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Huiting Wu

China University of Geosciences, Peking University

G R. Shi

University of Wollongong, guang@uow.edu.au

Yuanlin Sun

Peking University

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Abstract

Although there have been many studies of biological patterns along latitude, less attention has been paid on how latitude might affect the large-scale spatial patterns of ornament among shelled invertebrate organisms. Based on a newly designed set of four quantitative metrics of shell ornaments and the measurement and quantification of shell ornaments from 2654 Changhsingian (Late Permian) brachiopods (representing 702 species) spanning 80° south to 30° north in paleolatitude, this paper analyzes the relationship between the degree of shell ornament development of Changhsingian brachiopods and paleolatitude. For the first time, we report the presence of statistically significant latitudinal gradient patterns in the development of a multitude of brachiopod shell ornament types for the Permian, generally characterized by the tendency of an increased proportion of brachiopods with more complicated and stronger ornament towards the paleotropics. The gradient pattern is manifested not only in the individual types of ornament (e.g., radial ornament, body spines) but also pronounced when all the studied ornament types are integrated and analyzed together. Two scenarios are offered to account for the latitudinal gradient of Changhsingian brachiopod shell ornaments. First, in consistency with most previous similar studies, the latitudinal gradient of brachiopod shell ornament is explained by G. Vermeij's escalation theory, in that shell ornaments are regarded as defence apparatuses against predation, and that shell ornament of Changhsingian brachiopods is interpreted to have become stronger and more elaborate in lower paleolatitudes as an adaptive response to the progressively increased predation pressure towards the paleotropics. Second, the latitudinal gradient pattern of Changhsingian brachiopod shell ornaments could also be explained by the varied calcification rate in the oceans as a function of the latitudinal temperature gradient. The CaCO₃ solubility is known to increase in colder, high-latitude areas. This means it is more difficult for marine organisms to extract calcium carbonate to generate their shells in higher latitudes, consequently resulting in less developed ornament for shelled marine benthic organisms living in colder water habitats. This second interpretation potentially complements and extends the G. Vermeij's escalation theory in explaining the observed latitudinal gradients of Changhsingian brachiopod shell ornaments, but the theory itself requires both experimental and empirical testing with respect to living shelled marine invertebrates and their production of shell ornament.

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The latitudinal gradient of shell ornament – a case study from Changhsingian (Late Permian)
brachiopods

Huiting Wu¹, G.R. Shi^{2,*}, Yuanlin Sun¹

¹ School of Earth and Space Sciences, Peking University, Beijing 100871, China

² School of Earth, Atmospheric and Life Sciences, University of Wollongong, Northfields
Ave, NSW 2522, Australia (guang@uow.edu.au)

* Corresponding author

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theory, in that shell ornaments are regarded as defence apparatuses against predation, and that shell ornament of Changhsingian brachiopods is interpreted to have become stronger and more elaborate in lower paleolatitudes as an adaptive response to the progressively increased predation pressure towards the paleotropics. Second, the latitudinal gradient pattern of Changhsingian brachiopod shell ornaments could also be explained by the varied calcification rate in the oceans as a function of the latitudinal temperature gradient. The CaCO_3 solubility is known to increase in colder, high-latitude areas. This means it is more difficult for marine organisms to extract calcium carbonate to generate their shells in higher latitudes, consequently resulting in less developed ornament for shelled marine benthic organisms living in colder water habitats. This second interpretation potentially complements and extends the G. Vermeij's escalation theory in explaining the observed latitudinal gradients of Changhsingian brachiopod shell ornaments, but the theory itself requires both experimental and empirical testing with respect to living shelled marine invertebrates and their production of shell ornament.

Keywords: Changhsingian brachiopods; shell ornament; latitudinal gradient; escalation; calcification rate.

1. Introduction

The global latitudinal gradient is known to be a pervasive force in governing and regulating a plethora of biological (including evolutionary) and biogeographical processes and patterns (Schemske et al., 2009). Among these patterns, the global latitudinal gradient of biodiversity is clearly the best known and most extensively studied (Fischer, 1960; Willig et al., 2003). Other parallel but relatively less-studied latitude-related biotic patterns are represented by a

number of long-recognized, albeit some still remaining controversial, biological/biogeographical rules, including: the Bergmann's rule, the tendency of organisms to increase body size with latitude (Bergmann, 1847; Lomolino et al., 2006); Allen's rule, the tendency of vertebrates living in higher latitude and colder regions to grow shorter protruding body parts (e.g., beaks, tails, ears and legs) relative to their body size compared to counterparts living in a warmer climate (Allen, 1877; Lomolino et al., 2006); Jordan's rule, the tendency of marine fish to increase the number of vertebrae with increasing latitude (Jordan, 1892; Lomolino et al., 2006); and the Rapoport's rule, a tendency of species to increase their geographic ranges in higher latitude (Gaston et al., 1998; Veter et al., 2013). In this context, interestingly, relatively few studies have examined how latitude might affect the large-scale spatial patterns of shell ornament among shelled invertebrate organisms despite their prevalence and abundance in both the fossil record and present-day environments. The only possible exception to this observation is the presence of a body of studies concerning the variation of shell ornament in relation to latitude, which regards the degree of shell ornament as a response to predation pressure that increases with the decrease of latitude (e.g., Vermeij, 1977, 1978; Signor and Brett, 1984). In this case, shell ornament has been used as a means to test whether variation in the level of predation would follow a particular latitudinal gradient. Thus far, published evidences from both neontological and paleontological records seem to well support the hypothesis (neontological case studies: Stanley, 1970; Vermeij, 1987; Watson, 2009; paleontological case studies: Leighton, 1999; Dietl and Kelley, 2001), although rare exceptions also exist (Vörös, 2014). Among the paleontological case studies, Brachiopoda has been among the main clades for investigation, probably because of their possession of a diverse array of shell ornaments, coupled with a wide range of paleogeographic, paleoenvironmental and stratigraphic distributions, making them ideal materials for exploring the possible latitude–ornament relationships. However, published information concerning the variation of

brachiopod shell ornament in connection to paleolatitude is very limited and, to our knowledge, only available for the Devonian (Leighton, 1999), the Carboniferous (Dietl and Kelly, 2001), and the Jurassic (Vörös, 2014). Among these three previous studies, however, inconsistent patterns have been reported: for the two Paleozoic studies, both Leighton (1999) and Dietl and Kelly (2001) found that brachiopod ornament gradually increased towards lower paleolatitudes, as would be expected by the latitude–predation hypothesis; for the Jurassic, Vörös (2014) found that the distribution of two main types of ornament showed opposite trends (spinosity was confined to higher paleolatitudes whereas ribbing was somewhat stronger in low latitudes), partly contrary to the observations made for the Paleozoic case studies. To explain this discrepancy between the Paleozoic and Jurassic case studies within the framework of the latitude–predation hypothesis, Vörös (2014) suggested that the Jurassic gradient of the shell-crushing predation might be rather similar to that recorded in the mid-Paleozoic, while the drilling predation might prevail in the higher paleolatitudes in the Jurassic.

In this paper, we provide the first case study of the co-variation between brachiopod shell ornament and latitude for the Permian Period, using an array of newly designed and quantified ornament metrics applied to a comprehensively compiled and biostratigraphically well-resolved global database of Changhsingian (Late Permian) brachiopod species. The specific aims of this paper are twofold. First, we want to test which of the shell–ornament latitudinal relationships documented for the Devonian, Carboniferous and Jurassic holds also for the Permian. Second, given the ornament–latitude relationship revealed in this study, which could be either positive, negative or random (un-correlated), how should it be best explained? The basic hypothesis in the present study is that the relative strength of Permian brachiopod shell ornament was inversely correlated with latitude: that is, brachiopod shell ornament became stronger and more elaborate towards lower latitudes. An acceptance of this hypothesis thus would support (though not necessarily prove) the notion that predation pressure increases with

decrease of latitude. A rejection of the hypothesis, on the other hand, would mean that the commonly perceived inverse ornament strength–latitude relationship needs to be reassessed and other possible mechanisms explored.

To our knowledge, this is the first such study undertaken for the Permian, although Zhang and He (2008) had carried out a study of the temporal patterns of Permian brachiopod ornament changes across the Permian–Triassic boundary based on a regional (South China) database. Changhsingian (last stage of the Permian Period) brachiopods are of considerable global interest because of their close association with the end-Permian mass extinction. For this reason, they have been extensively sampled and systematically described around the world, leading to a wealth of literature on their taxonomy and biostratigraphy, as well as excellent illustrations of a range of morphological characteristics (e.g., Chen et al., 2006; Shen and Shi, 2007; Posenato, 2011; Zhang et al., 2014; He et al., 2014, 2019; Wu et al., 2018a), enabling the characterization and measurement of shell ornament on a large spatial scale. Not surprisingly, in addition to Zhang and He (2008), several other studies have also specifically addressed the global Changhsingian brachiopod fauna as a whole, respectively connected to their global paleobiogeography (Shen et al., 2001), global nearshore–offshore body-size change patterns (Shi et al., 2016), as well as extinction and survival patterns (Chen et al., 2005; Posenato et al., 2009; He et al., 2015; Zhang et al., 2016; Wu et al., 2018b), but none has specifically explored the latitudinal patterns of shell ornament. In this sense, the present study may be regarded as both a complementary and a supplementary contribution to the existing knowledge concerning the global Changhsingian brachiopod fauna.

2. Data and methods

2.1. The global Changhsingian brachiopod database

We compiled a global Changhsingian brachiopod database from 147 references published up to the end of 2016, built on and expanded from an earlier version of the same database used by Shi et al. (2016). The database encompasses a range of basic information, including order name, family name, genus name, species name, collection localities, age and age range, paleolatitude, length and width of shell, as well as shell ornament types (hinge spine, body spine, costa and ruga) and frequency (density), mostly directly extracted from the original references with the exception of paleolatitude. Paleolatitude for each Changhsingian brachiopod locality was obtained either directly from the original literature or, if no such data were available, calculated using the software PointTracker (Scotese, 2004). The final dataset contains 702 brachiopod species and 2654 specimens, extending from 80° south to 30° north in paleolatitude (Fig. 1). All taxonomic classifications were checked and updated following the Treatise on Invertebrate Paleontology Part H Brachiopoda (Williams et al., 2000, 2002, 2006, 2007).

2.2. Quantifying and estimating brachiopod shell ornament strength

Brachiopods as a whole are a very diverse group with a great variety of ornament types (Cooper, 1970; Harper and Moran, 1997), most of which are difficult to quantify. Therefore, not surprisingly, there is yet no single quantitative ornament index developed that can capture the degree of variability of all ornaments in a given brachiopod shell. Presumably for this reason, previous studies of brachiopod ornaments have simply categorized ornament into four categories: (1) weak, ornament absent (i.e., shells smooth) or capillate; (2) costate ornament; (3) strongly costate, rugose, or plicate ornament; and (4) spinose ornament anterior to hingeline (Leighton, 1999; Dietl and Kelly, 2001; Vörös, 2010, 2014), with the implication that the larger the category number the stronger the ornament represented. This classification scheme may be

appropriate for certain selected brachiopod taxa, as it was in the case of Leighton (1999) and also Dietl and Kelly (2001), both of which were focused on planoconvex strophomenates and excluded chonetides; or as in the case of Vörös (2014), which only referred to Jurassic biconvex rhynchonellides and terebratulides. This relatively simple treatment of shell ornament classification is considered inappropriate for the present study because Changhsingian brachiopods are very diverse (>700 species) with a great proliferation of ornaments. Consequently, we use a new approach, carried out in a multitude of consequential steps. First, similar to some previous studies (Leighton, 1999; Zhang and He, 2008), brachiopod ornaments were categorized into four broad groups: hinge spine, body spine (excluding hinge spine), costa (radial ornament), ruga (concentric ornament) (Fig. 2; Table 1). Second, for each of these categories, we then measured the frequency (i.e., density per centimetre) of each of these ornament types: frequency of hinge spine was measured along the hingeline while that for the other three ornament types was measured on the middle-valve of a specimen. For each such measurement, the frequency of an ornament type was obtained, in most cases, from the ventral valve of the holotype of a species, and was taken as the typical ornament (or standard) for all other specimens assigned to the same species. In cases where the frequency of an ornament type could not be obtained from the holotype of a species due to poor preservation, we directly measured the frequency of the ornament type from the actual specimen in the literature. For cases where neither the holotype nor other specimens of a Changhsingian brachiopod species were suitable for measuring ornament frequencies, we used ornament frequency data of the type species of the genus to represent the species concerned.

Next, in order to explore the degree of brachiopod ornament development in relation to paleolatitude, a number of ornament metrics were created. The ideal metric for evaluating the possible latitudinal gradient of shell ornament would be to estimate the proportion of specimens bearing simple ornament within a latitudinal zone with respect to those bearing relatively more

complex ornament, and then to plot this ratio over a gradient of evenly spaced latitudinal bins. If a latitudinal gradient in the variation of ornament strength is apparent, a significant trend should be detectable with an appropriate statistical test (see below). To facilitate this analysis and also considering the range of ornament types concerned in this paper, four different ornament metrics were quantified and calculated (Table 2). First, we devised a single ornament complexity index (OCI), integrating all four ornament types (hinge spine, body spine, costa and ruga) included in Table 1, defined as the percentage of the number of specimens with no ornament or only one type of ornament over the number of specimens with more than one type of ornament (Table 2, Supplementary Data Table 1). In addition to OCI, the degree of shell ribbing (radial ornament) and spinosity was also considered but treated separately to allow further comparison, each with its own index (Table 2). Thus, the radial ornament index, or ROI, refers to the degree of shell ribbing, quantified as the percentage of the number of specimens with radial ornament frequency equal to or less than 10/cm to the number of specimens with radial ornament frequency more than 10/cm (see Supplementary Data Table 2). In a similar manner, the body spine index (BSI) describes the degree of shell spinosity demonstrated by body spines (i.e., excluding hinge spine), and was calculated as a ratio between the number of specimens with body spine frequency equal to or less than 8/cm and the number of specimens with body spine frequency more than 8/cm (see Supplementary Data Table 3). Finally, a composite ornament index, or COI, was also employed as a proxy of the overall degree of ornament on a specimen by summing the values of hinge spine frequency, body spine frequency, radial ornament frequency, and ruga frequency of a specimen. It should be pointed out that in calculating OCI, ROI and BSI the cut-off point between two broad groups of ornament in each case was randomly chosen. This approach is admittedly arbitrary, but is consistent with some other comparable studies (Linse et al., 2006; Powell and Glazier, 2017).

For the gradient analyses of OCI, ROI and BSI, the size of latitudinal bins was set at 20 degrees, following Dietl and Kelly (2001), but for the analysis of COI, because a greater spatial resolution was possible as the data used for this analysis combine frequencies of all ornament types which allowed the inclusion of more collections for the analysis, we conducted an analysis and comparison of COIs at two different levels of spatial scaling: one at 20-degree latitudinal intervals, the other at 10-degree latitudinal intervals.

2.3. Statistical analyses

To test whether the degree of brachiopod shell ornament variation followed a latitudinal gradient during the Changhsingian, we used the two-tailed Cochran–Armitage Z-statistic-based trend test. This is a special test designed for categorical data and has been used for similar studies (Sanvito et al., 2007; Gardner et al., 2016; Mack et al., 2018). Such a test was conducted respectively on the ornament complexity index (OCI), radial ornament index (ROI) and body spine index (BSI) (Table 2, Figs. 3, 4, 5). Since the Cochran-Armitage trend test could not be performed for regions containing less than three latitudinal bins, no such tests were possible for the northern hemisphere where there are only two latitudinal bins with Changhsingian brachiopod occurrences.

When comparing the composite ornament index (COI) between latitudinal bins, which uses frequency data, an analysis of box plot was conducted and pairwise differences between adjacent latitudinal bins were compared with the Mann-Whitney U-test to check for statistical significance. Because this test is not constrained by the number of latitudinal bins in each hemisphere, a comparison of the two latitudinal bins in the northern hemisphere was possible (Fig. 6).

To further investigate the relations between ornament frequency and latitude, correspondence analysis (CA) was adopted and conducted on the data matrix containing the frequency distribution, expressed by number of specimens, of COI categories at two different spatial scales, respectively at 20-degree and 10-degree latitudinal bins (see Supplementary Data Tables 4–5). In this exercise, the COI was divided into four graded categories in an ascending order of ornament complexity: category 1 has COI < 10, category 2 with COI ranging between 10 and 30, category 3 with COI falling between 31 and 50, and category 4 with COI > 50 (Figs 7, 8). For each paleolatitudinal bin, the makeup and relative abundance of all represented COI categories in a latitudinal bin constitutes a profile specific to the latitudinal bin, and these profiles are here depicted as pie charts (Fig. 9). To test for statistically significant differences between profiles (i.e., between paleolatitudinal bins), chi-square distances between each profile and the mean profile (Table 3) as well as the chi-square distances between each pair of profiles (Table 4) were calculated. The mean profile was conceptualized as the centre of axes, where there is no difference between profiles (Greenacre, 2007; Alberti, 2013). The comparison of profiles was used to verify the results derived from CA, which used essentially the same data matrix (see Supplementary Data Table 5), but was conducted at a higher spatial resolution using 10-degree latitudinal bins. This is possible because if two latitudinal bins have similar profiles, they would plot close together in the CA plot. A similar CA was also used by Dietl and Kelly (2001) in a comparable study. To see how closely the latitudinal variation of ornament (expressed by the pie diagrams of profiles) tracks paleolatitude, a linear regression analysis was conducted with the line of best fit and r^2 values obtained and depicted (Fig. 9).

The Cochran-Armitage trend test and correspondence analysis were performed using XLSTAT (www.xlstat.com/en/) while the Box plot, Mann-Whitney U-test and linear regression analysis were performed using PAST (Hammer et al., 2001). For all the statistical comparisons between paleolatitudinal bins with respect to a particular ornament index, a

significant result means that the proportion of specimens bearing a particular type of ornament is dependent on latitude, thus confirming the hypothesis that a latitudinal gradient in ornament existed.

3. Results

For the ornament complexity index (OCI), our analysis shows that there is a significant latitudinal gradient, with the proportions of brachiopod specimens with no or only one type of ornament increasing with paleolatitude in the southern hemisphere (Cochran-Armitage trend test, $p < 0.05$) (Fig. 3) (note that Changhsingian brachiopods in the northern hemisphere fall into only two latitudinal bins, thus insufficient for a Cochran-Armitage trend test, hence no northern hemisphere data can be shown in Fig. 3; same reason for ROI and BSI analyses, see below). In other words, Changhsingian brachiopods living in lower latitudes tended to have a significantly higher proportion of individuals with a greater diversity of shell ornament types. The relationships of brachiopod radial ornament (ROI) and body spine (BSI) with respect to paleolatitude were separately investigated, both of which decreased in frequency as latitude increased, thus demonstrating a significant latitudinal gradient (Fig. 4 shows a significant trend for ROI at $p < 0.05$; Fig. 5 shows a significant trend for BSI at $p < 0.05$). For instance, the high latitudinal area (60° – 80° S paleolatitudinal bin) contains over four times more specimens with sparse radial ornament than those of the paleo-equatorial area (0° – 20° S paleolatitudinal bin) (Fig. 4). Although the proportion of specimens with body spine frequency equal to or less than 8/cm in the 20° – 40° S paleolatitudinal band is higher than that in the 60° – 40° S paleolatitudinal band, there is still an overall significant trend of decreasing proportions of specimens with sparse body spines as latitude decreased in the southern hemisphere (Cochran-Armitage trend test at $p < 0.05$) (Fig. 5).

The COI of specimens were calculated and portrayed in box plots by paleolatitudinal bins (Fig. 6). As for the results from the preceding analysis, there are also significant increases in COI median values from 80°–60°S to 60°–40°S, and from 60°–40°S to 40°–20°S (Mann-Whitney U-test with $p < 0.05$), as well as an increase of COI median values from 40°–20°S to 20°–0°S, the latter matched by a significant increase of COI median values from 40°–20°N to 20°–0°N (Mann-Whitney U-test with $p < 0.05$). The consistent paleolatitudinal trends of COI suggest that the degree of overall brachiopod shell ornament, expressed by integrating the relative frequencies of hinge spine, body spine, radial ribbing and concentric ruga, increased towards lower paleolatitudes, a pattern that is conspicuously displayed in Figure 6.

Correspondence analysis (CA) of the data matrix consisting of COI and 20-degree paleolatitudinal bins (Fig. 7) shows that the distribution of the paleolatitudinal bins is partitioned into three areas, each constrained by a specific range of COI values. In the 80°–60°S and 60°–40°S paleolatitudinal bins, brachiopods had a higher proportion of specimens with COI smaller than 10; by comparison, brachiopods from the 40°–20°S and 40°–20°N areas had a higher proportion of specimens with COI ranging from 10 to 30, and those from 20°–0°S and 0°–20°N areas had a higher proportion of specimens with COI larger than 30. Another notable feature of the CA biplot is the disposition of paleolatitudinal bins and COI values with respect to the first principal axis (F1) of the CA biplot (Fig. 7): COI values decrease as F1 increases in values; data points of 80°–60°S and 60°–40°S are distributed farthest in the positive direction of F1, whereas those of the lower paleolatitudinal bins (20°–0°S and 0°–20°N) are disposed to the most negative end of F1. As such, one inescapable conclusion from this pattern of polarized depiction of the data points is that the COI values are inversely correlated with paleolatitude with respect to F1, which accounts for 60.2% of the total variance of the data; in other words, the proportion of brachiopods with more complex ornament (i.e., higher COI values) decreased with an increase of paleolatitude.

To verify whether or not this observation is dependent on the choice of the paleolatitudinal bin size (i.e., the size of samples for comparison), we conducted a CA on a similar data matrix but with a finer paleolatitudinal gradient, at 10° bins. The result of this analysis is shown in Figure 8: in high paleolatitudinal areas (80°–70°S and 60°–50°S) a higher proportion of brachiopods had COI smaller than 10; in middle latitudinal area (50°–40°S, 30°–20°S and 20°–30°N), a higher proportion of brachiopod had COI at 10–30; in low latitudinal areas (10°–0°S, 0°–10°N and 10°–20°N), a higher proportion of brachiopod had COI larger than 30.

Notably, the patterns revealed in Figure 8 are also corroborated by tests of the chi-square distances between the profile of each 10-degree paleolatitudinal bin and their mean profile (Table 3, Fig. 9), showing a progressive drop in pairwise distance towards the paleo-equator in both hemispheres, with the exception of the 20°–10°S paleolatitudinal bin. This bin possibly is a statistical outlier because it is also shown to be out of place in Figure 8 when compared to the dispositioning of the other 10-degree paleolatitudinal bins. In Table 4, which compares the chi-square distances between all pairs of paleolatitudinal bins, a consistent feature is that the distances between neighbouring pairs of paleolatitudinal bins are generally shorter than when they are farther apart, suggesting that the COI profile of a paleolatitudinal bin is most similar to its nearest bin (see also Fig. 9). As was found in Table 3, one possible outlier here is the 10°–20°N paleolatitudinal bin.

In brief, results of both CA biplots show that brachiopod ornament frequency, as expressed by COI values, decreased as latitude increased (Fig. 7, 8), and this pattern is particularly obvious in Figure 6 where the secular COI decline from the middle paleolatitudinal zone (20°–40°S) through to the high (60°–80°S) paleolatitudinal zone was found statistically significant (Mann-Whitney test, $p < 0.05$) (while the COI change between 0°–20°S and 20°–40°S paleolatitudinal zones is statistically insignificant, albeit still displaying a small decline). Furthermore, the progressive decline in the degree of shell ornament towards higher latitudes

appears to be a rather robust pattern because (1) it seems independent of the spatial scaling used for testing (similar patterns were revealed at two different paleolatitudinal scales), and (2) it is strongly corroborated by the highly linear distribution of the COI profiles when plotted with respect to paleolatitudes and their mutual chi-square distances (Tables 3, 4; Fig. 9)

4. Discussion

Despite using a different methodology in quantifying shell ornament and a different taxonomic and chronostratigraphic dataset, the results of our study support the conclusions reached in two previous studies focused on mid-Paleozoic brachiopods (Leighton, 1999; Dietl and Kelley, 2001), in both of which the degree of brachiopod shell ornament was found to decrease significantly with increasing latitude, a common biotic pattern that has also been noted for many living shelly benthos (Nicol, 1967; Vermeij, 1987; Trussell, 2000; Watson et al., 2012). This consistent pattern suggests that the latitudinal gradient of shell ornament is a pervasive and recurring feature at a global scale, and therefore it must have been driven and maintained by some persistent underlying ecological and/or evolutionary mechanisms. To date, two leading hypotheses have been proposed to account for the development of shell ornament, including predation (Leighton, 1999; Vörös, 2010, 2014) and calcification (solubility of CaCO_3 , Watson et al., 2012).

Predation. Among the published hypotheses, the most widely cited model is predation. In this scenario, the function of shell ornament is thought to serve as a defence system against predation and, therefore, the degree of ornament represents an adaptive response to the level of predation pressure at a particular location (habitat) at a particular time, leading to a dynamic

positive relationship between predation pressure and ornament enhancement, the so-called escalation or “arms race” theory (Vermeij, 1987).

In modern marine ecosystems, numerous studies have shown that the degree of marine predation, mainly manifested by shell-crushing (durophages) and shell-drilling predators, increases towards the equatorial area, leading to the formation of a conspicuous latitudinal gradient of predation (Aronson et al., 2007; Schemske et al., 2009). Similarly, from the fossil record there also exists a large body of literature documenting a strong positive correlation between the degree of ornament of marine shelly benthos and the intensity of predation (e.g., Alexander, 1981, 1986; Harper and Skelton, 1993; Stone, 1998; Leighton, 1999; Dietl and Kelley, 2001; Zuschin et al., 2003; Klompmaker and Kelley, 2015). Most notable examples of these studies come from the Mesozoic–Cenozoic fossil record in support of the theory of the Mesozoic Marine Revolution (Vermeij, 1977). But, as initially suggested by Signor and Brett (1984) and later documented by Leighton (1999), the escalation between predation and shell ornament predated the Mesozoic Marine Revolution and actually began as early as in the Devonian, coinciding with the first major diversification of marine vertebrates during the Age of Fish. A subsequent study, undertaken by Dietl and Kelley (2001), raised two previously under-appreciated features of this escalation. First, it is apparent that the large-scale escalation between predation and ornament in the marine realm continued into the Carboniferous. Second, the strength of the latitudinal gradient of brachiopod ornament varied temporally during the Carboniferous, in that it was found most pronounced in the Tournaisian when the latitudinal temperature gradient was steepest.

Regarding the first feature highlighted in the Dietl and Kelley’s study (2001) and considering the results from the present study, we may conclude that an active escalation between predation and the enhancement of anti-predatory ornament of brachiopods also prevailed for at least part of the Permian, namely the Changhsingian, the last stage of the

Permian just prior to the end-Permian mass extinction. To evaluate the validity of this inference, we may refer to the empirical evidence of predation on Permian brachiopods to see if there indeed existed a significant latitudinal gradient in predation in the marine realm during the Permian. Such evidence may be provided by the relative frequency or intensity of predation of marine shelly invertebrate fossils in relation to paleolatitude. To our knowledge, to date no such global statistical study has been undertaken for the Permian despite a number of large-scale studies on the temporal variation of marine predation through the Phanerozoic (e.g., Signor and Brett, 1984; Alexander, 1986; Kowalewski et al., 1998, 2005; Klompmaker et al., 2019). We attempted to collect the global predation data on Permian brachiopods, bivalves, gastropods and echinoids, mainly referring to drill holes and repair scars in fossil records which are commonly used in predation studies (Harper et al., 2009; Harper, 2016). Unfortunately, too few studies have been focused on such records (see Supplementary Data Table 6), and we were unable to collect sufficient data to permit a statistically robust analysis between marine predation intensity and paleolatitude during the Permian. Nevertheless, there is published evidence suggesting that (1) marine predation was ubiquitous across many environments and latitudes throughout the Permian, albeit relatively rare when compared with Mesozoic–Cenozoic molluscs (Kowalewski et al., 2000, 2005); and that (2) Permian bivalves from west Texas in the southwestern USA, then located in the northern subtropical zone, were drilled more intensely (drilling frequency 7.43%) than Permian bivalves from Brazil and Greece (drilling frequency respectively 0.57% and about 1.5%), both then located in the middle to high latitudes of Gondwana (Grant, 1988; Kowalewski et al., 2000; Hoffmeister et al., 2004). If the latter can be taken as an indication of at least a crude expression of a latitudinal gradient in marine predation for the Permian, the latitudinal gradient pattern of predation is certainly correlated with, and thus may account for, the conspicuous latitudinal gradient of

Changhsingian brachiopod ornament found in the present study, thus confirming the existence of an active predator–prey escalation during at least part of the Permian.

Calcification. Concerning the coincidence between the latitudinal gradient of brachiopod ornament and a contemporaneous steep latitudinal temperature gradient, another important finding revealed by Dietl and Kelley’s (2001) study, an inference can be drawn that temperature may also have some bearing on the degree of shell ornament development. The latitudinal gradient of global temperature variation is a well-known natural phenomenon, generally expressed as a function of declining solar insolation per unit area with increasing latitude (e.g., Fu and Rich, 1999). The mechanism by which the global latitudinal thermal gradient may potentially influence shell ornament formation and variation in relation to latitude is via the thermodynamic relationship between temperature and the solubility of calcium carbonate (CaCO_3) in seawater. Generally, CaCO_3 and CO_2 solubility decreases as temperature increases towards equatorial areas (Watson et al., 2012). Thus, it is perceivable and predictable that the higher CaCO_3 solubility in colder marine environments will increase the energetic cost for calcification (Clarke, 1990, 1993). This makes it more difficult for marine organisms to produce calcium carbonate to generate their shells, including the production of shell ornaments. Although this scenario potentially could explain the observed latitudinal gradient pattern of Permian brachiopod ornament characterized by less developed ornament in higher-latitude brachiopods, the theory itself requires both experimental and empirical testing with respect to living marine invertebrates with calcified shells. We are not yet aware of any published studies as far as the relationship between latitude-related calcification rate and shell ornament development of living marine invertebrates is concerned.

5. Conclusions

(1) A higher proportion of Changhsingian brachiopods living in higher paleolatitude habitats were found possessing smooth or only one type of ornament, compared to those inhabiting lower paleolatitudinal areas;

(2) Higher proportions of Changhsingian brachiopod shells with denser radial ornament (ribbing) and body spines were found in lower paleolatitudinal areas;

(3) The composite ornament index, comprised of the sum of hinge spine frequency, body spine frequency, radial ornament frequency and ruga frequency of Changhsingian brachiopods, was found to decrease with increase of paleolatitude;

(4) The conspicuous latitudinal gradient patterns of Changhsingian brachiopods revealed in this study are comparable with the results of two previous studies focused on mid-Paleozoic (Devonian and Carboniferous, respectively) brachiopods;

(5) The latitudinal gradient patterns of Changhsingian brachiopods can be well explained by Vermeij's escalation theory, in that brachiopod ornaments are regarded as self-defense adaptations against predation, and thus an inversely correlated latitude-ornament gradient, such as the patterns revealed here for the Changhsingian brachiopods, could develop as a response to increased predation pressure towards the tropics;

(6) A second, probably or potentially complementary and supplementary explanation for the conspicuous latitudinal gradient patterns of Changhsingian brachiopods is the varying calcification rate of brachiopod shells in relation to latitude. This interpretation is based on the fact that CaCO_3 and CO_2 solubility increases with increasing latitude in marine environments, making it difficult for marine organisms to produce calcium carbonate to form shells and produce more elaborate shell ornament. This scenario may explain the observed latitudinal gradient pattern of Permian brachiopod ornament characterized by less developed ornament in

higher-latitude brachiopods, but both experimental and empirical testing of this hypothesis is required.

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Appendix A. Supplementary Data Tables 1–6

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641 **Caption**

642 Figure 1. Paleogeographic distribution of Changhsingian brachiopods, paleomap modified
643 from Scotese (2001).

644

645 Figure 2. Ornament combination types and corresponding examples of brachiopods and
646 sketches. 1. *Costatumulus* from He et al. (2014); 2. *Paryphella* from Zhang et al. (2015); 3.
647 *Transennatia* from Williams et al. (2000); 4. *Fusichonetes* from Zhang et al. (2013); 5.
648 *Licharewiella* from Williams et al. (2000); 6. *Spinomarginifera* from Williams et al. (2000); 7.
649 *Huatangia* from Williams et al. (2000); 8. *Quinquenella* from Williams et al. (2000); 9.
650 *Strophalosia* from Williams et al. (2000); 10. *Spiriferella* from Williams et al. (2006); 11.
651 *Crurithyris* from Williams et al. (2006).

652

653 Figure 3. OCI (ornament complexity index) expressed as relative frequencies of occurrences
654 of specimens across paleolatitudinal areas of the southern hemisphere and its changing trend.
655 Note the distinct linear latitudinal gradient tested by the Cochran-Armitage trend statistic. Full
656 explanation of OCI is given in Table 2.

657

658 Figure 4. ROI (radial ornament index) expressed as relative frequencies of occurrences of
659 specimens across paleolatitudinal areas of the southern hemisphere and its changing trend. Note
660 the distinct linear latitudinal gradient tested by the Cochran-Armitage trend statistic. Full
661 explanation of ROI is given in Table 2.

662

663 Figure 5. BSI (body spine index) expressed as relative frequencies of occurrences of specimens
664 across paleolatitudinal areas of the southern hemisphere and its changing trend. Note the
665 distinct linear latitudinal gradient tested by the Cochran-Armitage trend statistic. Full
666 explanation of BSI is given in Table 2.

667

668 Figure 6. Box plot of COI (composite ornament index) changes along paleolatitude in the
669 Changhsingian. Circles represent outliers; upward arrows indicate significant changes (Mann-
670 Whitney U test, $p < 0.05$) between adjacent paleolatitudinal bins.

671

672 Figure 7. Biplot of correspondence analysis (CA) of 20-degree paleolatitudinal bins and COI
673 values (green numbers). See text for more explanation.

674

675 Figure 8. Biplot of correspondence analysis (CA) of 10-degree paleolatitudinal bins and COI
676 values (green numbers). See text for more explanation.

677

678 Figure 9. Linear regression of paleolatitudinal bins (using the mean paleolatitude value in each
679 paleolatitudinal bin as the centroid for each pie diagram) to chi-square distance between each
680 profile and mean profile. The COI profile of each paleolatitudinal bin is shown as a pie chart.

681

682 Table 1. Definitions of four types of Changhsingian ornaments and their measurement methods.

683

684 Table 2. Definitions and mathematical formulae of the ornament metrics used in this paper to
685 quantify and estimate the relative degree of brachiopod ornament strength within a
686 paleolatitudinal bin during the Changhsingian.

687

688 Table 3. Chi-square distances to the origin, showing the dissimilarity between the category
689 profile and the mean profile of ornament composition.

690

691 Table 4. Chi-square distances between category profiles, giving information about the
692 dissimilarity of ornament composition between each category. Bold numbers are distances of
693 every pair of the nearest paleolatitudinal bins, numbers written in italics are outliers.

694

Caption

Figure 1. Paleogeographic distribution of Changhsingian brachiopods, paleomap modified from Scotese (2001).

Ornament combination type	Examples of brachiopod	Sketch of ornament type
Hinge spine+ body spine+ costa+ruga	1 4mm
Hinge spine+ costa+ruga	2 2mm
Body spine+ costa+ruga	3 2mm
Hinge spine+ costa	4 2mm
Body spine+costa	5 2mm
Body spine+ruga	6 5mm
Costa+ruga	7 2mm
Hinge spine	8 2mm
Body spine	9 5mm
Costa	10 4mm
smooth shell	11 2mm

7

8 Figure 2. Ornament combination types and corresponding examples of brachiopods and
9 sketches. 1. *Costatumulus* from He et al. (2014); 2. *Paryphella* from Zhang et al. (2015); 3.
10 *Transennatia* from Williams et al. (2000); 4. *Fusichonetes* from Zhang et al. (2013); 5.
11 *Licharewiella* from Williams et al. (2000); 6. *Spinomarginifera* from Williams et al. (2000); 7.
12 *Huatangia* from Williams et al. (2000); 8. *Quinquenella* from Williams et al. (2000); 9.
13 *Strophalosia* from Williams et al. (2000); 10. *Spiriferella* from Williams et al. (2006); 11.
14 *Crurithyris* from Williams et al. (2006).

16

17 Figure 3. OCI (ornament complexity index) expressed as relative frequencies of occurrences
 18 of specimens across paleolatitudinal areas of the southern hemisphere and its changing trend.
 19 Note the distinct linear latitudinal gradient trend tested by the Cochran-Armitage trend statistic.
 20 Full explanation of OCI is given in Table 2. (Note that Changhsingian brachiopods in northern
 21 hemisphere fell into only two latitudinal bins, insufficient for a Cochran-Armitage trend test,
 22 hence no northern hemisphere data could be shown here; same reason for ROI and BSI analyses
 23 in Figs. 4, 5)

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Figure 4. ROI (radial ornament index) expressed as relative frequencies of occurrences of specimens across paleolatitudinal areas of the southern hemisphere and its changing trend. Note the distinct linear latitudinal gradient trend tested by the Cochran-Armitage trend statistic. Full explanation of ROI is given in Table 2.

Figure 5. BSI (body spine index) expressed as relative frequencies of occurrences of specimens across paleolatitudinal areas of the southern hemisphere and its changing trend. Note the distinct linear latitudinal gradient trend tested by the Cochran-Armitage trend statistic. Full explanation of ROI is given in Table 2.

Figure 6. Box plot of COI (composite ornament index) changes along paleolatitudes in the Changhsingian. Circles represent outliers; upward arrows indicate significant changes (Mann-Whitney U test, $p < 0.05$) between adjacent paleolatitudinal bins.

Figure 7. Biplot of correspondence analysis (CA) of 20-degree paleolatitudinal bins and COI values (light green numbers). See text for more explanation.

Figure 8. Biplot of correspondence analysis (CA) of 10-degree paleolatitudinal bins and COI values (light green numbers). See text for more explanation.

Figure 9. Linear regression of paleolatitudinal bins (using the mean paleolatitude value in each paleolatitudinal bin as the centroid for each pie diagram) to Chi-square distance between each profile and mean profile. The COI profile of each paleolatitudinal bin is shown as a pie chart.

Figure 10. Histogram of proportion of Productida and record from muddy substrate in different latitude areas.

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Four types of ornament	Definition	Frequency measurement
Hinge spines	Spines located along the hingeline	Number of hinge spines in 1 cm
Body spines	Macro spines dispersed on the external surface of the shell, but excluding hingeline	Number of hinge spines in 1 cm
Costa	Radial ornamentation distributed on external shell surface	Number of costae across 1 cm
Ruga	Concentric ornamentation on shell external surface	Number of rugae across 1 cm

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Table 1. Definitions of four types of Changhsingian ornaments and their measurement methods.

Name of ornament metric	Abbreviation	Definition	Mathematical formula
Ornament complexity index	OCI	Percent of number of specimens with no ornament or only one type of ornament (N₁) to number of specimens with more than one type of ornament (N₂)	$OCI = N_1/N_2 * 100\%$
Radial ornament index	ROI	Percent of number of specimens with radial ornament frequency equal to or less than 10/cm (N₃) to the number of specimens with radial ornament frequency more than 10/cm (N₄)	$ROI = N_3/N_4 * 100\%$
Body spine index	BSI	Percent of number of specimens with body spine frequency equal to or less than 8/cm (N₅) to number of specimens with body spine frequency more than 8/cm (N₆)	$BSI = N_5/N_6 * 100\%$
Composite ornament index	COI	Sum of hinge spine frequency (F₁), body spine frequency (F₂), radial ornament frequency (F₃) and ruga frequency (F₄)	$COI = F_1 + F_2 + F_3 + F_4$

96 Table 2. Definitions and mathematical formulae of the ornament metrics used in this paper to quantify and estimate the relative degree of
97 brachiopod ornament strength within a paleolatitudinal bin during the Changhsingian.

	Distance between profile of each latitudinal bin and mean profile
80°–70°S	1.05
60°–50°S	0.6
50°–40°S	0.56
30°–20°S	0.31
20°–10°S	0.52
10°–0°S	0.23
0°–10°N	0.09
10°–20°N	0.6
20°–30°N	0.62

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101 Table 3. Chi-square distances to the origin, showing the dissimilarity between the category
 102 profile and the mean profile of ornament composition.

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	80°–70°S	60°–50°S	50°–40°S	30°–20°S	20°–10°S	10°–0°S	0°–10°N	10°–20°N	20°–30°N
80°–70°S	0	0.462	0.979	1.169	0.61	1.271	1.087	1.396	1.398
60°–50°S	0.462	0	0.581	0.712	0.195	0.824	0.648	1.033	0.96
50°–40°S	0.979	0.581	0	0.366	0.419	0.714	0.645	1.153	0.448
30°–20°S	1.169	0.712	0.366	0	0.568	0.378	0.383	0.865	0.311
20°–10°S	0.61	<i>0.195</i>	0.419	0.568	0	0.74	0.579	1.033	0.804
10°–0°S	1.271	0.824	0.714	0.378	0.74	0	0.189	0.502	0.622
0°–10°N	1.087	0.648	0.645	0.383	0.579	0.189	0	0.516	0.68
10°–20°N	1.396	1.033	1.153	0.865	1.033	0.502	0.516	0	1.117
20°–30°N	1.398	0.96	0.448	0.311	0.804	0.622	0.68	1.117	0

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110 Table 4. Chi-square distances between category profiles, giving information about the dissimilarity of ornament composition between each

111 category. Bold numbers are distances of every pair of the nearest paleolatitudinal bins, numbers written in italics are outliers.

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113 **Supplementary data:**

114 Data for analyzing OCI changes

Paleolatitude bins	Number of specimens with no or only one type of ornament	Number of specimens with more than one type of ornament
80°–60°S	25	1
60°–40°S	301	87
40°–20°S	39	22
20°–0°S	582	409
0°–20°N	728	398
20°–40°N	18	30

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116 Data for analyzing ROI changes

Paleolatitude bins	Number of specimens with radial ornament frequency equal to or less than 10/cm	Number of specimen with radial ornament frequency more than 10/cm
80°–60°S	21	1
60°–40°S	147	81
40°–20°S	15	27
20°–0°S	145	500
0°–20°N	285	539
20°–40°N	22	23

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119 Data for analyzing BSI changes

Paleolatitude bins	Number of specimens with body spine frequency equal to or less than 8/cm	Number of specimen with body spine frequency more than 8/cm
80°–60°S	2	0
60°–40°S	76	55
40°–20°S	15	8
20°–0°S	82	117
0°–20°N	40	51
20°–40°N	16	11

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123 Data for CA of 20-degree paleolatitudinal bins

Paleolatitude bins	Category 1: specimen number of brachiopod with COI less than 10	Category 2: specimen number of brachiopod with COI ranging between 10 and 30	Category 3: specimen number of brachiopod with COI ranging between 31 and 50	Category 4: specimen number of brachiopod with COI more than 50
80°–60°S	25	1	0	0
60°–40°S	254	90	40	4
40°–20°S	25	24	10	2
20°–0°S	374	291	296	30
0°–20°N	545	187	351	43
20°–40°N	17	26	9	0

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125 Data for CA of 10-degree paleolatitudinal bins

Paleolatitude bins	Category 1: specimen number of brachiopod with COI less than 10	Category 2: specimen number of brachiopod with COI ranging between 10 and 30	Category 3: specimen number of brachiopod with COI ranging between 31 and 50	Category 4: specimen number of brachiopod with COI more than 50
80°–70°S	25	1	0	0
60°–50°S	157	35	20	2
50°–40°S	92	71	7	2
30°–20°S	24	24	11	2
20°–10°S	98	34	10	4
10°–0°S	279	242	276	41
0°–10°N	436	243	297	47
10°–20°N	33	10	49	5
20°–30°N	16	27	7	1

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Species name	Geographic area	Age	Palaeo-latitude	Data source	Numbers of holes	hole size (mm)	References
Athyris pectinifera (Spiriferida)	Kirillow, Novgorod region, Russia	Permian	~ 40	Yakovlev, 1926	1	?	Kowalewski et al., 2000
Athyris pectinifera (Spiriferida)	Kirillow, Novgorod region, Russia	Permian	~ 40	Yakovlev, 1926	1	?	Kowalewski et al., 2000
Camarophoria superstes (Rhynchonellida)	Kirillow, Novgorod region, Russia	Permian	~ 40	Yakovlev, 1926	1	?	Kowalewski et al., 2000
Camarophoria superstes (Rhynchonellida)	Kirillow, Novgorod region, Russia	Permian	~ 40	Yakovlev, 1926	1	?	Kowalewski et al., 2000
Camarophoria superstes (Rhynchonellida)	Kirillow, Novgorod region, Russia	Permian	~ 40	Yakovlev, 1926	1	?	Kowalewski et al., 2000
Strophalosia horrescens (Strophomenida)	Kirillow, Novgorod region, Russia	Permian	~ 40	Yakovlev, 1926	-	?	Kowalewski et al., 2000
Productus hemisphaerium (Strophomenida)	Kirillow, Novgorod region, Russia	Permian	~ 40	Yakovlev, 1926	-	?	Kowalewski et al., 2000
Athyris pectinifera (Spiriferida)	Sok River, Russia	Permian	~ 40	Hecker, 1965	1	1.2	Kowalewski et al., 2000

Derbyoides nebrascensis (Strophomenida)	West Texas	Permian	~ 10	Cooper & Grant, 1974	1?	1.4	Kowalewski et al., 2000
Paucispinifera (Spiriferida)	West Texas	Permian	~ 10	Cooper & Grant, 1975	1?	2.8	Kowalewski et al., 2000
Cooperina subcuneata (Strophomenida)	West Texas	Permian	~ 10	Cooper & Grant, 1975	1?	0.3	Kowalewski et al., 2000
Penicularis subcostata (Strophomenida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1?	?	Kowalewski et al., 2000
Craspedona newelli (Strophomenida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1?	?	Kowalewski et al., 2000
Echinauris lateralis (Strophomenida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	2.1	Kowalewski et al., 2000
Rhamnaria vinnula (Strophomenida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	1.2	Kowalewski et al., 2000
Nudauris enigmatica (Strophomenida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1?	?	Kowalewski et al., 2000
Rugatia paraindica (Strophomenida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	2.8	Kowalewski et al., 2000

Rugatia paraindica (Strophomenida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	2.6	Kowalewski et al., 2000
Xestosia schucherti (Strophomenida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	1.8	Kowalewski et al., 2000
Peniculauris subcostata (Strophomenida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1?	?	Kowalewski et al., 2000
Peniculauris costata (Strophomenida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	2.6	Kowalewski et al., 2000
Anemonaria sublaevis (Strophomenida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	1.4	Kowalewski et al., 2000
Paucispinifera sulcata (Strophomenida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	2.2	Kowalewski et al., 2000
Siphonosisa alleni (Strophomenida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1?	?	Kowalewski et al., 2000
Institella leonardensis (Strophomenida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	1.6	Kowalewski et al., 2000
Dyoros (Dyoros) intrepidus (Strophomenida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1?	?	Kowalewski et al., 2000

Rugaria hessensis (Strophomenida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1?	?	Kowalewski et al., 2000
Amphipella arcara (Rhynchonellida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1?	0.75	Kowalewski et al., 2000
Holosia ovalis (Rhynchonellida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	1.8	Kowalewski et al., 2000
Tautosia fastigiata (Rhynchonellida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	1.4	Kowalewski et al., 2000
Petasmatherus pumilus (Rhynchonellida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	1.8	Kowalewski et al., 2000
Stenoscisma exutum (Rhynchonellida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	0.8	Kowalewski et al., 2000
Stenoscisma exutum (Rhynchonellida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	0.8	Kowalewski et al., 2000
Stenoscisma exutum (Rhynchonellida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	1.6	Kowalewski et al., 2000
Stenoscisma exutum (Rhynchonellida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	1.2	Kowalewski et al., 2000

Stenoscisma fabarium (Rhynchonellida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	1.8	Kowalewski et al., 2000
Stenoscisma fabarium (Rhynchonellida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	3	Kowalewski et al., 2000
Stenoscisma oblisum (Rhynchonellida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1?	1.4	Kowalewski et al., 2000
Stenoscisma triquetrum (Rhynchonellida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1?	1	Kowalewski et al., 2000
Torynechus caelatus (Rhynchonellida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1?	2.2	Kowalewski et al., 2000
Cartorhium chelomatum (Spiriferida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1?	5.1	Kowalewski et al., 2000
Eliva shumardi (Spiriferida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1?	1.3	Kowalewski et al., 2000
Neophricadothyris cordata (Spiriferida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1?	1.7	Kowalewski et al., 2000
Rallacosta actina (Spiriferida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	1.6	Kowalewski et al., 2000

Rallacosta xystica (Spiriferida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	2.8	Kowalewski et al., 2000
Rallacosta laminata (Spiriferida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	1.4	Kowalewski et al., 2000
Composita enormis (Spiriferida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1?	1.8	Kowalewski et al., 2000
Composita pilula (Spiriferida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	1.2	Kowalewski et al., 2000
Composita mexicana (Spiriferida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1	0.4	Kowalewski et al., 2000
Composita parasulcata (Spiriferida)	West Texas	Permian	~ 10	Cooper & Grant, 1976a	1?	1.6	Kowalewski et al., 2000
Parenteletes cooperi (Rhipidomellida)	West Texas	Permian	~ 10	Cooper & Grant, 1976b	1?	?	Kowalewski et al., 2000
Rhynchopora hebetata (Uncertain)	West Texas	Permian	~ 10	Cooper & Grant, 1976b	1?	1.1	Kowalewski et al., 2000
Metrioilepis scrupea (Spiriferinida)	West Texas	Permian	~ 10	Cooper & Grant, 1976b	1	1.6	Kowalewski et al., 2000

Hustedia trita trita (Spiriferinida)	West Texas	Permian	~ 10	Cooper & Grant, 1976b	1?	1.1	Kowalewski et al., 2000
Thedusia bucrenata (Spiriferinida)	West Texas	Permian	~ 10	Cooper & Grant, 1976b	1	1.2	Kowalewski et al., 2000
Dielasma sulcatum (Terebratulida)	West Texas	Permian	~ 10	Cooper & Grant, 1976b	1?	0.6	Kowalewski et al., 2000
Cryptacanthia sinuata (Terebratulida)	West Texas	Permian	~ 10	Cooper & Grant, 1976b	1?	0.6	Kowalewski et al., 2000
Disphenia myiodes (Terebratulida)	Hydra Island, Greece	Baisalia n	~ 35	Grant, 1988	1	1	Kowalewski et al., 2000
Disphenia myiodes (Terebratulida)	Hydra Island, Greece	Baisalia n	~ 35	Grant, 1988	1	0.6	Kowalewski et al., 2000
Disphenia myiodes (Terebratulida)	Hydra Island, Greece	Baisalia n	~ 35	Grant, 1988	1	0.6	Kowalewski et al., 2000
Disphenia myiodes (Terebratulida)	Hydra Island, Greece	Baisalia n	~ 35	Grant, 1988	1	0.4	Kowalewski et al., 2000
Disphenia myiodes (Terebratulida)	Hydra Island, Greece	Baisalia n	~ 35	Grant, 1988	1	0.4	Kowalewski et al., 2000

Martinia	Cathedral Mtn. Fm., west Texas	Permian	~ 10	Kowalewski et al 2005	10	1.9	Kowalewski et al., 2005
Composita	Cathedral Mtn. Fm., west Texas	Permian	~ 10	Kowalewski et al 2005	7	2	Kowalewski et al., 2005
Composita	Road Canyon Fm., west Texas	Permian	~ 10	Kowalewski et al 2005	5	1.7	Kowalewski et al., 2005
Pinzonella illusa	Brazil	Permian	~ -60	Kowalewski et al 2000	1	3.1	Kowalewski et al 2000
Pinzonella illusa	Brazil	Permian	~ -60	Kowalewski et al 2000	1	0.6	Kowalewski et al 2000
Pinzonella illusa	Brazil	Permian	~ -60	Kowalewski et al 2000	1	0.5	Kowalewski et al 2000
Pinzonella illusa	Brazil	Permian	~ -60	Kowalewski et al 2000	1	0.6	Kowalewski et al 2000
Pinzonella illusa	Brazil	Permian	~ -60	Kowalewski et al 2000	1	0.5	Kowalewski et al 2000
Pinzonella illusa	Brazil	Permian	~ -60	Kowalewski et al 2000	1	0.5	Kowalewski et al 2000

Pinzonella illusa	Brazil	Permian	~ -60	Kowalewski et al 2000	1	0.9	Kowalewski et al 2000
Pinzonella illusa	Brazil	Permian	~ -60	Kowalewski et al 2000	1	1.8	Kowalewski et al 2000
Pinzonella illusa	Brazil	Permian	~ -60	Kowalewski et al 2000	1	0.4	Kowalewski et al 2000
Plesiocyprinella carinata	Brazil	Permian	~ -60	Kowalewski et al 2000	1	2.4	Kowalewski et al 2000
Plesiocyprinella carinata	Brazil	Permian	~ -60	Kowalewski et al 2000	1	5.5	Kowalewski et al 2000
Plesiocyprinella carinata	Brazil	Permian	~ -60	Kowalewski et al 2000	1	3	Kowalewski et al 2000
Plesiocyprinella carinata	Brazil	Permian	~ -60	Kowalewski et al 2000	1	5.8	Kowalewski et al 2000
Cowperesia anceps	Brazil	Permian	~ -60	Kowalewski et al 2000	1	1.1	Kowalewski et al 2000
Cowperesia anceps	Brazil	Permian	~ -60	Kowalewski et al 2000	1	0.8	Kowalewski et al 2000

Casterella gratiosa	Brazil	Permian	~ -60	Kowalewski et al 2000	1	4.1	Kowalewski et al 2000
Pinegathyrus?	southeastern Alaska	Permian	~ 60	Rohr et al., 2016	1	2.5	Rohr et al., 2016
Spiriferella	southeastern Alaska	Permian	~ 60	Rohr et al., 2016	1	2.5	Rohr et al., 2016
Conclusive result							
Taxa	Geographic area	Age	Frequency of drilling		Reference		
brachiopods	West Texas	Permian	1.07%		Hoffmeister, 2002		
mollusks	West Texas	Permian	7.43%		Hoffmeister, 2003		
mollusks	Brazil	Permian	0.57%		Kowalewski et al 2000		
Minysphenia conopia	Greece	Permian	<1.5%		Grant, 1988		