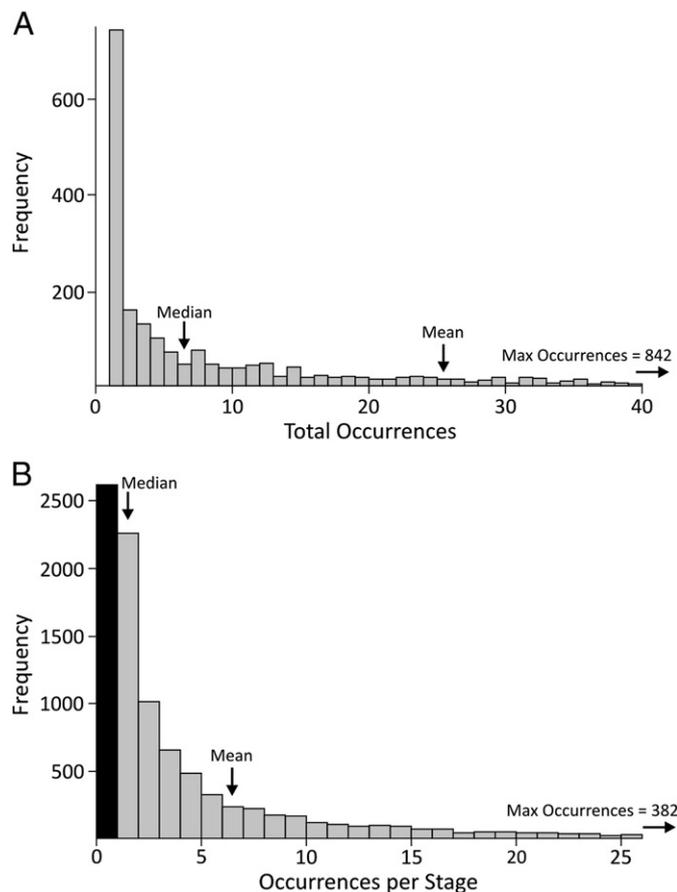


Fig. 3. Histograms showing the frequency of genus occurrences in the database. Only the left side of each distribution is shown for clarity; the maximum number of occurrences in each analysis is indicated. A. Total number of occurrences per genus, grouped over the entire range of the taxon. B. Number of occurrences per genus, subdivided at the stage level. Black bar at zero occurrences indicates the frequency of Lazarus taxa.

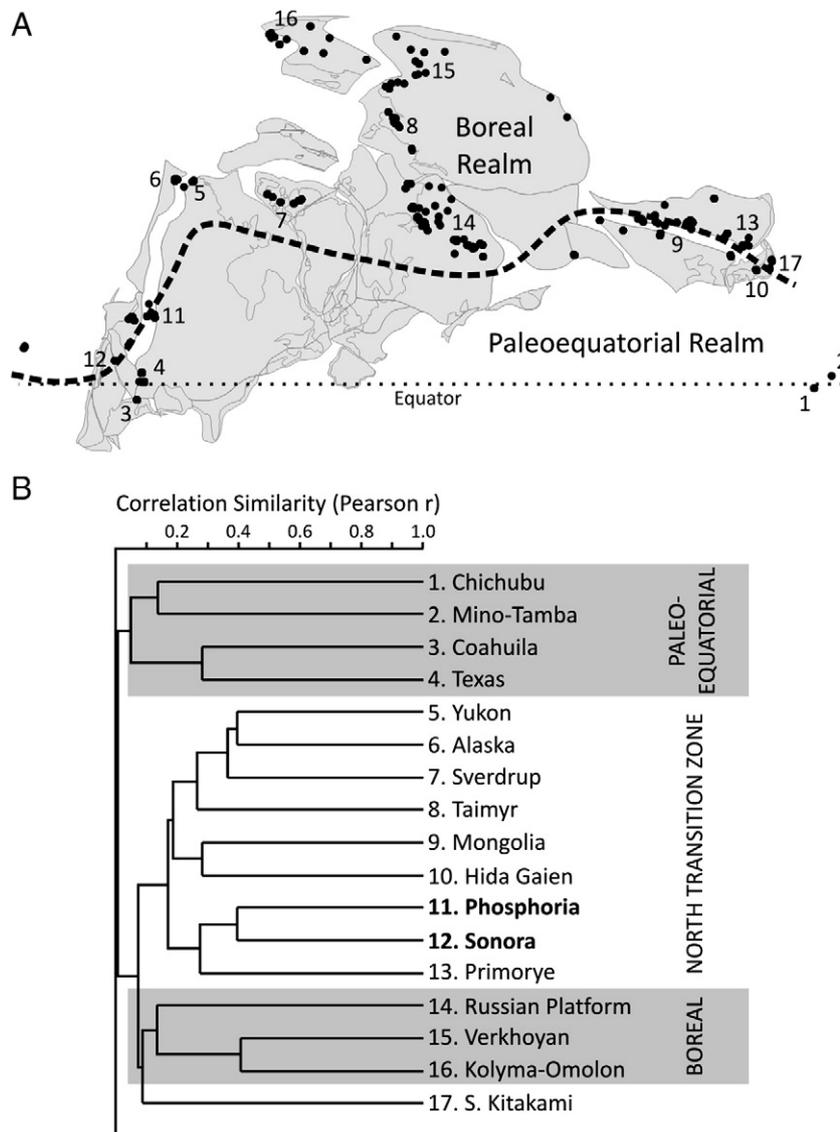


Fig. 4. Paleobiogeographic affinity of Roadian–Wordian brachiopods from northern Pangea. A. Paleogeographic map showing sampling stations (numbers) and spatial distribution of brachiopod collections in the database (filled circles). Dashed line indicates approximate position of biogeographic boundary between Paleotropical and Boreal realms. B. Cluster dendrogram of the 17 sampling stations from northern Pangea (correlation similarity, average linkage was chosen to facilitate comparison with the results of Shen et al. (2009)). Paleobiogeographic realms (Paleoequatorial, transitional, and Boreal, based on Shen et al. (2009)) are superimposed on the dendrogram, showing how western Laurentian localities such as the Phosphoria basin group with other regions in the northern transitional zone.

previous authors; for example, Ross (1978) and Ross and Ross (1990) subdivided Middle and Late Permian bryozoan faunas into biogeographic provinces and recognized that faunas from the central Cordillera were distinct from the west Texas bryozoan fauna. The transitional nature of the northeast Nevada fauna, with similarities to tropical regions as well as to localities Russian platform was also noted (Ross, 1978). Gilmour and Morozova (1999) also grouped Cordilleran localities in the Phosphoria basin and northeast Nevada with faunas from the Canadian Arctic and Russia, explicitly placing the western United States faunas in the Boreal realm.

Cluster analysis provides quantitative support for these biogeographic relationships and the resulting dendrogram highlights a paleobiogeographic pattern similar to that exhibited by brachiopods, but with some minor differences in the boundaries of the individual faunal provinces. For example, the Southern Transitional Zone (Cimmerian Province), which contained especially rich bryozoan faunas, extended further into western Tethys and into western Australia than observed among brachiopod faunas (Shen et al., 2009). It is possible,

however, that better coverage of localities from the poorly-represented Paleoequatorial Cathaysian Province in China or western Tethys may alter the grouping of more tropical Cimmerian localities in Iran and other regions of western Tethys. Similar to the provinces delineated by brachiopods, bryozoan-based Boreal and Gondwanan realms are distinct and consist of an Austrazean province in eastern Australia, an extended Verkolyma province that also includes localities in Mongolia, and a larger Northeast European province that extends into the northwestern United States. Like in previously published analyses, localities in Washington and the Phosphoria basin cluster with the Russian Platform. The Phosphoria basin contains boreal genera *Hinganella*, *Ruzhencevia*, and *Neoeridotrypella*, and the bipolar genus *Dyscritellina* (Gilmour and Walker, 1986; Gilmour et al., 1997), whereas Washington contains the cool-water genera *Neoeridotrypella*, *Pinegopora*, and *Dyscritellina* (Gilmour and Snyder, 2000). The boundary between Paleoequatorial and Boreal realms, as delineated by bryozoan faunas, is also much closer to the equator in western Pangea than in eastern Pangea (Fig. 5).

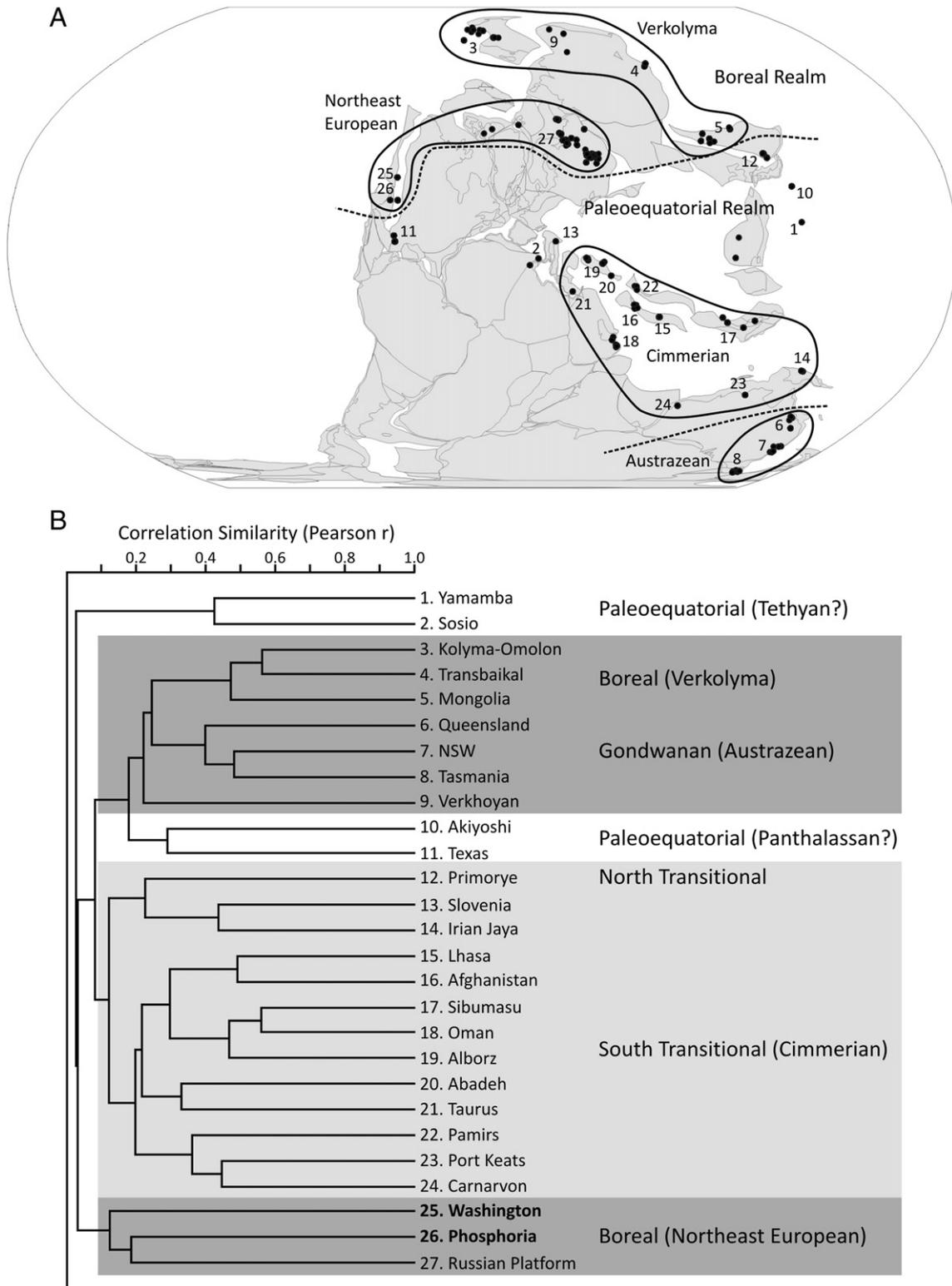


Fig. 5. Paleobiogeographic affinity of Roadian–Wordian bryozoans. A. Paleogeographic map showing sampling stations (numbers) and spatial distribution of bryozoan collections in the database (filled circles). Dashed lines indicate approximate position of biogeographic boundary between Gondwanan, Paleotropical, and Boreal realms. The boundaries of biogeographic provinces are indicated by solid lines. B. Cluster dendrogram of the 27 stations. The Phosphoria basin and Washington state localities group with the Russian platform in the Boreal Northeast European province.

3.3. Bivalves

Roadian–Wordian bivalves are also well represented, by 1065 occurrences from 368 localities; however, the paleobiogeographic patterns are much less refined because bivalve genera have larger

geographic ranges than brachiopod or bryozoan taxa and several localities contain only cosmopolitan taxa. Two provinces are exceptions: the Austrazean Province in the Gondwanan Realm and the Verkolyma Province in the Boreal Realm are clearly separated from all other localities (Fig. 6). The Verkolyma Province was dominated by

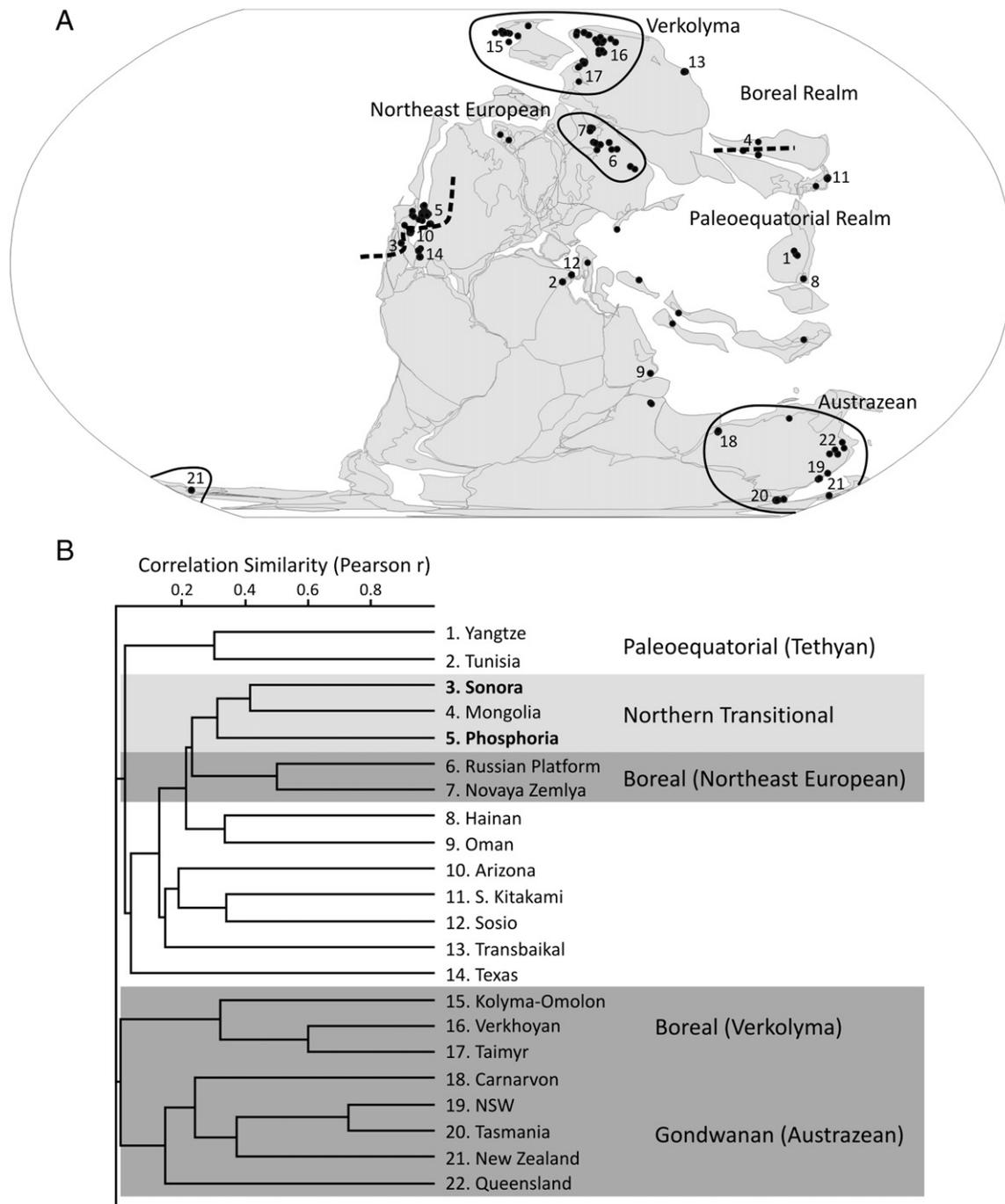


Fig. 6. Paleobiogeographic affinity of Roadian–Wordian bivalves. A. Paleogeographic map showing sampling stations (numbers) and spatial distribution of bivalve collections in the database (filled circles). Dashed lines in northeast Asia and Laurentia indicate approximate position of biogeographic boundary between Paleotropical and Boreal realms. The boundaries of better-differentiated biogeographic provinces are indicated by solid lines. B. Cluster dendrogram of 22 stations. Biogeographic provinces are poorly differentiated, except for the Verkolyima and Austrazean provinces, because of the cosmopolitan nature of Permian bivalve localities. Nevertheless, western Laurentian stations such as the Phosphoria basin seem to be more similar to transitional (Mongolia) or Boreal (Russian platform) regions.

kolymiid bivalves, such as *Kolymia*, *Cigarella*, *Cyrtokolymia*, and *Taimyrokolymia* (Biakov, 2008), whereas the Austrazean Province included many infaunal pholadomyoid bivalves such as *Myonia*, *Vacunella*, and *Megadesmus*. Differentiation of other provinces is more problematic due to the cosmopolitan nature of many faunas (e.g., Transbaikal) but localities in the Phosphoria basin group closer to Boreal localities in Russia rather than with the geographically closer west Texas basin (Fig. 6). The Sonora cluster contains five cosmopolitan genera so its position is uncertain. The Phosphoria basin shares some unique taxa with west Texas, such as *Fransonia*, but also

contains Boreal taxa such as *Vngripecten* (Newell and Boyd, 1995) and the kolymiids *Intomodesma* and *Aphanaia* (Kauffman and Runnegar, 1975). Localities in Mongolia have a similar transitional fauna, containing Boreal *Vngripecten* and *Kolymia* along with taxa like *Leptodesma* with a greater Paleoequatorial affinity. Together, the Mongolia and Phosphoria basin regions broadly trace a Northern Transitional Zone between Paleoequatorial and Boreal realms (Fig. 6). As was the case with Roadian–Wordian brachiopod and bryozoan faunas, the transitional faunas occur at a lower latitude in western Pangea than in eastern Pangea.

3.4. Other clades

Occurrences of other clades are too sparse to allow cluster analysis but previously published results qualitatively support the cool-water nature of faunas from western North America. Middle Permian corals were rare in western North America, but widespread Early Permian coral faunas have been grouped with faunas from the Ural Mountains in the *Thysanophyllum* coral belt (Stevens, 1982) of the Cordilleran–Arctic–Uralian realm (Fedorowski et al., 2007). Some analyses have suggested that faunas from accreted terranes in Laurentia were dissimilar from cratonal faunas (Belasky et al., 2002) but a comprehensive taxonomic revision has emphasized the similarity of localities throughout western North America to each other and to faunas from the Russian Platform and Arctic (Fedorowski et al., 2007). The occurrence of the conulariid *Diconularia meadepeakensis* in the Roadian Meade Peak Member of the Phosphoria Formation is another potential cool-water link, as Permian conulariids were most common in anti-tropical settings (Weldon and Shi, 2003), although a different conulariid (*Paraconularia leonardensis*) has also been reported from the Kungurian of west Texas (Finks, 1955). In contrast to most other groups, the biogeographic affinities of Permian ammonoids from the western United States were notably tropical, sharing almost no links with coeval faunas in the Arctic and Russia. Although some Cordilleran localities in Nevada have yielded Boreal ammonoids, such as the Artinskian *Uraloceras* (Schiappa et al., 2005) and the Roadian *Spirolegoceras* (Miller et al., 1957), the majority of taxa are widespread paleoequatorial genera such as *Properrinites*, *Daraelites*, and *Agathiceras* or taxa shared with west Texas faunas (*Stenolobulites*, *Glassoceras*) (Mikesh et al., 1988; Miller et al., 1957; Schiappa et al., 1995; Schiappa et al., 2005).

4. Discussion

4.1. Spatial variation of cool-water faunas

Roadian/Wordian faunas in the Phosphoria Basin were paleobiogeographically distinct from coeval faunas in Texas and instead had a strong affinity with the Boreal Realm, demonstrating the influence of cool waters along the western margin of Laurentia in the early Guadalupian. Transitional brachiopod, bryozoan, and bivalve faunas all extended to lower paleolatitudes on the western margin of Pangea in the Phosphoria basin and northern Nevada than on the eastern margin in Japan, Mongolia, and north China. Although cluster analysis provides strong paleobiogeographic evidence for cool conditions in western Laurentia, restriction of the data to stations along the continental margin means that the analysis cannot distinguish the relative importance of a southerly-flowing cool boundary current from coastal upwelling of cool, deep waters, both of which likely were present (e.g., Piper and Link, 2002). Likewise, it is not certain that Roadian/Wordian paleobiogeographic patterns are indicative of ocean circulation at other times in the Permian, given major fluctuations in global or regional climate and oceanography during that time (Fielding et al., 2008; Montañez et al., 2007; Reid et al., 2007).

Spatial variations in the paleobiogeographic affinity of fossil localities can instead be measured by calculating the mean paleolatitude score of all genera within 1 by 1° bins (containing 5334 fossil collections from northwestern Pangea with a total of 29,951 occurrences). Some cells contain few genera, but this approach allows assessment of both broader-scale patterns, by incorporating cells with too few for quantitative cluster analysis, and finer-scale variations within regions. The development of characteristically Boreal faunas on accreted terranes such as the Wrangellia–Alexander terrane (Fig. 7) is indicative of a more extensive southerly-flowing boundary current, suggesting that cool faunas in continental margin localities were not simply a signal of localized upwelling of cooler waters along the coastline (Piper and Link, 2002). For example, an Artinskian

locality from the Wrangellia terrane on Vancouver Island (Yole, 1963) contains tropical brachiopods but also shares several genera with a cratonal fauna from the Yukon Territory (Shi and Waterhouse, 1996). The Boreal rhynchonellid taxa *Septacamera* and *Callaiapsida* are also found in Asselian and Wordian localities from the Alexander terrane in Alaska (Grant, 1971). The occurrence of Arctic-type brachiopods at low latitudes in the Wrangellia–Alexander terrane may indicate longitudinal variations in the strength of the cool current (Belasky et al., 2002), but other Arctic brachiopod genera such as *Rhynoleichus* and *Komiella* were also present at similar paleolatitudes in the Phosphoria Basin. Guadalupian brachiopods from the Eastern Klamath terrane were similar to cool-water localities in the Phosphoria Basin on the craton (Coogan, 1960), suggesting that the overall faunal character of the accreted terranes was not unusual compared to localities such as the Phosphoria Basin, Washington, or British Columbia at similar paleolatitudes on the craton (Fig. 7).

4.2. Effects of upwelling

Although the widespread distribution of cool-water faunas both along the continental margin and on accreted terranes is consistent with a widespread southerly-flowing boundary current, upwelling of cool water (Piper and Link, 2002) or other variations in the depth of the thermocline may also have influenced the faunal composition in some regions. Absolute depth estimates are not feasible for the majority of published fossil collections but it is possible to use the Phosphoria Basin, a region with a well-defined relative paleobathymetry (Piper and Link, 2002), as a case study to assess bathymetric controls on faunal composition. The basin deepened to the west from nearshore units in central Wyoming to basinal units in western Wyoming and Idaho (Fig. 8A). Capitanian-age formations in the Phosphoria Basin (Phosphoria and Park City Formations) are also subdivided into lithologically-distinct members that occupy consistent positions along a paleobathymetric transect (Fig. 8A). The Shedhorn Sandstone was the most proximal unit, the Ervay Limestone was less proximal, the Tosi Chert formed on more distal parts of the ramp, and the Retort Phosphatic Shale was deposited in deepest parts of the basin (Ciriacks, 1963). The Gerster Formation is a time-equivalent unit in northeastern Nevada (Wardlaw and Collinson, 1978) deposited in environments similar to the Ervay or Tosi members.

The mean paleolatitude score for genera occurring in the distal Retort Phosphatic Shale is slightly higher than in the other four units (26° compared to a range of 15.3–21°; Fig. 8B) but the differences among the five units are not significant (ANOVA, $p = 0.28$). Facies are an imperfect predictor of bathymetry, however, and comparison of genus paleolatitude scores across a depth transect in Wyoming indicates a significant ($p = 0.03$) increase in paleolatitude score with increasing distance into the basin (Fig. 8C), consistent with effects of a depth-related thermal gradient. The common occurrence of cool-water taxa in more proximal collections (e.g., from the Ervay Limestone) may also suggest upwelling of cooler waters to shallow parts of the ramp, although it is difficult to evaluate the relative influence of upwelling versus ambient cool water without comparison of bathymetric faunal gradients with other regions.

4.3. Temporal variation of cool-water faunas

The occurrence of sparse Early Permian Boreal-type brachiopod faunas from the accreted terranes provides tentative evidence suggesting that a cool boundary current and/or related upwelling effects may have been a long-lived feature on the western Laurentian margin. Early Permian corals in western Laurentia also belong to the Cordilleran–Arctic–Uralian Province, with links to coeval cool-water faunas in Russia and the Arctic (Fedorowski et al., 2007), but brachiopods, bryozoans, and other groups have not been described in

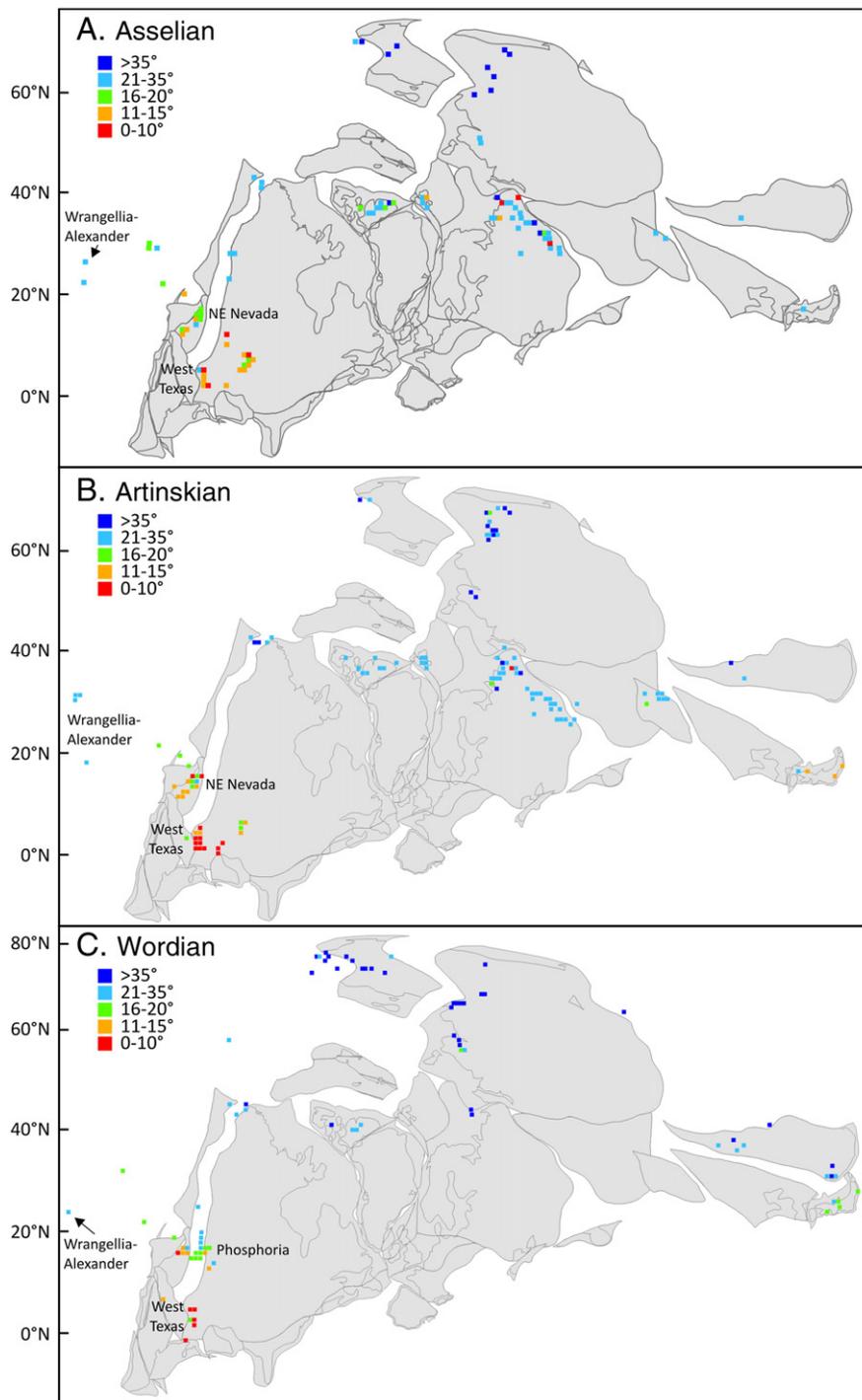


Fig. 7. Paleogeographic maps of northern Pangea showing the mean paleolatitude score for all genera in 1 by 1° bins during the Asselian (A), Artinskian (B), and Wordian (C). The results show cool conditions (as indicated by higher paleolatitude scores and green or blue colors) extending along the western margin of Laurentia to paleolatitudes of 20°, in NE Nevada and the Phosphoria basin. Cool conditions also affected the offshore Wrangellia–Alexander terrane during these time intervals.

sufficient numbers to allow quantitative paleobiogeographic analysis. Changes in the climatic affinity of faunas were instead quantified by calculating the mean paleolatitude of all recorded genera for Asselian through Capitanian stages within three regions: west Texas and the Guadalupe Mountains in New Mexico; northeastern Nevada and the Phosphoria Basin; and Yukon, eastern Alaska, and the Sverdrup Basin. The mean paleolatitude of genera in northeast Nevada and the Phosphoria basin increased consistently from the Asselian to Capitanian, whereas the mean paleolatitude of genera in west Texas exhibited a static or slightly opposite, but not significant, trend

(Fig. 9). Capitanian taxa from the Phosphoria basin had a significantly cooler faunal affinity than Asselian taxa (Wilcoxon rank sum test, $p = 0.027$), indicating that the cooling trend, although subtle, had a measurable influence on faunal composition.

Those diverging trends, especially the increasingly Boreal character of the Phosphoria fauna, suggest that the cool boundary current or upwelling were more pronounced in the Middle Permian than in the Early Permian, but also imply that the Delaware basin in west Texas became progressively isolated from that cool current. Cooling from the Early to Middle Permian in the Phosphoria basin was coincident

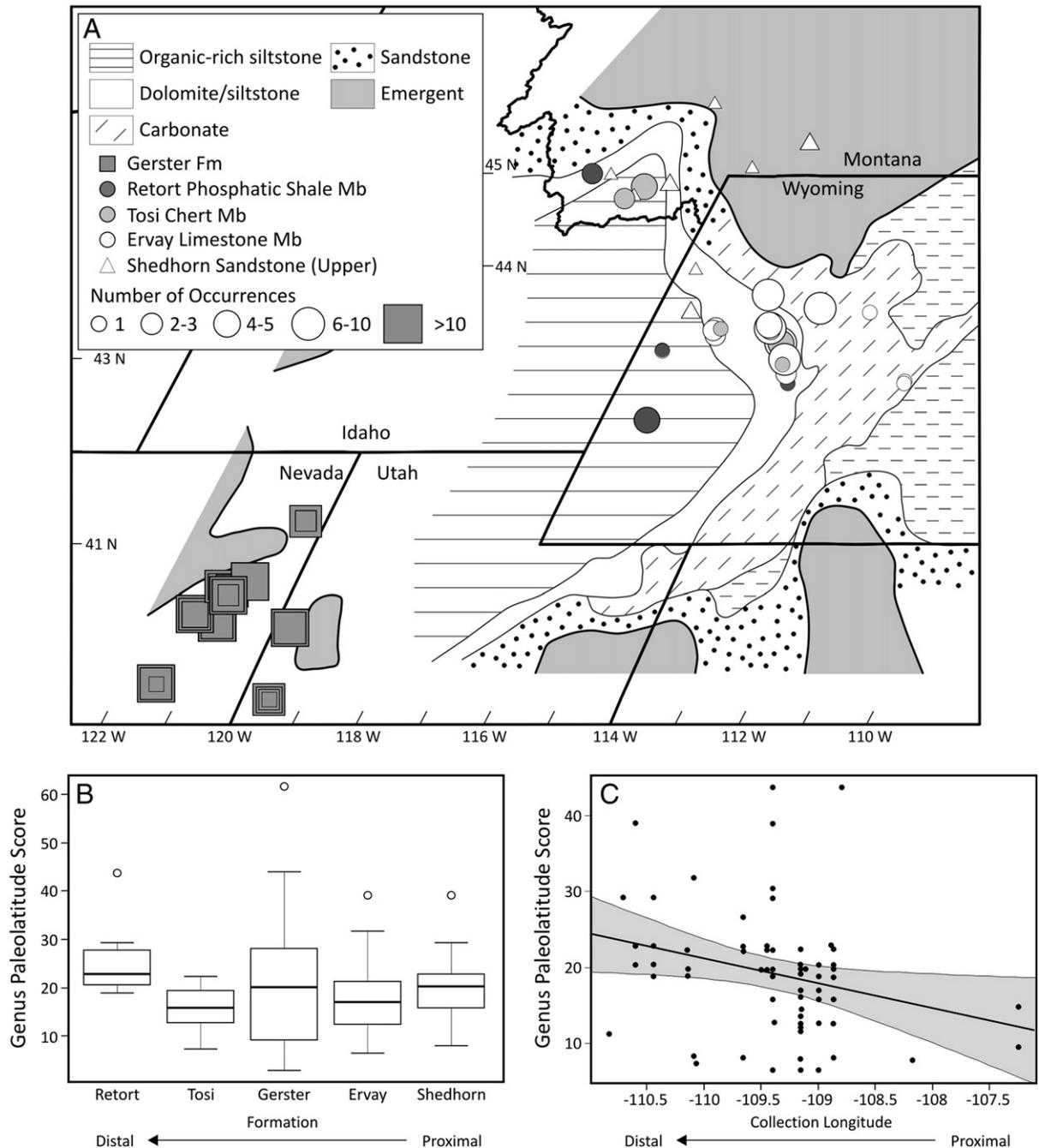


Fig. 8. Paleobathymetric changes in faunal composition in the Capitanian of the Phosphoria basin and northeastern Nevada. **A.** Paleogeographic map (based on a reconstruction for the Roadian from Piper and Link (2002)) showing distribution of facies from proximal siliciclastics in central Wyoming to basinal shale in western Wyoming and Idaho. Symbols indicate location and lithological unit of Capitanian fossil collections in this analysis (squares: Gerster Formation, dark gray circles: Retort Member, light gray circles: Tosi Member, white circles: Ervey Member, triangles: Shedhorn Sandstone). Fossil collections are Capitanian but the paleogeographic map is based on Roadian facies, resulting in occasional discordance between the two. Symbol size indicates the number of occurrences per collection. **B.** Box-and-whisker plot of the paleolatitude score for genera occurring in each lithological unit, arranged from the most proximal (Shedhorn Sandstone) on the right to the most distal (Retort Shale) on the left. Differences among the means are not significant (ANOVA, $p=0.28$). **C.** Genus paleolatitude score plotted against present-day longitude, a proxy for onshore–offshore position on the ramp, for collections from Wyoming. There is a significant inverse relationship ($p=0.03$) between paleolatitude score and collection longitude, indicating that more distal collections, on average, tend to contain a cooler-water fauna.

with cooling in Boreal regions, the result of oceanographic changes following the closure of the connection the Tethys sea in the southern Uralian basin (Reid et al., 2007). Thus, the boundary current may also have been cooler due to cooling in its Boreal source area. However, if water temperature are indicative of air temperatures along the Pangean margin, cooling at higher latitudes coupled with stable temperatures near the equator (e.g., Montañez et al., 2007) implies that an enhanced temperature gradient may have altered regional

wind patterns and driven more rapid flow of the boundary current and/or more intense upwelling.

5. Conclusions

Quantitative paleobiogeographic analysis demonstrates that Early and Middle Permian localities in the Phosphoria basin contained faunas distinct from those in contemporaneous localities in the

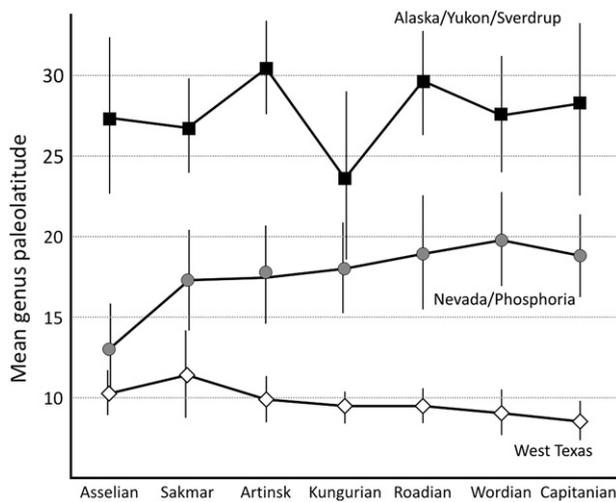


Fig. 9. Temporal changes in the mean paleolatitude of genera occurring in west Texas (open diamonds), northeastern Nevada and the Phosphoria basin (gray circles), and eastern Alaska, western Yukon, and the Sverdrup basin (black squares). Error bars are bootstrap 95% confidence intervals. The significant progressive cooling of the fauna in the Phosphoria basin ($p=0.027$ for difference between Asselian and Capitanian) contrasts with static conditions in west Texas. Temporal trends in Arctic faunas are obscured because the mean paleolatitude proxy is less sensitive and more susceptible to noise at high latitudes.

southwestern United States. Early Guadalupian brachiopod, bryozoan, and bivalve faunas contained a mixture of cool-water and warm-water taxa and had a greater affinity with other northern transitional zone localities situated near the biogeographic boundary between the Paleoequatorial and Boreal realms. Similar biogeographically mixed localities are found in northeastern Asia (Mongolia, North China, and Primorye) but were located at higher paleolatitudes than the Phosphoria basin. This discrepancy between the western and eastern sides of Pangea is consistent with the expected presence of a northerly-flowing warm-water boundary current along the eastern Pangean margin and a cool, southerly-directed eastern boundary current along western Pangea.

The distinct climatic affinities of Guadalupian marine invertebrates in the Phosphoria basin and west Texas was the result of a gradual divergence between the two regions throughout the Permian. The faunal composition in the Phosphoria basin acquired more of a mixed, cool-water aspect whereas Texas localities became more strongly paleoequatorial in character. These changes suggest that regional-scale climate change overprinted the general global trend of postglacial warming from the earliest Permian through the Middle Permian, highlighting the need for proxy reconstructions with detailed spatial resolution, such as those provided by quantitative paleobiogeography. Cooling in western Laurentia was likely influenced to a large extent by similar cooling in Boreal regions and enhanced effects of the cool boundary current. The entire region was decoupled from other regions in Laurentia, such as west Texas, as well as being decoupled from global changes.

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