

PHANEROZOIC EVOLUTION TRENDS WITHIN BENTHIC FORAMINIFERA

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Abstract

Foraminifera are marine protists that evolved and diversified throughout the Phanerozoic Eon. These protists construct their shells (called “tests”) from their surrounding environment. Foraminifera tests fossilize in great abundance and are sensitive to ocean chemistry and climate. In this study, the relative proportions of calcareous and agglutinated foraminifera are used to understand changes in ocean chemistry over 541 million years. With this data, I aim to answer the following question: How have benthic foraminifera responded to short- and long-term changes in global ocean chemistry? This was accomplished by aggregating diversity-level information from *Foraminifera Genera and their Classification*, published by Alfred R. Loeblich and Helen Tappan, the most recent and commonly-used reference literature for foraminiferal genera. I built a dataset by recording the accepted names, wall type, and time interval of 3,114 taxa (2,442 genera). Using the genera, binned by Epoch, I tracked wall-type diversity, compared the ratios of calcareous versus agglutinated foraminifera, and contextualized foraminiferal responses to geologically-significant events. I found a notable decrease in relative abundance of calcareous foraminifera during the mid-Carboniferous warming and the end-Permian mass extinction. These changes in the Paleozoic imply that benthic calcifiers organisms were more sensitive to changing ocean acidification and temperatures. However, despite documented climatic fluctuations throughout the Cenozoic, calcareous foraminifera remain stable around 80% diversity from the Eocene through the Pleistocene. This implies benthic calcifiers were more resilient to changes in the Cenozoic, which may be due to pelagic calcifiers stabilizing the carbonate saturation. Comprehensive datasets such as this are essential for research about faunal diversity and paleoclimate records, ocean chemistry, and conservation because it provides insight into how benthic marine organisms respond to and interact with their marine environment. This data has the potential to inform global trends of benthic foraminifera and ocean chemistry throughout the Phanerozoic, which can contextualize current changes in the marine ecosystem.

Introduction

Marine organisms like corals and bivalves use naturally-abundant calcium and dissolved inorganic carbon in the oceans to metabolically produce calcium carbonate (CaCO_3) for shell and skeletal growth (Ridgwell & Zeebe, 2005). The ocean is a sink for anthropogenic carbon emissions, leading to ocean acidification and a lower saturation state for carbonate ion formation (Masson-Delmotte, 2021; Hönlisch et al., 2012). This may lead to a decline in marine calcifiers since they are sensitive to changes in ocean chemistry (Cornwall, 2021). Benthic (bottom-dwelling) carbonate producers are especially vulnerable to changes in carbon dioxide fluxes due to their shells' retrograde solubility. Calcareous foraminifera rely on calcium carbonate supersaturation for the precipitation of their skeletons/tests, and benthic foraminifera are especially sensitive to changing ocean chemistry since their skeletons are thermodynamically unstable below the carbonate compensation depth (Ridgwell & Zeebe, 2005). This means increasing CO_2 levels may negatively impact benthic-ecosystem composition, and in order to conserve our oceans, calcifiers' response to changes in ocean chemistry must be studied. Looking at the geologic record for the response of benthic organisms to short- and long-term changes in ocean chemistry can help predict organismal responses to current changes in marine ecosystems.

The ocean's carbonate factory has shifted in meaningful ways in both the long and short term (Ridgwell 2005). In the short term, changes include acidification events like the Paleocene-Eocene Thermal Maximum and mass-extinction events like the Permian/Triassic and

Triassic/Jurassic mass extinction. Several ocean-acidification events have led to mass extinctions such as the end-Permian and end-Triassic mass extinctions (e.g., Knoll et al., 2007; Greene et al., 2012). While ocean chemistry has the potential to influence the biotic composition of reef ecosystems (Kiessling, 2009) and ocean acidification has been linked to several reef crises (Kiessling and Simpson, 2011), the overall impact of acidification on marine calcifiers has proven variable (Ries, 2009; Leung et al., 2022). I aim to understand the link between short-term ocean changes and marine evolution by addressing the following questions: How is the evolution of marine life impacted by 1) rapid mass-extinction events? and 2) rapid warming and cooling events?

In the long term, changes include the Mesozoic Marine Revolution (MMR) and transitions between calcite and aragonite seas. Carbonates are impacted by the recurring shift between aragonitic and calcareous seas (Reis, 2010); Mg/Ca ratios determine which carbonate minerals dominate in the ocean (Stanley & Hardie, 1998), and these changes in chemical compositions impact marine life. Research by Porter (2010) shows that calcite-aragonite seas influence the test type of newly evolved skeletons; however, Kiessling et al. (2008) show that these chemical shifts are less influential than mass extinctions in shaping Phanerozoic diversity trends. Moreover, the precipitation of CaCO_3 during the MMR (Ridgwell, 2005) is of interest. The MMR is characterized by an evolution of hard shells and infaunal (burrowing) benthic organisms (Vermeij, 1977), and the mid-Mesozoic radiation of pelagic (open-sea) calcifiers coincided with the scarcity of sedimentary tepees and pisoids (Smith et al., 2021). Changes in the carbonate factory, especially intervals like the MMR, likely impacted the biomineralization of marine invertebrates. I aim to understand the trends of long-term evolution by addressing the following questions: How is marine evolution impacted by 1) slower mass extinction events? 2) the MMR? 3) the shift between calcite and aragonite seas?

Benthic foraminifera are an ideal proxy for paleoecological responses to carbonate chemistry shifts because they are globally abundant throughout the fossil record as early as the Cambrian (Pawlowski et al., 2003). Foraminifera shells, are agglutinated from surrounding sediment (agglutinated), biomineralized from calcium carbonate (calcareous), or constructed out of organic material (organic), commonly proteins (e.g., Lipps, 1973). Studying the diversity of foraminiferal wall types during paleoenvironmental shifts provides insights into the general responses throughout the marine ecosystem (Saraswati, 2021). While there are excellent long-term reconstructions of the response of reef-forming organisms to ocean carbonate chemistry (e.g. Kiessling and Simpson, 2011) and planktic foraminifera's response to changing ocean chemistry (see review by Lowery et al., 2020), less is known about how benthic foraminifera respond to ancient changes in ocean carbonate chemistry. Benthic foraminifera are especially important to synthesize because their data extends 541 million years back to the Cambrian Period, compared to planktic foraminifera originating in the Jurassic Period. To address this gap, I focus on changes in benthic foraminifera diversity and wall type across the Phanerozoic Eon. In this paper, I present the first reconstruction of the relative abundance of benthic foraminifera test types throughout the Phanerozoic; these data are paired with biodiversity through time as well as extinction and origination rates of the different test types. Critical shifts in the benthic foraminiferal record are then discussed in the context of long- and short-term shifts in ocean chemistry.

Methods

Data were retrieved from *Foraminifera Genera and their Classification* (Loeblich and Tappan, 1988), which provides the best consensus on foraminiferal taxonomy at the time of publication.

While this book was published 35 years ago and likely no longer up to date, this is the most current exhaustive list of foram genera. The order, suborder, superfamily, family, subfamily, and genus were recorded along with origination interval, extinction interval, and wall type for a total of 3,114 taxa classifications. This dataset was reduced to focus on the 2,442 genera identified. Of these foraminifera, 160 genera are plankton. This reference is inconsistent with using stage and epoch levels to define foraminiferal occurrences, and to account for this, I binned the data at the epoch level.

For simplification, test types were merged into one of four groups: calcareous, agglutinated, organic, and unknown (Table 1). I classified all aragonitic and porcelaneous tests as calcareous because of their chemical similarities. Since calcareous-agglutinated wall types only account for 1.5% of total diversity and do not mineralize their tests, these wall types were combined with agglutinated tests. Some unknown genera in Loeblich and Tappan (1988) are fusulinids and other large reef-building foraminifera (e.g., BouDagher-Fadel 2008). Fusulinids physically built reef structures in the Paleozoic and lived on carbonate ramps and platforms (Lipps & Stanley, 2016). This Paleozoic superfamily originated during the Carboniferous, then went extinct near the end-Permian (Ross, 1979). Although it is still debated whether the microgranular calcite walls are calcareous or agglutinated (e.g., Hageman & Kaesler, 1998; Dubicka et al., 2021), most authors agree that fusulinids built calcareous walls (e.g., West, 1988); therefore, these taxa are classified as calcareous in the dataset.

Without the large benthic foraminifera, there were only three undefined genera: *Saudia*, *Sornayina*, and *Milammellus*. The *Saudia* and *Sornayina* wall types were classified as agglutinated, and *Milammellus* was classified as opaline based on its WoRMS (World Register of Marine Species) database description (WoRMS Editorial Board, 2023). *Milammellus* was excluded from analyses since it is the only genera classified as opaline in this dataset.

I performed analyses using R Statistical Software (v 4.0.0; R Core Team 2020) and binned diversity occurrences by the timescale used in Cohen et al. (2013). I calculated the diversity of foraminifera throughout each epoch, and I counted a genera as occurring in a bin if it was in one of the following categories: singleton (evolved and died in the interval), boundary crosser (evolved in an earlier interval and died in a later interval), originator (evolved in the interval then died outside the interval), or extinct (evolved in an earlier interval then died in the interval). I calculated origination and extinction rates based on Foote (2000). The null hypothesis code from Fraass (2015) was used to determine significant diversity fluctuations; I calculated the actual origination and extinction rates against the expected fluctuation rates. To account for preservation bias, I calculated the relative proportion of foraminifera wall type through time. Given the substantial differences in preservation between the earliest and latest parts of the Phanerozoic, caution must be used when comparing, for example, trends in the early Paleozoic with trends in the Neogene.

Table 1. Wall type categorization used in this study as compared to the Loeblich & Tappan (1988) descriptions.

Wall type described in Loeblich & Tappan	Simplified wall type (used in this study)
Agglutinated Calcareous and agglutinated Calcareous, porcelaneous, and agglutinated Porcelaneous and agglutinated Unknown (<i>Saudia</i> , <i>Sornayina</i>)	Agglutinated

Aragonite Calcareous Porcelaneous Calcareous and porcelaneous Calcareous and aragonitic Reef builders (BouDagher-Fadel, 2008)	Calcareous
Organic	Organic

Results

Paleozoic Era

During the Terreneuvian Epoch of the Cambrian Period, two agglutinated (*Platysolenites* and *Spirosolenites*) and one organic (*Chitinodendron*) foraminifera genera evolved. Agglutinated forms went extinct around the Series 2 Epoch (521-509 Ma), leaving only *Chitinodendron* for 23.6 million years (Ma).

During the transition from aragonite to calcite seas in the Lower Ordovician, total diversity increased from 1 to 8 genera as 2 more organic genera diversified (*Maylisoria* and *Archaeochitosa*), and agglutinated wall types reappear in the fossil record (5 genera). Early foraminiferal diversity doubled throughout the Ordovician (8 to 16 genera within 42 Myr), coincident with the Ordovician biodiversification event (Muscente et al., 2018). While the end-Ordovician mass extinction devastated marine communities, causing the extinction of 85% of marine species (Sheehan, 2001), foraminiferal diversity significantly increased as agglutinated foraminifera doubled from 11 to 21 genera (Figs. 1, 3).

During the Silurian, foraminifera with calcareous tests evolved and diversified from 2 genera in the Llandovery Epoch (~444 Ma) to 56 in the Upper Devonian (~359 Ma). Across the Devonian, foraminiferal diversity increased from 38 genera in the Lower Devonian to 82 genera in the Upper Devonian (115% increase) (Figs. 1, 2). Specifically, calcareous foraminifera diversified from 17 genera in the Lower Devonian to 56 genera in the Upper Devonian (229% increase). Only one organic-walled foraminifera, *Archaeochitosa*, was present from the Devonian to the Jurassic Period and made up less than 1% of the fossil data (Fig. 2). The Late Devonian biotic crisis (~370 Ma) led to more extinctions of calcareous tests (42 genera extinctions) compared to agglutinated tests (3 genera extinctions) (Figs. 1, 3).

During the Lower Mississippian (~327 Ma) there was a shift from calcite to aragonite seas (Kiessling, 2011), a decrease in atmospheric carbon, and an increase in oxygen (Scotese et al., 2021). Foraminifera diversified during this period (Fig. 3), and calcareous genera more than doubled from 56 to 146 genera in 36 million years (Upper Devonian to Lower Mississippian; Fig. 1). Calcareous and agglutinated wall-type proportions remained stagnant at 22% and 76% respectively (Fig. 2) until the Lower Pennsylvanian (323-315 Ma) when total diversity nearly halved; 111 genera went extinct, and calcareous wall types dropped to 60% proportional abundance (Fig. 2). Total diversity takes 230 Ma to get back to Mississippian-level numbers.

The Permian/Triassic mass extinction was caused by the eruption of the Siberian Traps, and while 90% of marine life went extinct during this event (e.g., Burgess et al., 2017; Erwin, 1994) no benthic foraminifera went extinct during the Lopingian (259-251 Ma). It was not until the Early Triassic (251-247 Ma) when 101 genera went extinct, and calcareous foraminifera experienced a 28% decrease in proportional abundance (103 to 27 genera). This was the first time since the

Early Devonian (419 Ma) that agglutinated tests were proportionally greater than calcareous forms (Fig. 2).

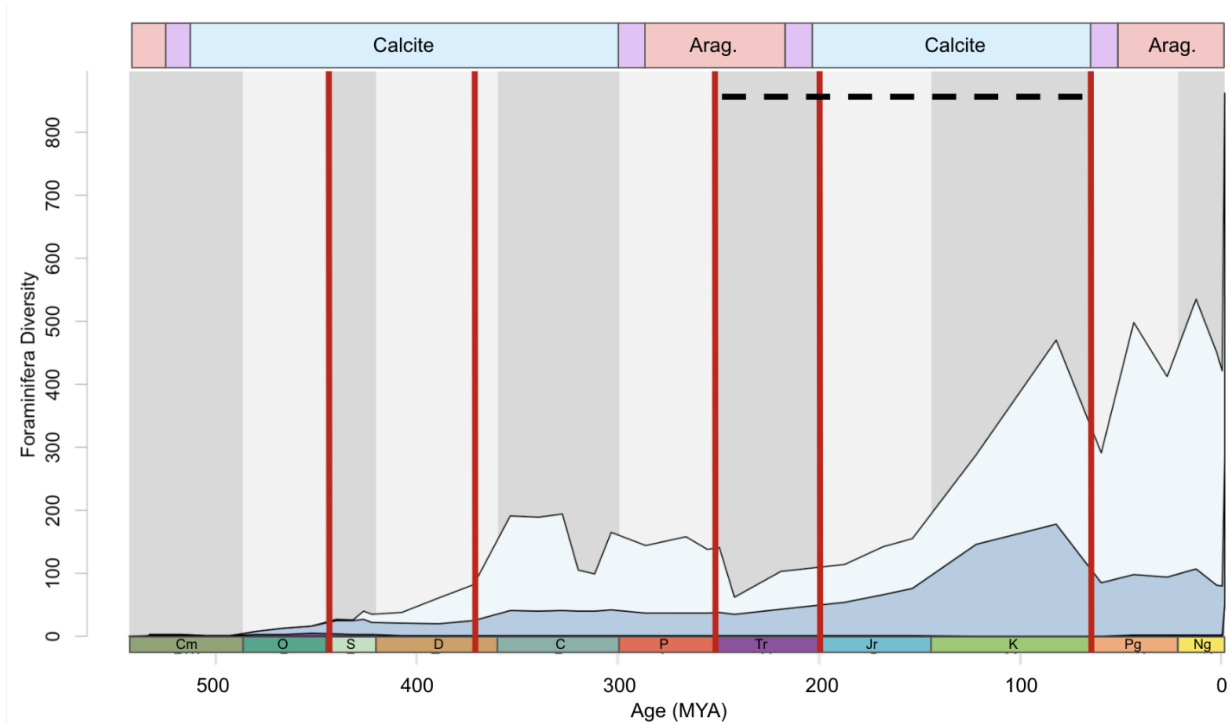


Figure 1. Foraminifera diversity through time based on the Loeblich and Tappan (1988) reference book. Generic diversity of foraminifera throughout the Phanerozoic; light blue = Calcareous, dark blue = Agglutinated, purple = Organic. Red indicates the “Big Five” mass-extinction events (Raup and Sepkoski, 1982), and the dotted line indicates the approximate duration of the MMR.

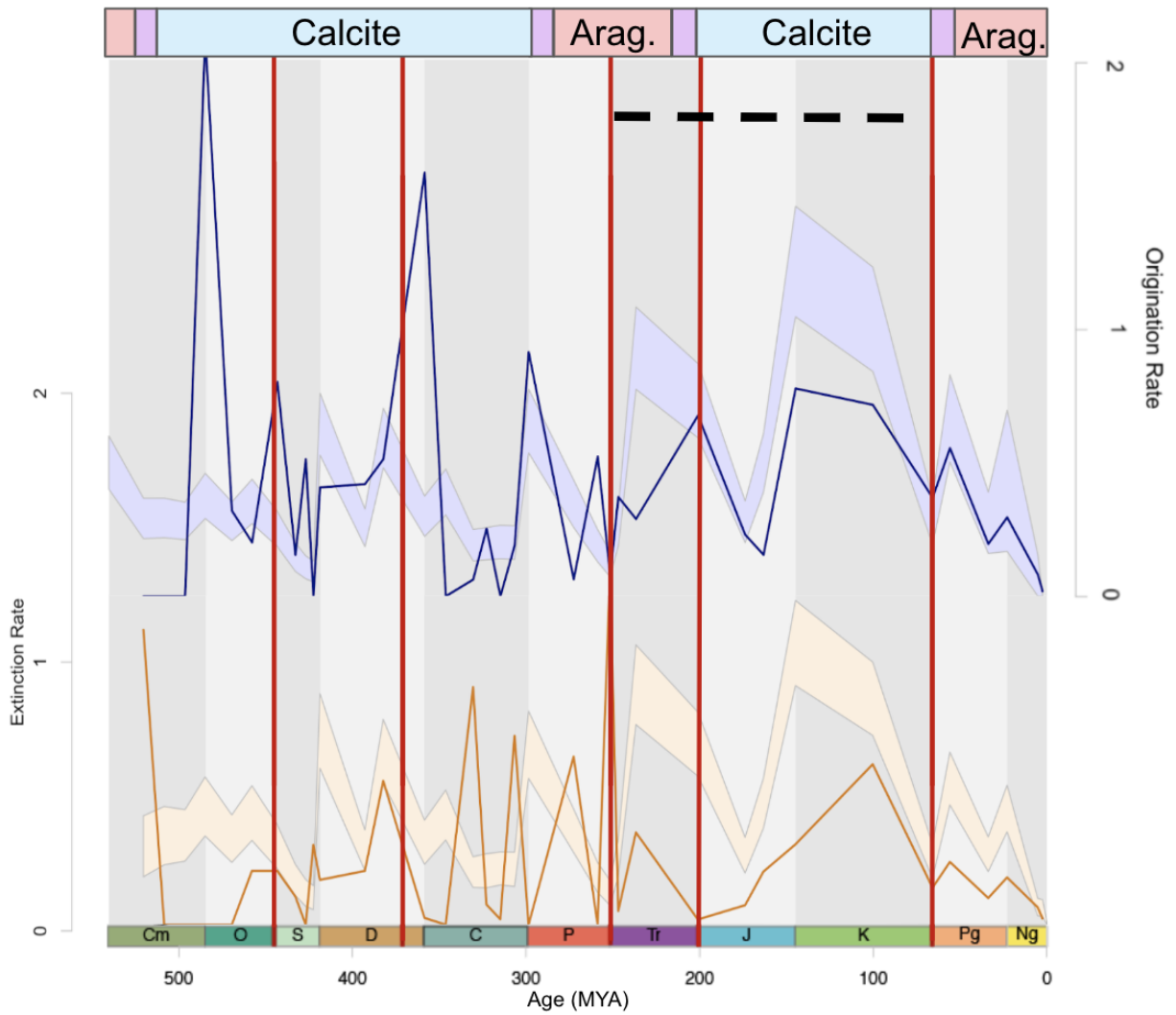


Figure 2. Origination (top) and extinction (bottom) rates of foraminifera in the dataset (dark blue for origination and dark orange for extinction) compared to the expected values within a 95% confidence-interval range (light blue for origination and light orange for extinction) throughout the Phanerozoic Eon.

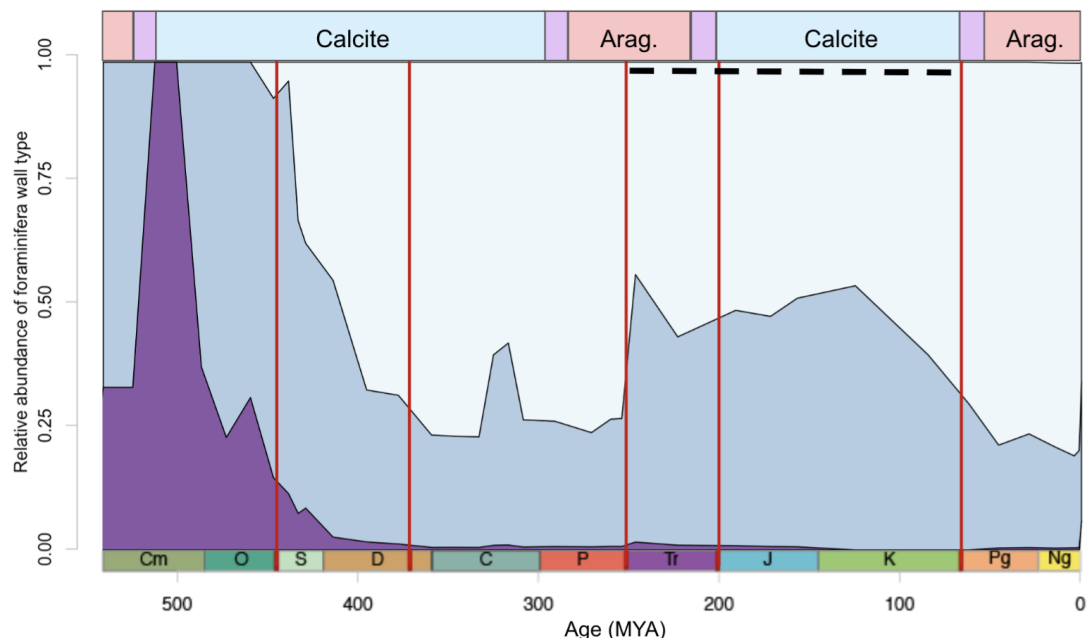


Figure 3. Relative abundance (percent) of foraminiferal wall types throughout the Phanerozoic Eon; transitions between calcite and aragonite seas are indicated at the top of the figure; light blue = Calcareous, dark blue = Agglutinated, purple = Organic. Red indicates the “Big Five” mass-extinction events (Raup and Sepkoski, 1982), and the dotted line indicates the approximate duration of the MMR.

Mesozoic Era

The MMR is a period of increased CaCO_3 production and calcareous plankton and occurred throughout the Mesozoic (252 to 66 Ma) (Vermeij, 1977). From the Middle to Late Triassic (247-201 Ma), total diversity increased from 62 to 103 genera (Fig. 1). Both calcareous and agglutinated genera increased in diversity, and calcareous foraminifera became the most abundant (by number of genera) again by the Late Triassic (Fig. 2). At the Triassic/Jurassic mass-extinction event, foraminifera diversity had a net increase of 11 genera; like the end-Ordovician mass extinction, agglutinated diversity increased (67 to 71 genera) (Fig. 1). At this time, aragonite seas began transitioning to calcite seas (Fig. 1).

After the Triassic/Jurassic extinction, foraminiferal diversity steadily increased throughout the Jurassic and Cretaceous. Agglutinated wall types grew in proportional abundance and reached a local maxima of 54% of total diversity by the Lower Cretaceous (145-105 Ma). This slight increase in agglutinated genera through time corresponds with Cretaceous Oceanic Anoxic Events (e.g., Schlanger and Jenkyns, 1976; Leckie et al., 2002; Jenkyns, 2010); however, the epoch-level resolution of this data makes it hard to ascribe trends associated with these changes.

While the net effect of the Triassic/Jurassic extinction was neutral for calcareous foraminifera, their relative proportion decreased (Figs. 1, 2). Meanwhile, agglutinated foraminifera had a net increase of 11 genera (44 to 55 genera) and became more proportionally abundant (Figs. 1, 2).

During the Middle Jurassic to Early Cretaceous (174.1 to 100.5 Ma) foraminifera diversity nearly doubled in 74 Ma (142 to 288 genera). The diversities of both agglutinated and calcareous wall

types increased, and their relative abundances were nearly even (Fig. 2). Although planktic foraminifera evolved in the Jurassic (Hart et al., 2003), these organisms did not noticeably impact the total foraminiferal diversity until the Cretaceous, and even then the vast majority of genera were benthic (Fig. 4). With little oceanic crust preserved before the Jurassic (Müller et al., 2008), the record of planktic foraminifera is especially limited. During the Late Cretaceous diversification, calcareous foraminifera increased rapidly and became the dominant form throughout the rest of the Mesozoic and Cenozoic (Fig. 2).

At the end-Cretaceous, there was a 38% net decrease in foraminifera diversity (470 to 291 genera), and agglutinated diversity was nearly halved (Fig. 1). While the relative proportion of agglutinated foraminifera decreased from 40% to 29%, calcareous shells increased proportionally from 60% to 70% (Fig. 2). Moreover, the end-Cretaceous coincides with the transition from calcite to aragonite seas (Fig. 2).

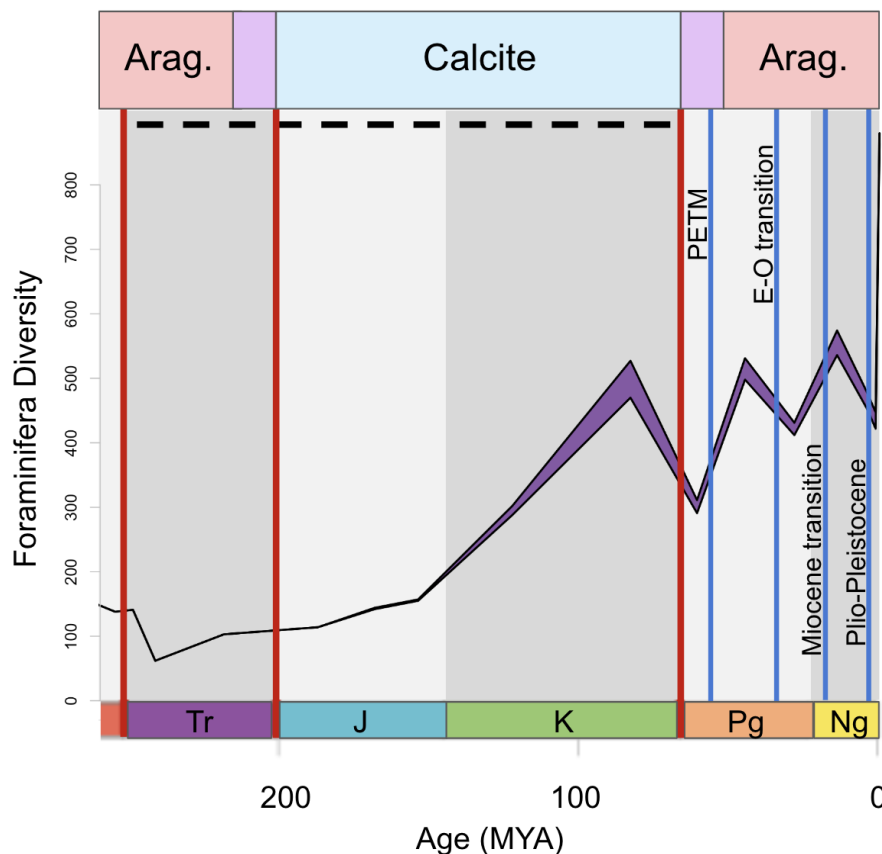


Figure 4. The diversity of foraminifera throughout the Mesozoic and Cenozoic based on Loeblich and Tappan (1988). The purple subset represents the number of planktic genera, whereas the rest of the diversity curve represents benthic foraminifera. Red lines indicate the “Big Five” mass-extinction events (Raup and Sepkoski, 1982), the perforated line represents the mid-Mesozoic, and the blue lines represent Cenozoic warming and cooling events (left to right: Paleocene-Eocene Thermal Maximum (PETM), Eocene-Oligocene (E-O) Transition, Miocene Climate Transition, and the Pliocene/Pleistocene boundary).

Cenozoic Era

During the Cenozoic, climate swings led to a multitude of warming events or intervals (e.g., Paleocene-Eocene Thermal Maximum, the Early Eocene Climate Optimum, the Middle Eocene

Climate Optimum, and the Miocene Climate Optimum) and cooling events (e.g., Eocene/Oligocene boundary, the Middle Miocene Climate Transition, and the Mid-Pleistocene Transition). Despite the rapid fluctuations between cold and warm climate throughout the Quaternary, the Eocene through the Pleistocene (56 Myr) maintained a constant relative ratio of foraminifera wall types (~80% calcareous and ~20% agglutinated) and the origination and extinction rates remained within their expected range (Figs. 2, 3).

Throughout the entirety of the Cenozoic Era, all origination rates occurred at an expected level, and extinction levels were lower than expected (Fig. 3). At the beginning of the Cenozoic, ocean chemistry once again switched from calcite to aragonite seas (Fig. 2); we remain in aragonite seas today. In the Paleocene Epoch, foraminiferal generic diversity had returned to pre-Cretaceous/Paleogene mass-extinction levels (498 genera) (Fig. 1). During the Paleocene-Eocene Thermal Maximum, there was a diversification from 291 to 498 genera over 32 Ma with a total of 359 originations and 213 extinctions (most of which were calcareous). There was a net decrease of 86 genera (77 of which were calcareous) during the Eocene-Oligocene transition to an icehouse climate (34 Ma). While the data resolution is not fine enough to distinguish diversity changes during the Middle Miocene Climate Transition (~14 Ma), total diversity (536 genera) is the highest of all Cenozoic epochs excluding the Holocene (Fig. 1). The increase in diversity comes solely from calcareous wall types, which have a net gain of 27 genera. After the Miocene, there was a net decrease in diversity of 85 genera (59 of which were calcareous). During the global cooling at the Plio-Pleistocene boundary (~5 Ma) total foraminiferal diversity decreased by 29 net genera; 18 of these genera had calcareous wall types.

From the Pleistocene to Holocene, there is a Pull of the Recent (Jablonski et al., 2003), which is associated with preservation bias. This is evident as diversity increases from 422 to 866 foraminifera (103% increase), which is likely biased by sample availability since geologic data is generally focused on the recent (Lloyd et al., 2012). The modern ocean contains 246 agglutinated genera (28%), 565 calcareous genera (65%), and 51 organic genera (6%).

Discussion

Foraminiferal diversity trends throughout the Phanerozoic

The early history of benthic foraminifera is difficult to decipher due to low sample abundance, but in general there is a gradual increase in diversity starting in the Cambrian and continuing through the Devonian. Undersampling of biotas from the Paleozoic is common (Tarver et al., 2007); this dataset's low organic-test diversity and disappearance and resurgence of agglutinated wall types during the Miaolingian and Furongian Epochs (509-485 Ma) may be related to preservation bias. The majority of the fossil record has only 1 organic genus, but the Holocene has 51 genera, which implies this may not be 100% of ancient diversity. Previous studies have recorded undersampling of biotas from the Paleozoic (Tarver et al., 2007); thus further, targeted research is needed to provide a more comprehensive review of Cambrian and Ordovician diversity.

Organic and agglutinated foraminifera were the most common forms through the Ordovician, with calcareous forms evolving in the Late Ordovician. Benthic diversity decreased on marine shelves during the end-Ordovician due to Gondwanan glaciation, lowering sea level, changing carbon cycle, and anoxia (Brenchley et al., 2001; Harper et al., 2014). While five foraminiferal genera went extinct during this event, my data suggests extinction rates were at an expected rate and origination rates were higher than expected (Figs. 1, 2). The benthic foraminifera's

elevated origination rates during the end-Ordovician mass extinction may be explained by the eustatic changes in sea level due to melting ice caps (Johnson & McKerrow, 1991). Agglutinated foraminifera diversify during sea-level rise (Kaminski et al., 2010), which tracks with the proportional turnover seen between organic and agglutinated wall types during this period (Figs. 1, 2).

Calcareous foraminifera's rapid origination and diversification throughout the Silurian and into the Devonian may be due to the greenhouse climate. Benthic foraminifera with CaCO_3 tests flourish in warmer climates (Greiner, 1969), which may explain how these genera became proportionally dominant within 61 Ma of their appearance (Fig. 2). Interestingly, there is an even number of originations and extinctions during the Upper Devonian biotic crisis (41 and 42 genera respectively), which may be due to stage-level averaging as fluctuations in warming and cooling occurred in the Frasnian and Fammenian (Kalvoda, 2006). Since benthic calcareous shells are sensitive to temperature changes, it is likely the radiations occurred during warming events while the extinctions occurred during cooling events.

The peak and trough in Carboniferous diversity (Figs. 2, 3) is similar to the foraminiferal abundance dynamics in Groves & Yue (2009). This may be explained by warming and cooling events during the Carboniferous. The peak in benthic foraminifera origination rates (Fig. 3) coincided with increasing oxygen and decreasing carbon in the atmosphere, signaling a greenhouse climate (Pfefferkorn et al., 2014). The shallow, warm waters and ocean circulation of the early Carboniferous allowed for the diversification of larger benthic foraminifera (BouDagher-Fadel, 2008), which may explain the 126 calcareous originations at the Lower Mississippian (Fig. 1, 3). In contrast, the icehouse climate in the mid-Carboniferous (Pfefferkorn et al., 2014) coincided with increased extinction rates and decreased calcareous shells (Figs. 2, 3). Agglutinated foraminifera are able to build tests in colder ocean temperatures (Greiner, 1969) compared to their calcareous counterparts, which may explain why 96 calcareous genera went extinct and agglutinated forms nearly doubled in proportional abundance (Figs. 1, 3).

Although the diversity of agglutinated forms remained stable throughout the Carboniferous-Permian Icehouse and transition into an aragonite sea (Fig. 1), the diversity of calcareous forms increased in the late Carboniferous and remained relatively high throughout the Permian, despite the end-Guadalupian (late Permian) extinction (Feng et al., 2020). The Permian/Triassic extinction selectivity may be due to the deoxygenation and high ocean acidification caused by the mass extinction (Erwin, 1990). The increase in extinction rates at the Permian/Triassic mass extinction (Fig. 3) and selectivity against calcareous wall types (Figs. 1, 2) coincided with general extinction selectivity against carbonate skeletons and the extinction of fusulinid foraminifera (Payne et al., 2007; Groves & Altiner, 2005). Unlike the Devonian's longer-term biotic crisis, the end-Permian is a geologically brief mass extinction. Due to enhanced anoxia and ocean acidification, this event was selective against larger carbonate producers, such as large benthic foraminifera (Dal Corso et al., 2022), which explain the sudden and substantial change in calcareous foraminifera (Fig. 2). While the epoch-level time scale is too large to view this punctuated event in detail, the extinction rate is much more distinct compared to slower mass-extinction events like the Upper Devonian biotic crisis (Figs. 1, 2, 3).

In contrast to the Permo-Triassic mass extinction, the end-Triassic extinction appears to have little impact on the diversity of either agglutinated or calcareous benthic foraminifera (Figs. 1, 2, 3, 4). The Triassic/Jurassic extinction event is linked to widespread volcanism, increased atmospheric carbon, and increased ocean acidification (Hallam, 1990). Despite these global phenomena, the Triassic/Jurassic does not indicate any major changes, and total diversity increased across the boundary (Fig. 1). Of the five mass extinction events, the Triassic/Jurassic

extinction had the lowest impact on marine ecology (Muscente et al., 2018). Although the majority of the marine ecosystem was not impacted by this extinction, reef communities did experience restructuring at the end-Triassic (Muscente et al., 2018), which may explain the proportional decrease and higher extinction levels of benthic calcifiers at this interval (Fig. 1, 3).

An increase in agglutinated genera during the end-Triassic complements the agglutinated generic richness described by Kaminski et al. (2010). At the same time, calcareous foraminifera were diversifying (Fig. 1), and as generic diversity increased throughout the end-Triassic and Jurassic (92 Ma), agglutinated and calcareous shells both maintained 50% relative proportion (Fig. 3). The upward trajectory of benthic genera (Fig. 1) and the 1:1 proportional ratio of shell types (Fig. 3) implies that all foraminifera were diversifying during this period. Moreover, extinction rates are lower than expected (Fig. 3), which may be due to a slower extinction over time (Hallam, 2002).

The Cretaceous Period is of particular interest because it is one of the largest intervals of steady diversification (288 to 470 genera throughout the Cretaceous), which may be due to the warming and ocean acidification events. The shift in proportional abundance toward calcareous foraminifera during the Late Cretaceous is likely due to the evolution of pelagic calcifiers (Henehan et al., 2016; Ridgwell, 2005). This increase of calcareous shells during the MMR is likely caused by the evolutionary arms race associated with predation and increasing calcium-carbonate shells (Vermeij, 1977). Cretaceous pelagic calcification rapidly increased and stabilized the carbonate cycle (Hull, 2017). Moreover, increased calcium and alkalinity in the Cretaceous seawater may have allowed for increased precipitation of CaCO_3 (Arvidson et al., 2014), which may explain the high diversity of calcareous benthic foraminifera (Fig. 3). Although this data's resolution is too broad for shorter-term changes in the Mesozoic (e.g., ocean anoxic events), it is clear from the originations and extinctions (Figs. 1, 2) that environmental perturbations led to ecological turnovers within the epochs.

The end-Cretaceous is the most recent major mass extinction and was caused by a bolide impact (e.g., Schulte et al., 2010). The foraminiferal response to the Cretaceous/Paleogene (K/Pg) mass extinction was similar to the end-Devonian mass extinction because it was one of the few times throughout the Phanerozoic (outside the end-Triassic) that I see calcareous tests proportionally increase after a mass-extinction event (Fig. 2). The origination and extinction rates (Fig. 3) support previous work (e.g., Culver, 2003; Alegret & Thomas, 2013) suggesting extinctions were not as significant during the K/Pg, but benthic diversity still clearly decreased (Fig. 4). The 331 generic extinctions across the boundary and a decrease in agglutinated tests confirm the suggestions within Lowery et al. (2020) and Culver (2003) that agglutinated wall types were more vulnerable to this event compared to calcareous tests.

The rise of calcareous forms may be due to the severe but brief nature of this extinction event (Smit & Hertogen, 1980); unlike previous mass-extinction events, the K/Pg extinction resulted from the Chicxulub bolide (e.g., Pope et al., 1994; Henehan et al., 2019). While this event may have initially impacted benthic calcifiers, these organisms likely stabilized due to the surplus of organic detritus on the shelf and deep sea during this period, which would provide opportunities for calcareous forms to diversify after the extinction event (Alegret & Thomas, 2013). Moreover, the abundance of pelagic calcifiers allowed benthic calcifiers to become more resilient to ocean acidification since carbonate saturation was more established (Hull, 2017; Henehan et al., 2019), which suggests that calcareous forms are not always sensitive to abrupt mass-extinction events as long as there is a saturation of carbonate for test construction. Similar to the end-Permian, this punctuated biotic crisis is more difficult to distinguish at the epoch level compared to slower events, but the change is especially clear for larger benthic foraminifera

(Macleod et al., 1997; Brasier & Larwood, 1988). There have been significant improvements in records of planktic foraminiferal diversity (in terms of both temporal and taxonomic resolution) since Loeblich and Tappan (1988), see Fraass et al. (2015) for a detailed discussion of planktic foraminiferal macroevolutionary trends.

Despite rapid warming and cooling intervals, origination and extinction rates during the Cenozoic (Figs. 2, 3) are relatively stable and within expected ranges, which supports previous work documenting stable foraminiferal communities (e.g., Alegret et al., 2021; Thomas, 2007). During the Eocene, large benthic foraminifera began to expand latitudinally (BouDagher-Fadel, 2008), and the mixing of ocean water as the Southern Ocean passages opened (Cramer et al., 2009) may have led to more global resilience to changes in paleotemperature, including the ability to expand and contract zonation (Berggren & Miller, 1989). Moreover, the carbonate cycle's stabilization during the MMR likely made calcareous foraminifera more resilient to environmental perturbations by the Cenozoic (Hull, 2017; Henehan et al., 2019). While there is a Pull of the Recent, it should be noted that the sharp changes are not significant (Fig. 3) and are likely biased by preservation and sample availability.

Phanerozoic Trends in Ocean Chemistry and their Impact on Foraminifera

Calcium carbonate's precipitated polymorph is controlled by the transitions between calcite and aragonite seas (Hardi, 2003). Although calcite is more stable (Sun et al., 2015), the magnesium content in today's seawater is preferential to aragonitic precipitation. Additionally, calcite exhibits a co-precipitation with aragonite at 20°C temperatures, but calcite is unable to precipitate when aragonite seas are warmer than 20°C (Balthasar & Cusack, 2015). Despite this, there are no clear transitional patterns seen between calcite/aragonite seas and the diversity of foraminifera (Figs. 1, 3).

Ocean acidification has the potential to influence the biotic composition of reef ecosystems (KieSSLing, 2009), but the overall impact of acidification on marine calcifiers has proven variable (Ries, 2009). This variability is seen throughout my data, as some intervals of ocean acidification lead to high extinction rates (e.g., Permo-Triassic mass extinction) while others do not (e.g., end-Triassic mass extinction) (Fig. 3).

While reef-forming organisms appear particularly susceptible to ocean acidification, pelagic calcifiers like planktic foraminifera, calcareous nannoplankton, and pteropods appear to be more resilient (e.g., Leung et al., 2022). My data provides evidence that Mesozoic and Cenozoic benthic calcifiers may also be more resilient, as calcareous forms were resilient during the end-Cretaceous and Cenozoic (Figs. 2, 3). This tracks with Jurassic to Recent extinction rates of planktic foraminifera and calcareous nannoplankton, which do not appear to be driven by ancient changes in pH (e.g., Lowery et al., 2020).

The rapid increase in $p\text{CO}_2$ levels associated with the end-Permian volcanic eruptions would have put reef builders like fusulinids at a disadvantage as the carbonate saturation state would have been reduced (Hönisch, 2012). Calcareous shells are more fragile when calcium carbonate is undersaturated (Corliss & Honjo, 1981), which may explain the extreme sensitivity of calcareous benthic foraminifera at the Permian/Triassic mass extinction (Figs. 1, 2, 3). These findings suggest that with rapidly increasing $p\text{CO}_2$ levels in the atmosphere, benthic reef builders and calcareous organisms are likely to decrease.

Similar to the end-Permian mass extinction, the Triassic/Jurassic extinction was likely caused by a series of pulsed volcanism associated with the Central Atlantic Magmatic Province (Percival et

al., 2017, Blackburn et al., 2013). The emplacement of these flood basalts caused $p\text{CO}_2$ levels to spike (Schaller et al., 2011; 2012) and ocean acidification to increase (Greene et al., 2012), which impacted reef communities (Martindale et al., 2012), and the calcareous foraminifera living in them. However, unlike the Permian-Triassic mass extinction, the Triassic/Jurassic extinction rate is much lower and at expected levels (Fig 2). This difference is likely due to the difference in $p\text{CO}_2$ levels. At the Permian-Triassic mass extinction, $p\text{CO}_2$ levels increased 6-fold (Wu et al., 2021), which would have led to ocean acidification and deoxygenation. While the Central Atlantic Magmatic Province was still detrimental to 50% of marine life (Ruhl et al., 2011), the impact on $p\text{CO}_2$ levels was smaller. This suggests the magnitude of $p\text{CO}_2$ change may play a role in foraminiferal biodiversity.

The MMR restructured the community of shallow marine benthic organisms and the coevolution between predator and prey (Buatois & Mángano, 2016). During this period, planktic foraminifera emerged from the fossil record (Fig. 4). The diversification of planktic foraminifera and calcareous nannoplankton provided a second oceanic sink and stabilized the carbonate cycle (Hull, 2017). Interestingly, the origination and extinction rates at the mid-Mesozoic are lower than expected despite the Cretaceous having high levels of origination and extinction (Fig. 3).

Despite foraminiferal diversity increasing throughout the Cenozoic, the proportion of wall types remains consistent (Figs. 1, 2, 3, 4); this is surprising since multiple rapid warming and cooling events occurred throughout the Cenozoic, which would be expected to impact calcareous taxa. As stated above, the MMR and the evolution of pelagic calcifiers provided saturation of carbonate in the oceans (Hull, 2017), so it is likely that benthic organisms are more resilient to rapid warming and cooling events in the Cenozoic. These findings provide new information about the relative stability of Cenozoic foraminifera wall types compared to their rapidly increasing diversity.

Conclusion

The dataset presented here shows the unique responses that foraminifera have to mass extinctions and changes in ocean chemistry through the Phanerozoic Eon. The majority of foraminiferal diversity trends are driven by changes in the diversity of the benthic foraminifera; planktic foraminifera do not noticeably influence trends until the Late Jurassic. The biodiversity of benthic foraminifera and the shifts in test types are tied to both short- and long-term oceanic and atmospheric fluctuations. Foraminiferal diversity only noticeably decreases after the end-Permian and end-Cretaceous mass extinctions, and calcareous foraminifera appear to stabilize their proportional abundance prior to the evolution of pelagic calcifiers. Planktic foraminifera and large benthic foraminifera are more impacted by the K/Pg mass extinction compared to smaller benthic foraminifera, which is likely due to more detritus when the sun is less available. Moreover, Cenozoic diversity fluctuates at an expected range throughout the Cenozoic, which may be due to the stabilization of the carbonate compensation depth.

One limitation of these findings is their temporal scale. The epoch-level data makes interpretation of short-term oceanic anoxic events and punctuated extinctions difficult. A higher resolution dataset may highlight important events that occurred at the stage level and thus would be necessary to determine how smaller scale events impact benthic foraminiferal diversity.

Seas	Era	Period	Epoch	Bottom (MVA)	Top (MVA)	Total genera	agglutinated	agglutinated %	calcareous	calcareous %	organic	organic %	originations	calc orig	agg orig	extinctions	calc extinct	agg extinct	
Aragonite	Cenozoic	Quaternary	Holocene	0.0117	0	863	246	28.51%	565	65.47%	51	5.91%	442	231	158	-	-	-	
			Pleistocene	2.58	0.0117	422	84	19.91%	335	79.38%	2	0.47%	7	4	3	1	1	0	
		Neogene	Pliocene	5.333	2.58	451	85	18.85%	363	80.49%	2	0.44%	42	42	0	36	32	4	
			Miocene	23.03	5.333	536	111	20.71%	422	78.73%	2	0.37%	168	145	20	127	101	26	
			Oligocene	33.9	23.03	412	96	23.30%	314	76.21%	2	0.49%	74	58	16	44	37	7	
		Paleogene	Eocene	56	33.9	498	105	21.08%	391	78.51%	2	0.40%	260	221	30	160	135	20	
			Paleocene	66	56	291	87	29.90%	204	70.10%	0	0.00%	99	77	20	53	34	19	
		Cretaceous	Upper	100.5	66	470	188	40.00%	282	60.00%	0	0.00%	302	208	90	278	155	113	
			Lower	145	100.5	288	156	54.17%	132	45.83%	0	0.00%	177	77	93	120	58	58	
			Upper	163.5	145	155	79	50.97%	75	48.39%	1	0.65%	40	16	22	44	20	22	
Calcite	Mesozoic	Jurassic	Middle	174.1	163.5	142	67	47.18%	74	52.11%	1	0.70%	42	26	16	27	15	12	
			Lower	201.3	174.1	114	55	48.25%	58	50.88%	1	0.88%	62	39	21	14	10	4	
		Triassic	Upper	237	201.3	103	44	42.72%	58	56.31%	1	0.97%	48	36	10	51	39	10	
			Middle	247.2	237	62	34	54.84%	27	43.55%	1	1.61%	22	17	5	7	5	2	
		Lower	251.902	247.2	141	37	26.24%	103	73.05%	1	0.71%	3	2	1	101	43	8		
Aragonite		Permian	Lopingian	259.1	251.902	138	36	26.09%	101	73.19%	1	0.72%	56	29	0	0	0	0	
			Guadalupian	272.95	259.1	158	37	23.42%	120	75.95%	1	0.63%	14	5	0	76	21	0	
		Carboniferous Pennsylvanian	Cisuralian	298.9	272.95	144	37	25.69%	106	73.61%	1	0.69%	86	20	5	0	0	0	
			Upper	307	298.9	165	43	26.06%	121	73.33%	1	0.61%	68	13	4	107	49	10	
			Middle	315.2	307	99	41	41.41%	57	57.58%	1	1.01%	0	0	0	2	0	2	
	Paleozoic	Carboniferous Pennsylvanian	Lower	323.2	315.2	105	41	39.05%	63	60.00%	1	0.95%	22	10	12	6	6	0	
			Upper	330.9	323.2	194	44	22.68%	149	76.80%	1	0.52%	5	4	1	111	96	13	
		Carboniferous Mississippian	Middle	346.7	330.9	189	43	22.75%	145	76.72%	1	0.53%	0	0	0	0	0	0	
			Lower	358.9	346.7	191	44	23.04%	146	76.44%	1	0.52%	151	126	19	2	1	1	
		Calcite		Devonian	Upper	382.7	358.9	82	25	30.49%	56	68.29%	1	1.22%	41	31	9	42	38
Middle	393.3				382.7	61	19	31.15%	41	67.21%	1	1.64%	28	27	1	20	16	4	
Silurian	Lower			419.2	393.3	38	20	52.63%	17	44.74%	1	2.63%	12	7	4	5	3	2	
	Pridoli			423	419.2	35	19	54.29%	13	37.14%	3	8.57%	0	0	0	9	4	3	
	Ludlow			427.4	423	40	24	60.00%	13	32.50%	3	7.50%	19	12	7	5	0	5	
		Ordovician	Wenlock	433.4	427.4	26	22	84.62%	1	3.85%	3	11.54%	6	0	6	5	0	5	
			Llandovery	443.8	433.4	27	21	77.78%	2	7.41%	4	14.81%	16	2	12	7	1	5	
			Upper	458.4	443.8	16	11	68.75%	0	0.00%	5	31.25%	5	0	3	5	0	2	
		Cambrian	Middle	470	458.4	13	10	76.92%	0	0.00%	3	23.08%	5	0	5	2	0	2	
			Lower	485.4	470	8	5	62.50%	0	0.00%	3	37.50%	7	0	5	0	0	0	
Aragonite		Furongian	Maolingian	497	485.4	1	0	0.00%	0	0.00%	1	100.00%	0	0	0	0	0	0	
			Series 2	509	497	1	0	0.00%	0	0.00%	1	100.00%	0	0	0	0	0	0	
			Terreneuvian	521	509	3	2	66.67%	0	0.00%	1	33.33%	0	0	2	0	2	0	
					Series 2	541	521	3	2	66.67%	0	0.00%	1	33.33%	3	0	2	0	0
					Terreneuvian	541	521	3	2	66.67%	0	0.00%	1	33.33%	3	0	2	0	0

Appendix

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