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SANTA CRUZ

THE ROLE OF SUBSTRATE PREFERENCE IN MESOZOIC BRACHIOPOD DECLINE

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Table of Contents

Marko Manojlovic

The Role of Substrate Preference in Mesozoic Brachiopod Decline

Abstract

Brachiopods dominated the seafloor from the Ordovician to the Permian as one of the primary members of the Paleozoic fauna. Despite the devastating effects of the Permian-Triassic extinction, the group mounted a successful recovery during the Triassic and Jurassic, which was followed by their final decline. One proposed cause of this decline is the large increase in bioturbation associated with the Mesozoic Marine Revolution, leading to brachiopods shifting to harder substrates. This hypothesis was explored using occurrence and abundance data downloaded from the Paleobiology Database, with carbonate lithologies serving as a proxy for hard substrates and siliciclastics as a proxy for soft substrates. Brachiopods were more common on carbonate substrates in the Mesozoic which suggests a shift to harder substrates due to rapidly increasing bioturbation during the era. The resulting restriction to harder substrates is a contributor to the Mesozoic decline of brachiopods. Though increasing bioturbation has been previously proposed as a cause of brachiopod decline, this study provides additional quantitative support for this hypothesis.

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Introduction

The brachiopod-bivalve transition

Articulate brachiopods were the primary constituents of the Paleozoic fauna and were a dominant member of communities completely unlike those found in the modern ocean. Instead of the primarily-infaunal bivalves, motile gastropods and crustaceans that dominate today's seafloor, Paleozoic communities featured sessile suspension-feeding brachiopods, crinoids, and bryozoans. The transition from the brachiopod-dominated Paleozoic Fauna to the bivalve-dominated Modern Fauna shaped life in the oceans as we know it (Sepkoski, 1985), and massively increased the available energy within marine food webs, due to the much larger metabolic activity of bivalves (Payne, 2014).

Though the Paleozoic Fauna experienced a disastrous decline at the Permian-Triassic boundary [Gould and Calloway, 1980] (Figure 1), articulate brachiopods recovered during a Triassic "golden age" (Figure 2), culminating in a final peak in their diversity and relative abundance during the Jurassic (Dulai, 2003; Clapham and Bottjer, 2007; Greene et al., 2011) (Figure 3). Brachiopods then declined from the mid-Jurassic to approximately the mid-Cretaceous, a decline that remains poorly understood (Figure 2). The numerous proposed causes of brachiopod decline include predation (e. g., sea stars, Donovan and Gale, 1990), direct competition with bivalves (Steele-Petrovic, 1979; Thayer, 1985; Liow et al., 2015) as well as increasing bioturbation (Thayer, 1979) and grazing pressure (Vermeij, 1977).

The transition likely had multiple causes but the relative contributions of these prospective causes to brachiopod decline remains poorly tested. Predation appears to be a compelling cause of brachiopod decline, considering that their decline coincides with the mid-Mesozoic Marine Revolution (Vermeij, 1977). Brachiopod immobility and their limited chemical defenses make them an attractive choice for predators (Donovan and Gale, 1990, but see Vermeij, 1990), but the importance of predation is unclear due to limited direct evidence of predation on post-Paleozoic brachiopods (Harper, 2003) and predator preference for more calorie-dense mollusks (Tyler et al., 2014) as well as the chemical defenses of exposed structures such as the lophophore (McClintock et al., 1993).

Direct competition with bivalves is another proposed cause of brachiopod decline. Bivalves are thought to have displaced brachiopods due to their superior competitive ability (including higher metabolism, reproduction rates and adaptability), particularly in the wake of extinctions (Steele-Petrovic, 1979) (Figure 4) and high bivalve extinction rates are correlated with increases in brachiopod origination (Liow et al., 2015). Modern bivalves (specifically mussels) directly compete for space with brachiopods in cage experiments (Thayer, 1985). Direct competition for food resources appears to be ruled out by metabolic data with bivalve energy consumption massively increasing while brachiopod energy use decreased, with bivalves tapping food resources unavailable to brachiopods by either taking advantage of an increase in total available food or displacing other clades (Payne et al., 2014).

Another proposed cause for brachiopod decline is increasing bioturbation by deposit feeding organisms, characterized as "biological bulldozers" by Thayer (1979), with a pronounced and rapid increase in bioturbation depth to over 5 cm, compared to a gradual increase from 1 to 2 cm during the entire Paleozoic, with feeding depth reaching 6.5 cm by the end of the Cretaceous (Thayer, 1983; Sepkoski et al., 1993) (Figure 4). This led to decreasing substrate consistency, a potential contributor to brachiopod decline due to their dependence on firm substrates. Articulate brachiopods are sessile benthic organisms and permanently attach to the substrate using their pedicle. They are not able to reattach if dislodged (Vermeij, 1977) or recover from burial in soft sediment.

Though some extant brachiopods can occupy soft, muddy sediments (Richardson, 1981; Stewart, 1981), most living communities depend on hard calcareous substrates and low to moderate sedimentation rates (Aberhan 1994; Lee, 2008). One important reason for their substrate dependence is the ability of the brachiopod pedicle to dissolve carbonate through (presumed) chemical boring during attachment, a process observed in extant brachiopods (Bromley and Surlyk, 1973). Carbonates are known to form thin (10-30cm) hard crusts (in the absence of significant bioturbation) due to early diagenetic cements (Purser, 1978) offering both favorable attachment sites and cryptic refuges from grazing organisms such as teleost fish and echinoids (Vermeij, 1977). Carbonates are more likely to form these crusts with lower bioturbation rates. A direct example of this dependence is the far-reaching extinction of brachiopods following the end-Danian disappearance of the chalk sea covering Northern Europe and Asia that had existed since the Cenomanian (Lee, 2008). Brachiopod dependence on stable substrates has previously been identified in the Lias (Early Jurassic) of the Provence region of France with brachiopods “few or absent when sediments indicate confined silty biotype, turbulent bottom conditions, emersion marks or fast marly sedimentation” (Almeras, 1983), a pattern also identified in Jurassic strata in Central Asia (Prosorovskaya, 1995). The correspondence between substrate and brachiopods was so close that Prosorovskaya suggested they would be useful for local sedimentary environment interpretation. Modern community evidence includes high-abundance (outnumbering local bivalves and gastropods combined) communities directly associated with carbonate-rich substrates of the Brazilian Bight (Kowalewski et al., 2002) as well as various calcareous substrates of New Zealand (Lee, 1990). Living communities also occur on rocky non-carbonate sediments in the Bay of Fundy (Noble et al., 1976), Gulf of Maine (Wittman and Cooper, 1983), off Antarctica (Foster, 1974) and in fjord environments in British Columbia (Tunnicliffe and Wilson, 1988) and Chile (Forsterra et al., 2008). Brachiopods are a “relict group dominated by micromorphic species restricted to shallow, cryptic, hard-bottom environments of tropical, subtropical, and temperate shelves” and “with only some medium and large-sized species living on the open shelf in cool temperate and [polar regions]” (Evangelisti et al., 2012). Brachiopods are largely limited to such environments, which offer hard, often cryptic, attachment sites, by the burrowing and grazing activity of other organisms (Thayer, 1979) and even accidental ingestion or dislodging by predators feeding on other organisms (Witman and Cooper, 1983).

Due to this dependence on firm substrates, it is likely that brachiopods were negatively affected by the diversification of infaunal bivalves (Steele-Petrovic, 1979; Miller, 1990) and the post-Triassic increase in bioturbation (Thayer, 1983; Sepkoski et al., 1993) (Figure 4) both of which likely disrupted the firm seafloors that favored brachiopods. In order to test the hypothesis that brachiopods declined in response to changing substrate, I used literature data compiled in the Paleobiology Database (PBDB) to quantify brachiopod occurrence and abundance in carbonate and siliciclastic lithologies, with carbonate substrates treated as a proxy for hard bottoms and siliciclastic substrates treated as a proxy for soft substrates. The association between brachiopod and bivalve latitudinal distribution and presence on carbonates was also explored.

Methods

Substrate preference and occurrence

As part of the data collection for this study, over 6300 brachiopod and bivalve occurrences from 131 references were entered into the Paleobiology Database (PBDB), concentrating on regions of the world outside Western Europe, which was already well-represented in the data. In order to explore the substrate preference of brachiopods and bivalves, all brachiopod and bivalve occurrences were downloaded from the PBDB. Occurrences not resolved to the stage level were discarded, resulting in a dataset of 74,000 bivalve and 81,000 brachiopod occurrences. The lithology of occurrences was simplified as either carbonate or clastic (Table 1). Secondary lithologies and lithology adjectives (calcareous, muddy, etc.…) were ignored; only the primary lithology field was used to classify occurrences. Mixed lithologies (marl, "mixed carbonate-siliciclastic") were left out of the analysis, due to marl's status as an ambiguous term (Boggs, 2006) and the relatively small number of brachiopods and bivalves in marls, only 6% of all bivalves and 3% of all brachiopods. Carbonate occurrences were coded as 1 while siliciclastic occurrences were coded as 0, then the mean lithology of each group was calculated for each stage, producing a substrate preference trend (Figure 5a-5b) with a Wilson interval used to add 95% confidence interval lines to the proportion of brachiopods and bivalves in carbonates (Newcombe, 1998).

In order to compare brachiopods with similarly sessile, epifaunal bivalves, non-pteriomorph infaunal bivalves were excluded from the analysis by using the PBDB data service to request the Pteriomorphia subclass instead of the order Bivalvia (Figure 6a-6b).

Latitude trend

Due to the association between latitude and carbonate deposition, with carbonates primarily accumulating on tropical shelves (Walker, 2002), the latitudinal trend in the two groups was examined by classifying all occurrences with a paleolatitude of less than 30 degrees as tropical, and coding them as 1, while all non-tropical occurrences were coded as 0 (Hopkins, 2014). The mean tropicality of both groups was then plotted versus their mean carbonate preference (Figure 7a-7b). A linear regression of the tropicality and carbonate preference was performed to test whether carbonate occurrences may instead be explained by tropical distribution.

Substrate preference and abundance

Unlike global occurrence data, abundance data from single paleocommunity samples allows for substrate preference to be explored even during intervals when deposition in well-sampled areas such as Western Europe was dominated by carbonates. In order to explore the relationship between the relative abundance of brachiopods and substrate, all brachiopod, bivalve and gastropod occurrences for the Early Permian to the Late Cretaceous were downloaded from the Paleobiology Database. These occurrences were then matched to collections that had been previously filtered by manual examination as suitable for paleoecological analysis. Suitable collections were defined as those containing at least 30 total specimens of brachiopods, bivalves and gastropods. The only abundance units used in the analysis were individuals, specimens and fragments, excluding other abundance units such as elements, rank, grid-count or category.

Collections were excluded if species from either of the three groups (bivalves, brachiopods or gastropods) appeared in the taxonomic list but did not have associated count data. Collections tagged to indicate that “major groups of macrofossils were present, but not included in the faunal list”, were discarded. This indicator is used to signify that species from other groups were not counted, though present, as for example in a brachiopod taxonomy paper that disregarded any co-occurring bivalves or gastropods.

Due to potential silicification bias, particularly for Paleozoic data (Allison and Bottjer, 2010), PBDB collections that list silica as the replacement mineral in the preservation info were discarded from the analysis. Since many collections don't include this information, silicified collections were also filtered manually while determining whether collections were suitable for paleoecological analysis. They were generally evident based on factors such as the presence of very large numbers (100s to 1000s of specimens) of gastropods or infaunal bivalves in the collection, which are otherwise rarely preserved due to aragonite dissolution (Allison and Bottjer, 2010).

The lithology of collections was simplified identically to the occurrence analysis, with carbonate collections coded as 1 and siliciclastic collections as 0. The total number and relative percentage of brachiopods, bivalves and gastropods was calculated for each collection and collections were binned by epoch from the Early Permian to the Late Cretaceous. The relative brachiopod percentage in all siliciclastic and carbonate collections was plotted as points alongside lines showing the mean percentage of brachiopods in carbonates and siliciclastics for each epoch (Figure 8).

Lithological Adjectives and Lithologies

In addition to primary lithological information for each collection, the PBDB also sometimes includes extended lithological descriptions consisting of one or more lithological adjectives. Some of these adjectives, including glauconitic, ferruginous, muddy etc... can be treated as additional proxies for the relative firmness of sediments, going beyond the carbonate/siliciclastic binary. To explore this relationship, all brachiopod and bivalve occurrences were downloaded from the PBDB and then subset to the Permian to Cretaceous interval and binned by epoch.

Brachiopod and bivalve occurrences were analyzed to determine if their lithological description included the following lithological adjectives: glauconitic, ferruginous, calcareous, and muddy/argillaceous. The number of brachiopods and bivalves in sandstone and mudstone was determined, compared to other siliciclastic lithologies.

The association between brachiopod and bivalve occurrence and the glauconite/ferruginous lithological adjectives was tested using carbonate and siliciclastic data due to the association of glauconitic and ferruginous sedimentation with firmer substrates (Fursich et al., 2017) in both sedimentary regimes.

The calcareous occurrence of the two groups was only compared in siliciclastics, since it is difficult to know whether a “calcareous limestone” represents a firmer or softer substrate than a regular limestone. For similar reasons, muddy/argillaceous occurrences were only examined in data from carbonates.

Firm substrate preference within siliciclastic lithologies was explored by comparing brachiopod and bivalve occurrence in sandstone and mudstone, with sandstones representing generally firmer surfaces compared to mudstone.

For all the association between brachiopods and bivalves and each lithology or lithological adjective, a 2x2 contingency table was constructed for each epoch and then analyzed using a Fisher’s Exact Test. The relative percentage of brachiopod and bivalve occurrences associated with the adjective/lithology in each epoch was also determined, and epochs where less than 1% of brachiopods or bivalves occur in the lithology or adjective of interest were discarded.

Brachiopod Carbonate Occurrence by Order

One potential cause of brachiopod preference for carbonate substrates is the decline of siliciclastic adapted orders, such as productids and spiriferids. This was explored by comparing the overall brachiopod carbonate trend to the brachiopod trend with productids excluded and the trend with both productids and spiriferids excluded.

Results

Substrate Preference and Occurrence

A direct comparison of brachiopod and bivalve substrate preference shows a greater brachiopod preference for carbonates through the Paleozoic and into the mid-Cretaceous (Figure 5a), with the difference increasing during the Mesozoic (Figure 5b). The 95% confidence interval indicates that the carbonate preference trend of the two groups overlaps during periods such as the Devonian and Carboniferous and the aftermath of the P-T extinction, due to the limited number of occurrences in those intervals. Excluding burrowing bivalves, which may be less affected by substrate conditions resulted in similar trends of brachiopod and bivalve carbonate affinity and brachiopod/bivalve carbonate occurrence difference, particularly during the late Mesozoic (Figure 6a, 6b).

Latitude Trend

Modern carbonates preferentially accumulate on tropical to subtropical shelves, where seawater reaches its highest saturation with respect to calcite and aragonite, a pattern also observed in the rock record, with carbonates accumulating within 30° of the equator (Walker, 2002). Therefore, it is important to determine whether the concentration of brachiopod/bivalve occurrences is responsible for the observed preference for carbonates. The carbonate occurrence of brachiopods and bivalves appears to be independent from the proportion of occurrences in the tropics (Figure 7a, 7b). The linear regressions indicate that there is a weak relationship between tropicality and carbonate occurrence for brachiopods and a somewhat stronger relationship between tropicality and carbonate occurrence for bivalves (R^2 of 0.06 and 0.3, respectively).

Substrate Preference and Abundance

In addition to occurrence data, abundance data from paleoecological collections was also used to explore the substrate trend. Occurrence data can offer a limited view of substrate trends. For example, due to the sampling/literature bias for North American and Western European occurrences, the dominant lithology in these areas can dominate the occurrence trend. Analyzing the relative abundance of brachiopods in individual collections allows for preference to be explored even during carbonate-dominated intervals.

During the Middle and Late Permian, brachiopods show a statistically significant (Table 2) greater relative abundance in siliciclastic collections while showing a greater relative abundance in carbonate collections during the Middle Permian. The last epoch during which brachiopods show a greater relative abundance in siliciclastics is the Early Triassic, after which they show a consistently higher relative abundance in carbonate collections particularly during the Early to Middle Jurassic and during the Early Cretaceous (Figure 8).

Lithological Adjectives

In addition to the carbonate/siliciclastic, firm/soft lithological binary, the association between brachiopod and bivalve occurrences and specific siliciclastic lithologies (mudstone and sandstone) and lithological adjectives were also explored. All these associations were explored using Fisher's exact tests of 2x2 contingency tables. Any time intervals with a statistically significant difference between brachiopod and bivalve occurrences but in which the lithological adjective was associated with less than 1% of the occurrences of either group.

Firm Substrate Indicators

The firm substrate indicators used include the adjectives calcareous, glauconitic, and ferruginous as well as sandstone (as the primary lithology).

Brachiopod and bivalve occurrences were found to be significantly different between calcareous and non-calcareous siliciclastics during the Early, Middle, and Late Permian and brachiopods are consistently more common in calcareous siliciclastics compared to bivalves (Figure 9; Table 3). There are also significant differences between brachiopod and bivalve occurrences during the Early Triassic but no significant difference during the Late Triassic. During the Early Triassic and Middle Triassic, around 50% of brachiopod occurrences in siliciclastic are calcareous, compared to 7-9% of bivalves. In the Late Triassic, 3% of brachiopod and 2% of bivalve occurrences are calcareous. Middle Triassic results are not statistically significant and less than a 100 bivalves and brachiopods total occur in calcareous siliciclastics during the epoch (Table 3). There is a significant difference between brachiopod and bivalve calcareous siliciclastic occurrences during all Jurassic and Cretaceous epochs as well. Brachiopods are consistently more likely to occur in calcareous siliciclastics, though the difference narrows significantly in the Cretaceous (Table 3).

Another lithological adjective associated with firm substrates is glauconite. Glauconite is associated with low sedimentation rate, requiring sediment starvation to form (Amorosi, 1995, Fursich, 2017). The association between glauconite and brachiopod/bivalve occurrences was explored by examining data from both carbonates and siliciclastics, because glauconite is expected to be associated with both firmer siliciclastics and carbonates. Only three epochs met the criteria of at least 1% bivalves and brachiopods occurring in glauconite and had a statistically significant difference, the Middle Permian, Late Jurassic and Late Cretaceous. Only 1% of brachiopods and bivalves occur in glauconitic sediments during the Middle Permian, compared to 8% of brachiopods and 10% of bivalves in the Late Jurassic and 5% of brachiopods and 13% of bivalves in the Late Cretaceous (Figure 10; Table 4). Contrary to the hypothesis, bivalves are associated with firm sediments.

Another firm substrate adjective is ferruginous, which indicates sediment starvation (Fursich, 2017), whose association with bivalve and brachiopod occurrences was explored using carbonate and siliciclastic data. Ferruginous sedimentation indicates sediment starvation (Fursich, 2017). Only the Jurassic epochs had statistically significant results and >1% occurrences of both groups in ferruginous sediments (Table 5). Brachiopod occurrence in ferruginous sediments increases during the Jurassic. During the Early Jurassic, 2% of brachiopod and 3% of bivalve occurrences are ferruginous ($p<0.001$) compared to 9% of brachiopods and 4% of bivalves in the Middle Jurassic ($p<0.001$) and 9% of brachiopods and 4% of bivalves during the Late Jurassic ($p<0.001$) (Figure 11; Table 5).

Compared to other siliciclastic lithologies such as mudstones, sandstones are expected to create a firmer substrate due to their larger grain size; deposit feeders generally prefer clay to silt sized sediments (Fursich, 1976) and the burrowing ability of specialized deposit feeding bivalves is very limited outside of their preferred grain size range (Alexander et al., 1993). Siliciclastic brachiopod and bivalve occurrence data was used to test this association by comparing brachiopod and bivalve occurrence in sandstones or mudstones to occurrences in all other siliciclastic lithologies.

During the Permian, brachiopods are more common than bivalves in sandstones, with over 20% of occurrences in sandstones, compared to less than 10% of bivalves occurring in sandstones (Figure 12; Table 6). The results for the Early to Middle Triassic are not statistically significant but the difference is maintained during the Late Triassic, with 25% of brachiopods and 5% of bivalves occur in sandstones ($p<0.001$). Brachiopods are also more common in sandstones during the Jurassic. During the Early Jurassic, 32% of brachiopods and 9% of bivalves occur in sandstones ($p<0.001$) compared to 39% of brachiopods and 8% of bivalves in the

Middle Jurassic ($p<0.001$) and 48% of brachiopods and 22% of bivalves in the Late Jurassic ($p<0.001$). During the Early Cretaceous, 50% of brachiopods and 55% of bivalves occur in sandstones ($p<0.001$) while 21% of brachiopods and 42% of bivalves occur in sandstones during the Late Cretaceous ($p<0.001$).

Soft Substrate Indicators

The proxies used to examine brachiopod and bivalve occurrence trends in soft substrates included two lithologies, mudstone (in siliciclastics) and lime mudstone (in carbonates). Two lithological adjectives, muddy and argillaceous were combined (since they are difficult to clearly distinguish from each other) in order to examine their association with brachiopod and bivalve carbonate occurrences.

During the Early Permian, 9% of brachiopods and 12% of bivalves occur in mudstones ($p<0.001$) (Figure 13). In the Middle Permian, 12% of brachiopods and 14% of bivalves occur in mudstones, a difference that was not statistically significant ($p=0.091$) while 27% of brachiopods and 25% of bivalves occur in mudstones during the Late Permian, a non-statistically significant difference ($p=0.14$) (Table 7). In the Early Triassic, 7% of brachiopods and 23% of bivalves occur in mudstone ($p<0.001$) compared to 14% of brachiopods and 31% of bivalves in the Middle Triassic ($p<0.001$) and 2% of brachiopods and 31% of bivalves during the Late Triassic ($p<0.001$). During the Early Jurassic, 15% of brachiopods and 33% of bivalves occur in mudstones ($p<0.001$) compared to 2% of brachiopods and 23% of bivalves during the Middle Jurassic ($p<0.001$) and 4% of brachiopods and 16% of bivalves in the Late Jurassic ($p<0.001$). During the Early Cretaceous, 7% of brachiopods and 9% of bivalves occur in mudstones, a non-statistically significant result (p=0.235) compared to 1% of brachiopods and 15% of bivalves.

The association between brachiopod and bivalve occurrence and muddy/argillaceous carbonates was also explored. The analysis was limited to carbonates because it is difficult to determine how much of an influence the presence of mud or clay has on softer siliciclastic substrates. The only statistically significant differences between brachiopods and bivalves were during the Middle Permian, Middle Triassic, Early Jurassic and Early Cretaceous (Figure 14; Table 8). During the Middle Permian, 10% of brachiopods and 2% of bivalves occur in muddy/argillaceous carbonates (p<0.001). By the Middle Triassic, 4% of brachiopod and 3% of bivalve occurrences in carbonates are muddy/argillaceous (p=0.041) compared to 12% of brachiopods and 3% of bivalves during the Middle Jurassic (p<0.001) and 8% of brachiopods and 5% of bivalves during the Early Cretaceous (p=0.001).

<u>Discussion</u>

Paleozoic Brachiopod Substrate Preference

Paleozoic brachiopods were hypothesized to have a substrate preference generally similar to that of bivalves due to both lower rates of sediment disturbance (Thayer, 1983) and the occurrence of brachiopod groups with soft sediment adaptations such as the “snowshoe strategists” and those with pedicle rootlets (Rhoads, 1970). Contrary to expectations, brachiopods were found to prefer carbonates based on occurrence data, particularly during the Devonian and Permian

(Figure 5a, 5b), a carbonate preference strengthened by removing spiriferids and productids, both soft substrate adapted groups, from the analysis (Figure 15).

Substrate preference during the Permian was also examined using abundance data because it was the only Paleozoic period with enough such data in the PBDB. In contrast to the occurrence trend, abundance data shows similar brachiopod preference for carbonates and siliciclastics during the Permian (Figure 8), though occurrence data does show lower carbonate preference towards the end of the Paleozoic (Figure 5). This may be linked to the increasing dominance of the productids prior to the Permian/Triassic extinction. Permian lithological adjective data shows brachiopods have a consistently higher preference than bivalves for calcareous siliciclastics (Figure 10, Table 3).

Mesozoic Brachiopod Substrate Preference

Brachiopod carbonate preference increases significantly following the end-Permian mass extinction based on occurrence data (Figure 5a, 5b), an increase linked to the extinction of soft substrate adapted groups such as the productids (Figure 9). In contrast, brachiopods show a similar abundance in carbonates and siliciclastics during the Triassic (the difference during the Middle Triassic is not statistically significant) (Figure 8, Table 2). This likely reflects the continued presence of Paleozoic groups during the period (Chen, 2005).

During the Jurassic, brachiopods remained abundant in carbonates after declining in clastics, pointing to faster brachiopod decline in clastics than carbonates due to increasing bioturbation. The Cretaceous trend shows higher carbonate preference during the Early Cretaceous with lower preference during the Late Cretaceous in datasets (Figure 5, 8). The generally very low relative abundance of brachiopods, on both carbonates and siliciclastics, may indicate that the high depth and rate of burrowing was leading to brachiopod decline even on favorable substrates during the Cretaceous (Thayer, 1983). Overall, the later Mesozoic features a gradual restriction of brachiopods to firmer, carbonate substrates.

Bioturbation and Substrate Preference

A proposed cause of increasing brachiopod preference for hard substrates is increasing bioturbation intensity. One indirect proxy for bioturbation rate is the feeding depth of taxa present during a period, extrapolated from their modern analogues (Thayer, 1983). Another proxy is the increasing thickness of preserved event beds over time due to the destruction of thinner event beds by bioturbation (Sepkoski, 1991). Based on both proxies, the bioturbation rate slowly increases over the Paleozoic, alongside a general increase in brachiopod carbonate preference from the Devonian to the Permian (Figure 4, 5), possibly accounting for pre-Mesozoic brachiopod preference for carbonates. This is followed by a significantly faster increase in bioturbation intensity following the Middle Triassic as part of the Mesozoic Marine Revolution (Vermeij, 1977). Brachiopod carbonate preference increases significantly during the Triassic, though this trend is limited to occurrences. The trend is clearer during the Jurassic and Cretaceous with increasing carbonate preference supported by both occurrences and abundances, accompanied by a further increase in bioturbation intensity (Figure 5, 8). Overall, Mesozoic data demonstrate the link between brachiopod carbonate preference and increasing bioturbation, accompanied by general brachiopod decline.

Conclusion

An analysis of occurrence and abundance data from the PBDB was found to support a link between increasing brachiopod preference for firm substrates and the increase in sediment disturbance as part of the Mesozoic Marine Revolution (Vermeij, 1977, Thayer, 1983). This study provides further support for bioturbation as a contributing factor in brachiopod decline. The decline of brachiopods, the dominant representatives of the Paleozoic fauna, was a key element of the transition to the Modern fauna, which completely reshaped seafloor communities (Sepkoski, 1983) and drastically increased the available energy in marine food webs (Payne et al., 2014). Previous studies have linked the transition between the two faunas to a transition from carbonates to siliciclastics (Peters, 2008) and this study details one mechanism behind this shift. Further study of the substrate preference of individual groups within the Paleozoic fauna could show the role that substrate played in their decline, using similar methods to this study. By entering additional abundance data to the PBDB for the Palezoic, the abundance trend for brachiopods and bivalves on firm and soft substrates could be explored across the entire era.

In conclusion, increasing bioturbation and the resulting restriction of brachiopods to firm substrates played an important part in brachiopod decline and thus was a key component of the transition between the Paleozoic and Modern Fauna. A better understanding of this transition may help better understand the relationship between sedimentation patterns and various changes to marine ecosystems.

Figures

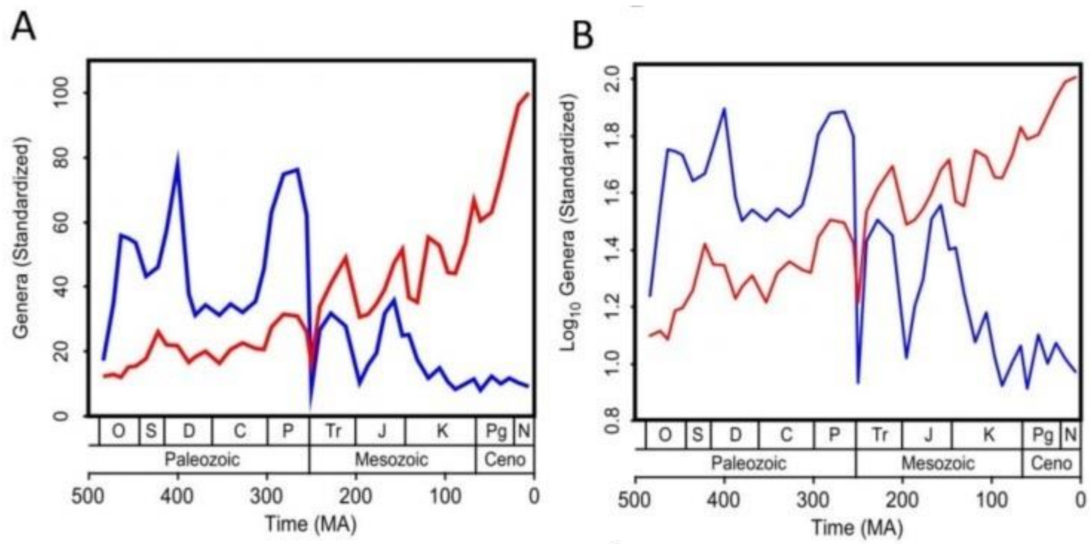

Figure 1: Sampling standardized generic diversity curves for brachiopods (blue) and mollusks (red). A is arithmetic scale while B is logarithmic scale

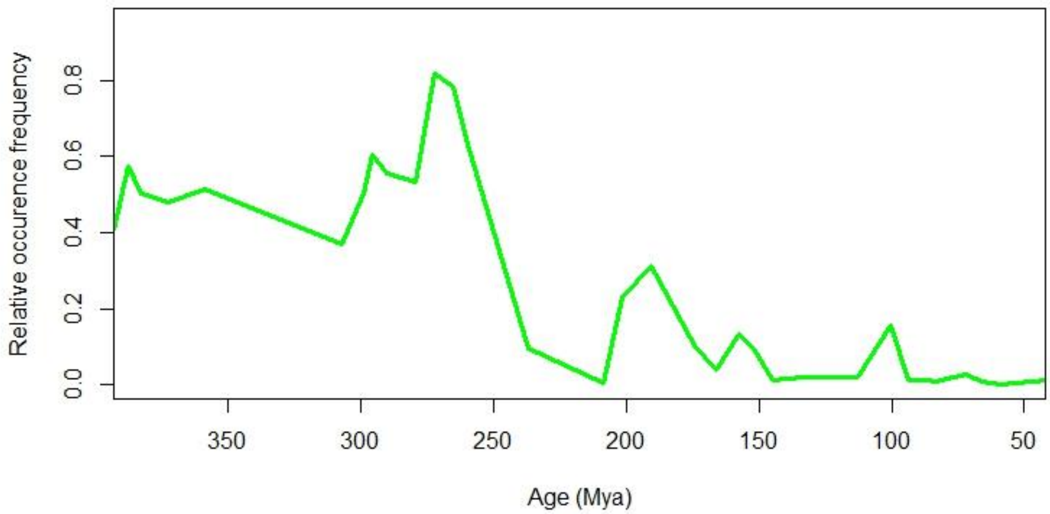

Figure 2: Relative abundance of brachiopods versus bivalves, gastropods, sponges and crinoids

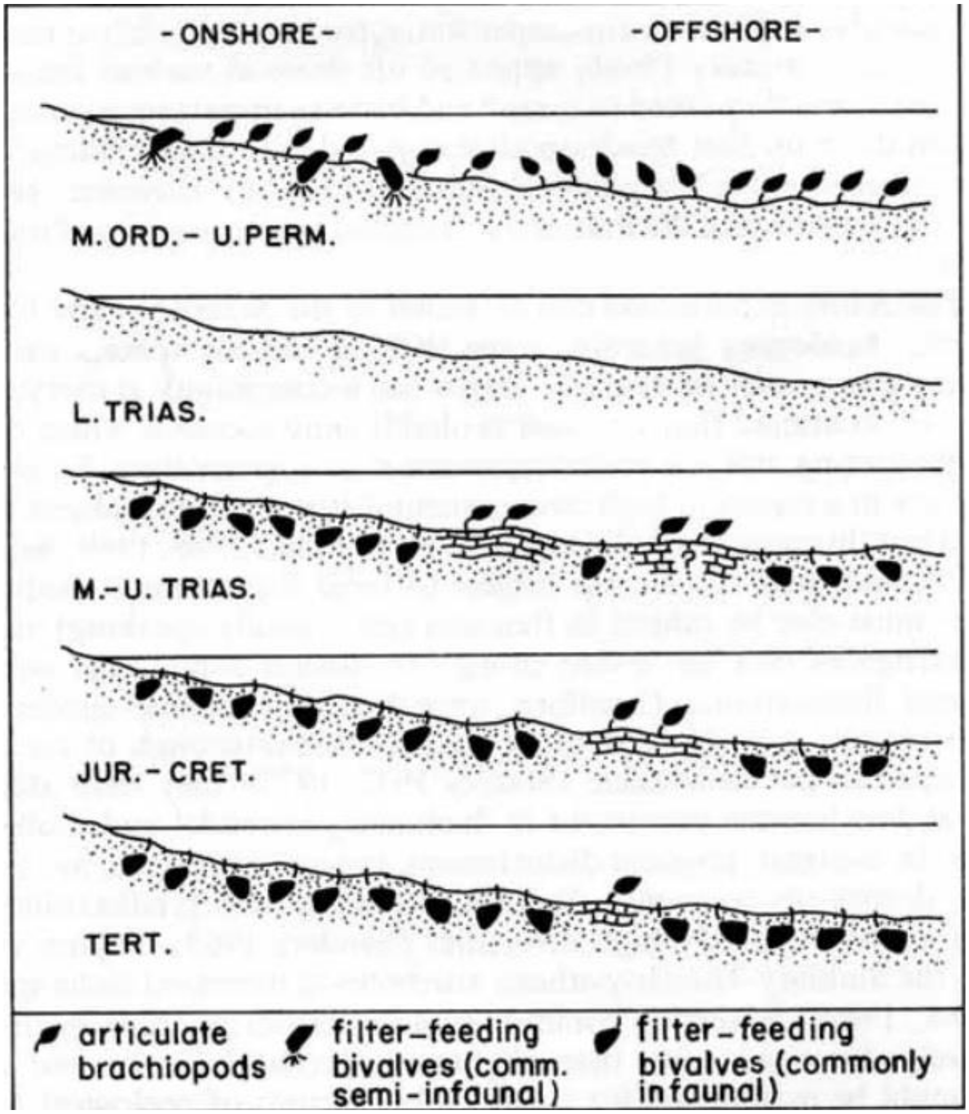

Figure 3: The displacement of brachiopods by bivalves (from Steele-Petrovic, 1975)

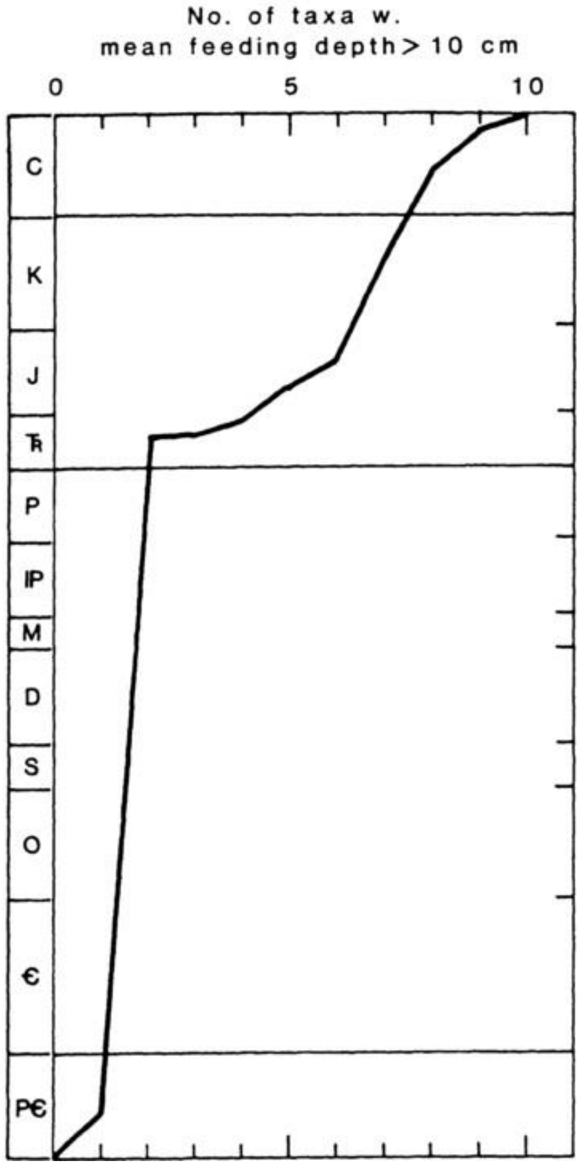

Figure 4: The increase in burrowing depth from the Pre-Cambrian to the Cenozoic

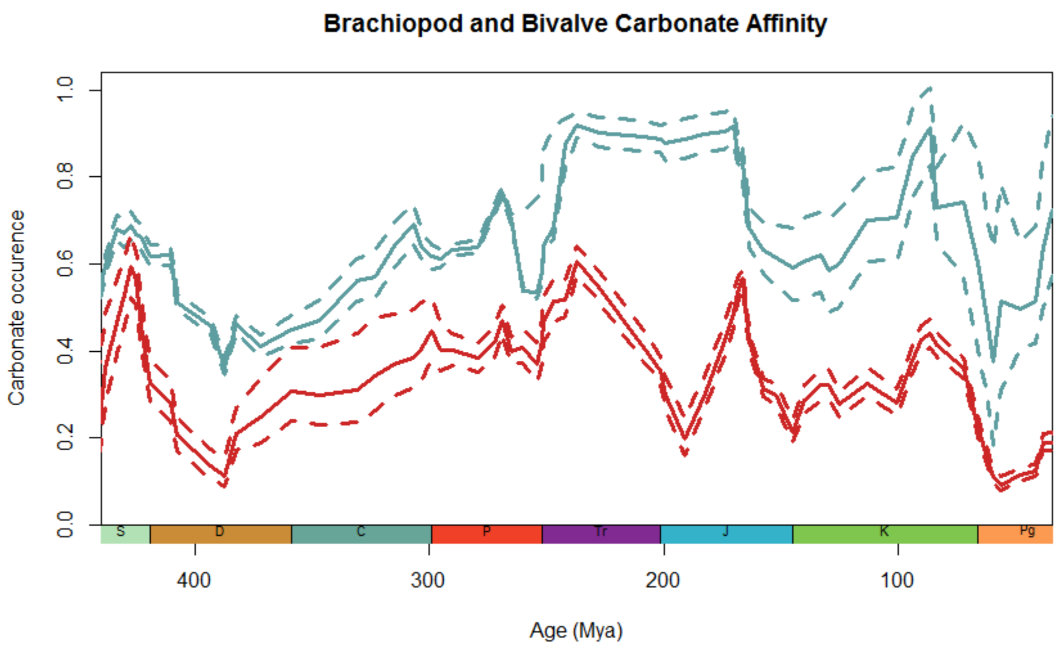

Figure 5a: The proportion of brachiopods and bivalves occurring in carbonates with proportion confidence interval added (dashed lines) (blue for brachiopods and red for bivalves)

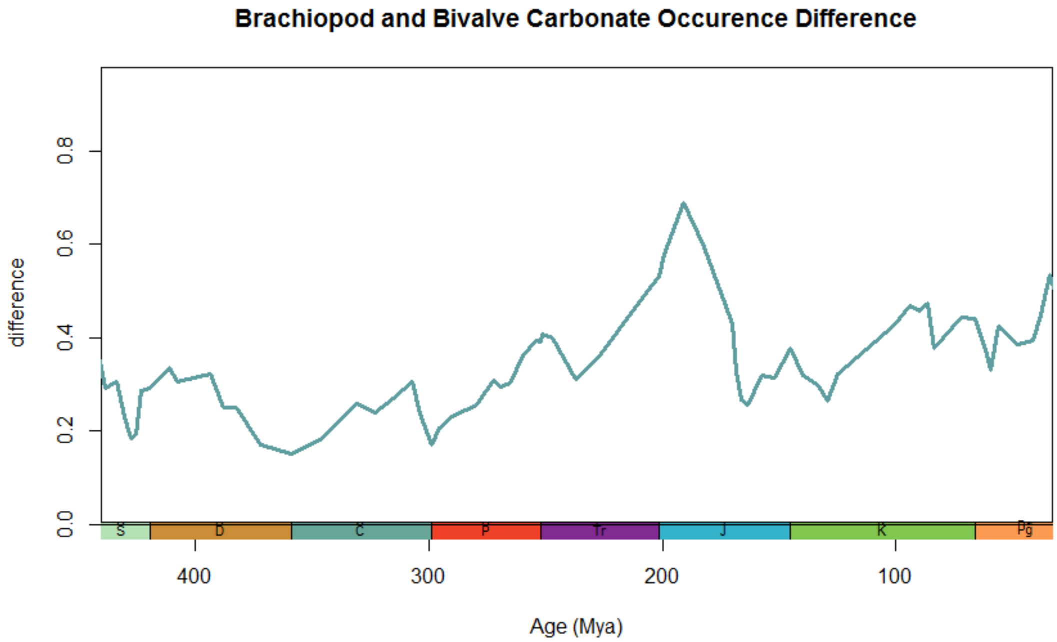

Figure 5b: The difference between brachiopod and bivalve carbonate occurrence

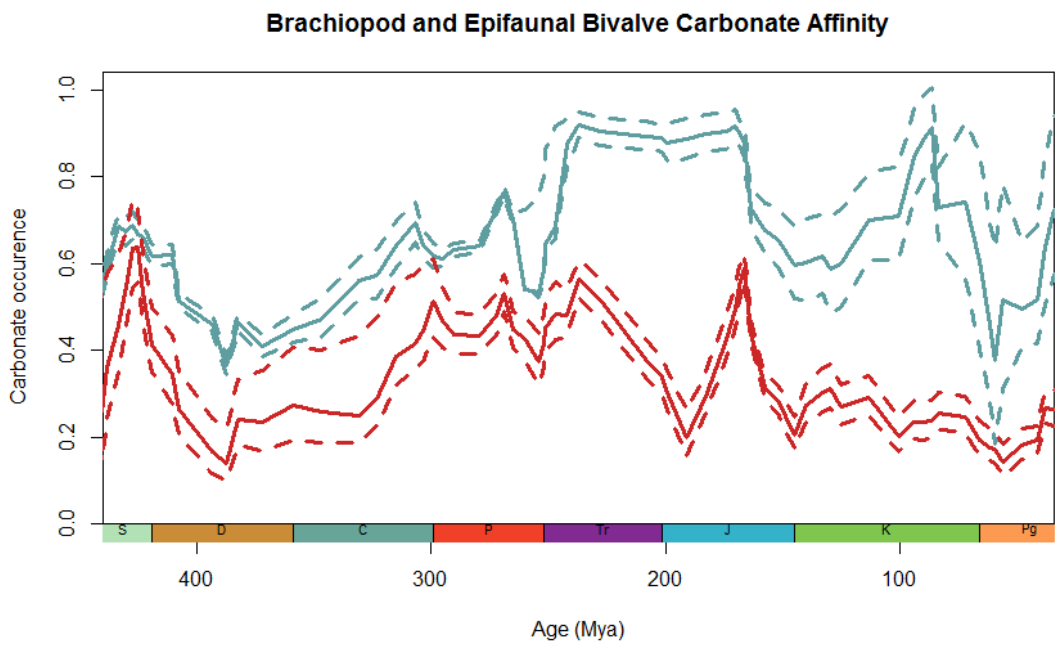

Figure 6a: The carbonate affinity trend with burrowing bivalves excluded

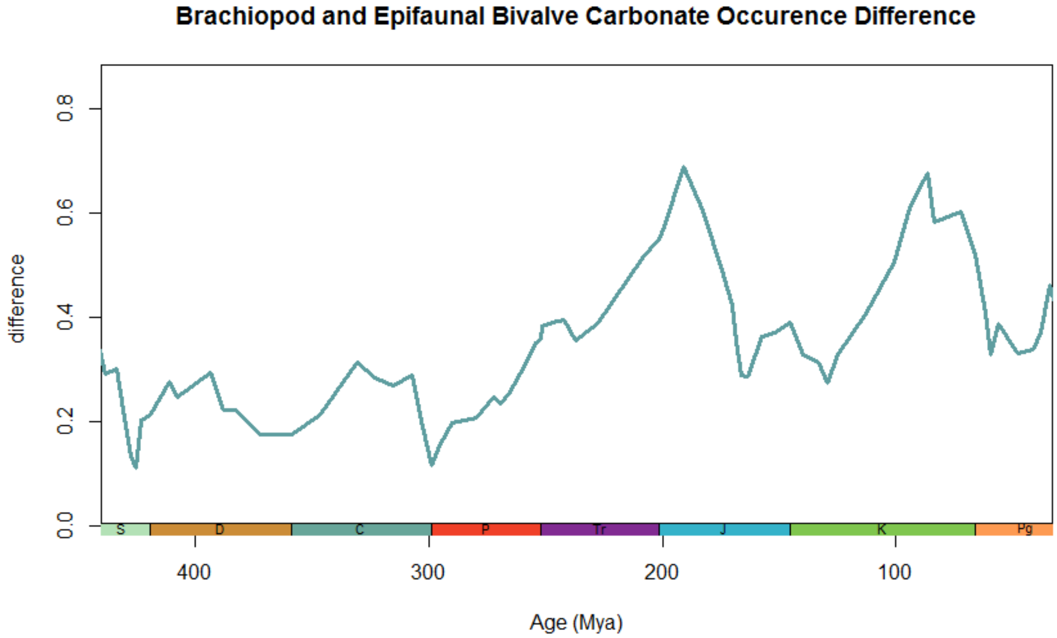

Figure 6b: Difference in carbonate occurrence with non-epifaunal bivalves excluded

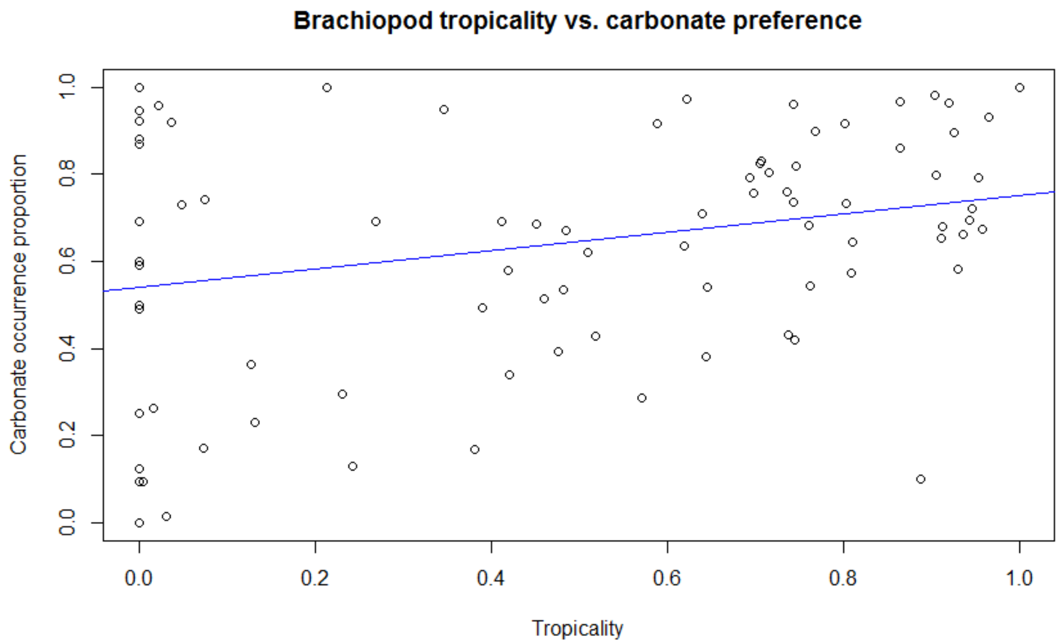

Figure 7a: Brachiopod carbonate occurrence vs tropicality

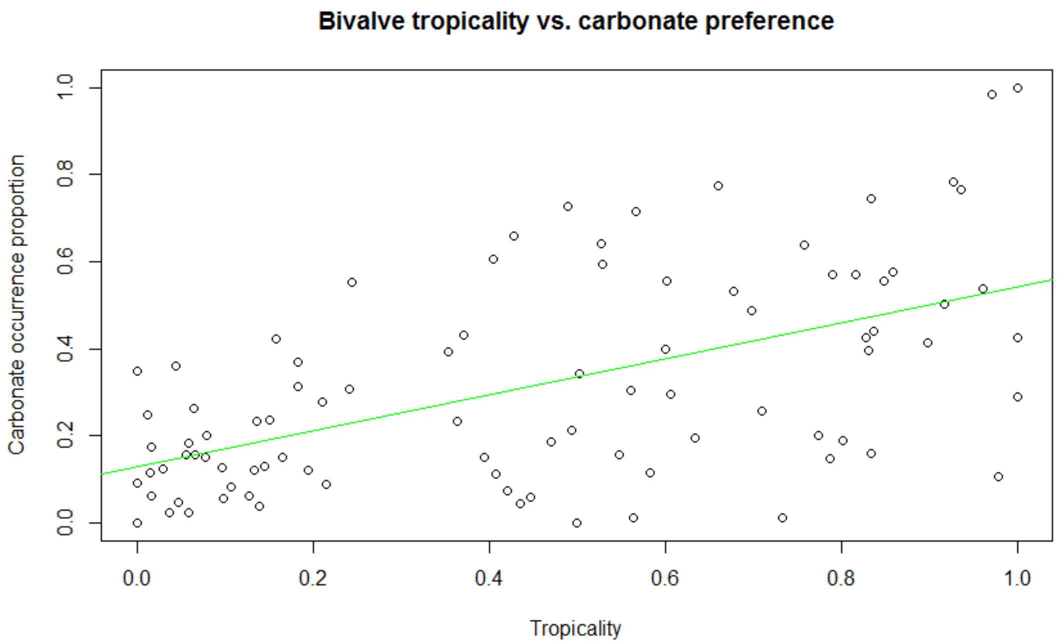

Figure 7b: Bivalve carbonate occurrence vs tropicality

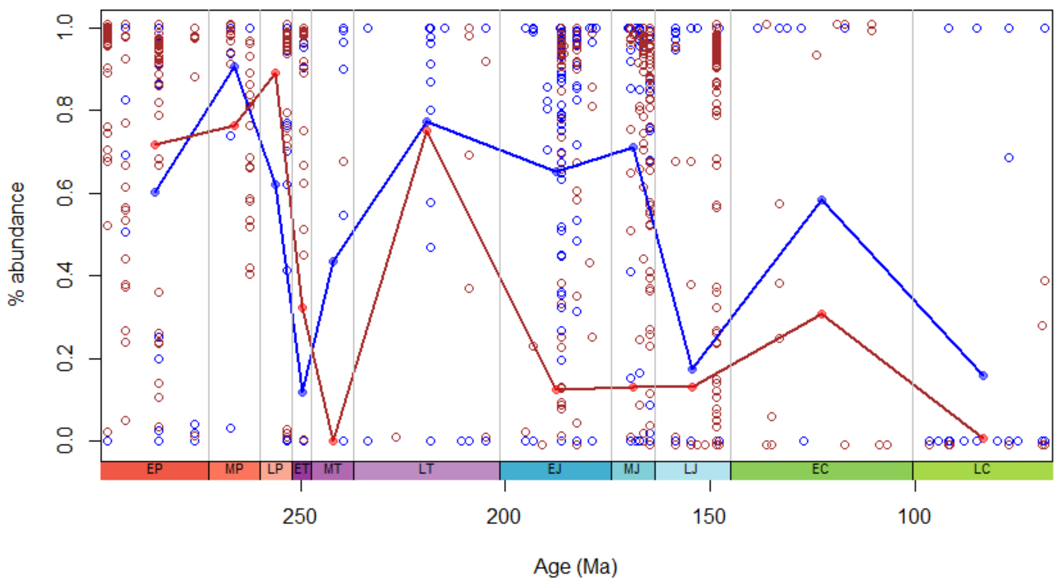

Figure 8: Relative brachiopod abundance in carbonate (blue) and siliciclastic (red) with individual collections plotted as points and the mean abundance in carbonate and siliciclastic collections for each epoch plotted as trendline

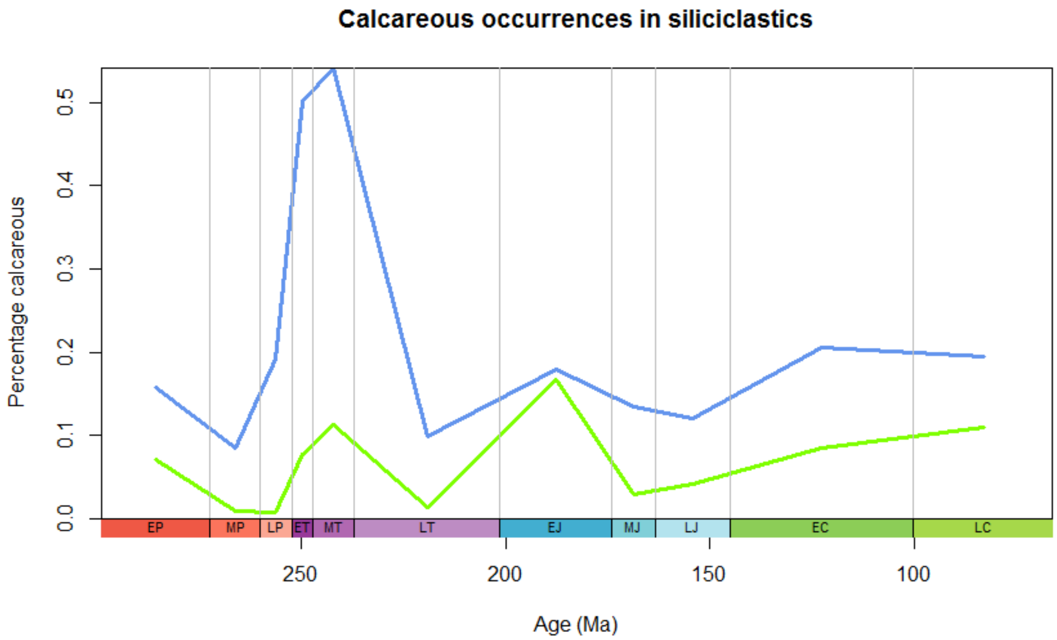

Figure 9: The proportion of brachiopods (blue) occurring in calcareous siliciclastics compared to bivalves (green)

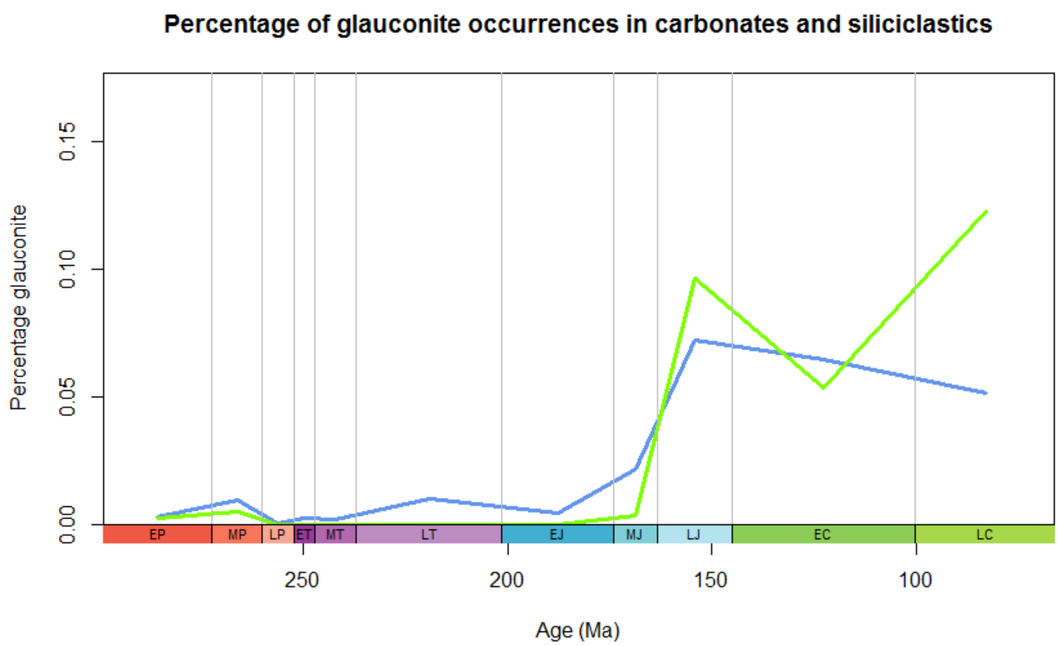

Figure 10: The proportion of brachiopods (blue) occurring in glauconitic lithologies compared to bivalves (green)

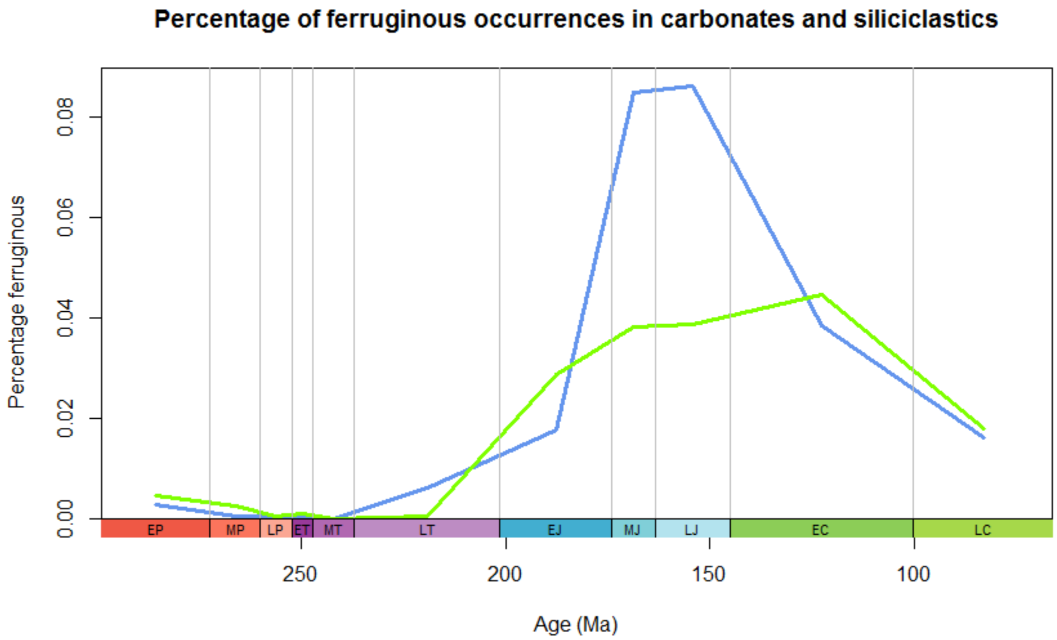

Figure 11: The proportion of brachiopods (blue) occurring in ferruginous lithologies compared to bivalves (green)

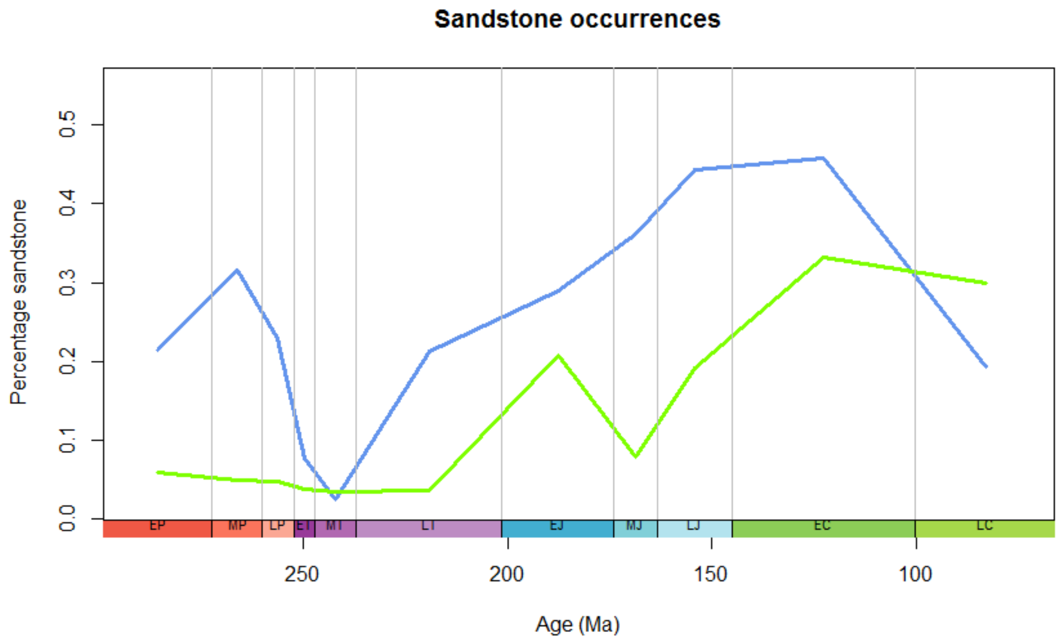

Figure 12: The proportion of siliciclastic brachiopods (blue) occurring in sandstones, compared to bivalves (green)

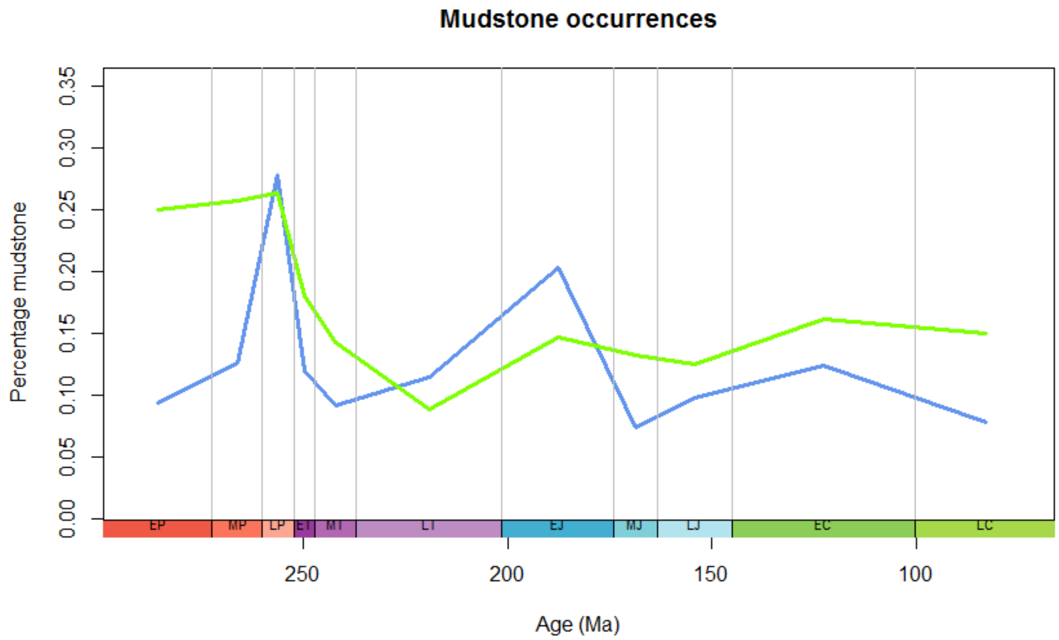

Figure 13: The proportion of siliciclastic brachiopods (blue) found in mudstones compared to bivalves (green)

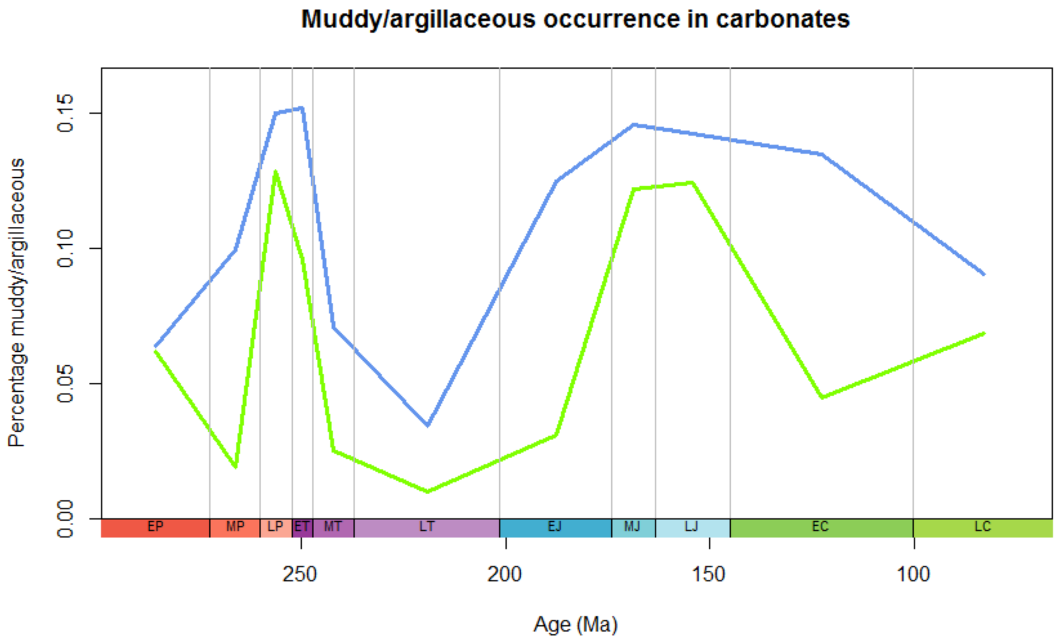

Figure 14: The proportion of carbonate brachiopods (blue) occurring in muddy and/or argillaceous lithologies, compared to bivalves (green)

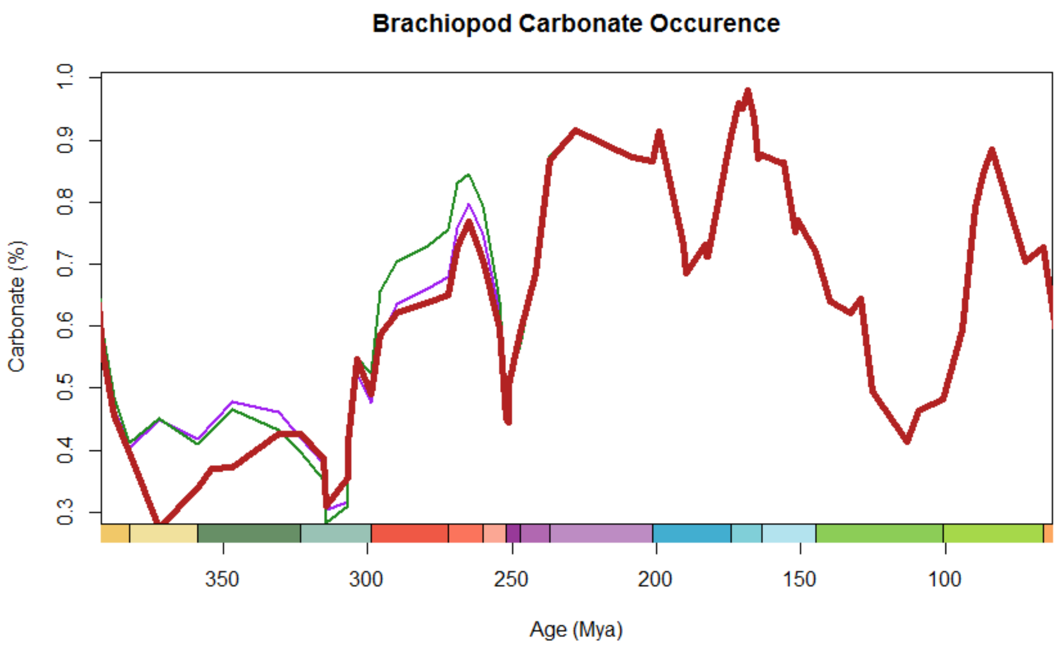

Figure 15: The proportion of brachiopods in carbonate with the thick red line representing all articulates, the green line representing all brachiopods – productids, and purple line representing all articulates – (productids and spiriferids)

TABLE 1. Lithologies assigned to principal lilthologic categories.

Category	Lithologies included
Carbonate	Limestone, dolomite, lime mudstone, packstone, grainstone, wackestone, ''reef rocks,'' bafflestone, framestone, bindstone, rudstone, floatstone, ''carbonate''
Clastic	Shale, mudstone, claystone, siltstone, sandstone, conglomerate, quartzite, phyllite, schist, slate, ''siliciclastic''
Mixed	Marl, ''mixed carbonate-siliciclastic''

Table 1: A list of the three lithology categories that are used to simplify PBDB lithological data (reproduced from Foote, 2006)

Table 2: Mann-Whitney U test of brachiopod carbonate/siliciclastic abundance

Epoch	P value	Brachiopod siliciclastic median	Brachiopod carbonate median	W
Early Permian	0.06	0.97	0.97	4447
Middle Permian	0.03	0.85	1	145
Late Permian	0.04	0.96	0.7	204
Early Triassic	<0.001	0.94	0	1509
Middle Triassic	0.84	0.68	0	10
Late Triassic	0.02	0.53	1	156.5
Early Jurassic	0.01	0.85	0.95	5288
Middle Jurassic	0.004	0.91	1	3364
Late Jurassic	0.03	0	0	5314
Early Cretaceous	0.001	0	1	90
Late Cretaceous	<0.001	0	0	222

Table 3: Calcareous occurrences in siliciclastics

Epoch	P value	Brachiopod calcareous %	Bivalve calcareous %
Early Permian	< 0.001	15	4
Middle Permian	< 0.001	8	3
Late Permian	< 0.001	19	4
Early Triassic	< 0.001	50	7
Middle Triassic	0.327	54	9
Late Triassic	< 0.001	3	2
Early Jurassic	< 0.001	14	5
Middle Jurassic	< 0.001	10	4
Late Jurassic	< 0.001	8	4
Early Cretaceous	0.006	18	13
Late Cretaceous	0.016	16	12

Table 4: Glauconitic occurrences

Epoch	p value	Brachiopod glauconite %	Bivalve glauconite %
Early Permian	0.652	0.3	0.3
Middle Permian	0.004	1	1
Late Permian	0.455	0.06	0.02
Early Triassic	0.004	0.3	0.01
Middle Triassic	0.017	0.2	0 (none)
Late Triassic	< 0.001	1	0 (none)
Early Jurassic	< 0.001	1	0 (none)
Middle Jurassic	< 0.001	2	0.4
Late Jurassic	0.001	8	10
Early Cretaceous	0.068	7	6
Late Cretaceous	< 0.001	5	13

Table 5: Ferruginous occurrences

Epoch	p value	Brachiopod ferruginous %	Bivalve ferruginous %
Early Permian	0.06	0.3	0.5
Middle Permian	< 0.001	0.05	0.3
Late Permian	0.72	0.05	0.07
Early Triassic	1	0.06	0.001
Middle Triassic	1	0	0
Late Triassic	< 0.001	0.6	0.05
Early Jurassic	< 0.001	2	3
Middle Jurassic	< 0.001	9	4
Late Jurassic	< 0.001	9	4
Early Cretaceous	0.43	4	5
Late Cretaceous	0.73	2	2

Table 6: Sandstone occurrences

Epoch	p value	Brachiopod sandstone %	Bivalve sandstone %
Early Permian	< 0.001	22	6
Middle Permian	< 0.001	32	8
Late Permian	< 0.001	23	9
Early Triassic	0.13	8	7
Middle Triassic	0.57	4	4
Late Triassic	< 0.001	25	5
Early Jurassic	< 0.001	32	9
Middle Jurassic	< 0.001	39	8
Late Jurassic	< 0.001	48	22
Early Cretaceous	< 0.001	50	55
Late Cretaceous	< 0.001	21	42

Table 7: Mudstone occurrences

Epoch	p value	Brachiopod mudstone %	Bivalve mudstone %
Early Permian	< 0.001	9	12

Middle Permian	0.09	12	14
Late Permian	0.14	27	25
Early Triassic	< 0.001	7	23
Middle Triassic	< 0.001	1	31
Late Triassic	< 0.001	2	31
Early Jurassic	< 0.001	15	33
Middle Jurassic	< 0.001	2	23
Late Jurassic	< 0.001	4	16
Early Cretaceous	0.24	7	9
Late Cretaceous	< 0.001	1	15

Table 8: Muddy/argillaceous carbonate occurrences

Epoch	p value	Brachiopod mudstone %	Bivalve mudstone %
Early Permian	0.88	6	6
Middle Permian	< 0.001	10	2
Late Permian	0.25	14	13
Early Triassic	0.26	11	10
Middle Triassic	0.04	4	3
Late Triassic	0.43	1	1

Early Jurassic	< 0.001	12	3
Middle Jurassic	0.07	14	12
Late Jurassic	0.77	12	13
Early Cretaceous	< 0.001	8	5
Late Cretaceous	0.47	6	7

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