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Morphological innovation did not drive biodiversification in Mesozoic brachiopods

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Abstract

Over long spans of geological time, various groups of organisms may wax and wane, experiencing times of apparent success and contraction. These rises and falls are often said to reflect either opportunities created by climate change or the relative success of innovative characteristics. The Phylum Brachiopoda was one of the most successful marine clades before the Permian-Triassic mass extinction (PTME), but after this event, they became marginal components of marine communities through to the present day. How brachiopod morphological innovations reacted to swiftly declining diversity has long remained poorly understood. Here we analyse morphological evolution over the 300 Myr (Permian–Holocene) history of the four major Mesozoic brachiopod orders. Unexpectedly, their disparities reached or exceeded pre-PTME levels, but were decoupled from species richness, which was generally lower. Distribution of taxa in morphospace and shifts in centroid indicate that all the four orders exploited new morphospaces when adapting to post-Permian environments. Comparison of morphospace occupation and diversity evolution suggests that the high extinction rate of brachiopods and the limited diversification of new forms may have

accounted for the depauperate nature of modern-day brachiopods.

Introduction

Biologists and palaeobiologists often refer to ‘success’ in evolution, by which they mean the achievement by a clade of high species richness, high abundance, and great breadth of morphological-functional adaptation. Among modern organisms, mammals, birds, molluscs, and angiosperms might be said to be successful against all those metrics. On the other hand, turtles, crocodylians, brachiopods, and ginkgos might be said to be less successful because of currently lower species numbers, lower global abundance, and more restricted functional and ecological diversities. In comparing so-called ‘successful’ and ‘unsuccessful’ clades, comparative studies often select pairs of close relatives, such as crocodylians and birds, that shared a single common ancestor, in this case some 252 million years ago (Ma) in the Triassic and ask why birds today comprise more than 10,000 species, and yet their sister clade, crocodylians, include ~25 extant species (Mannion et al., 2015; Stubbs et al., 2021; Payne et al., 2023). Among marine organisms, brachiopods and bivalves, are often taken as a pairing (Steele-Petrović, 1979; Gould and Calloway, 1980; Thayer, 1985; Sepkoski Jr, 1996; Payne et al., 2014; Liow et al., 2015; Guo et al., 2023), not because they shared a close common ancestor but because of many shared anatomical and functional features (Steele-Petrović, 1979). The classic story has been that brachiopods dominated seabeds until the Permian-Triassic mass extinction (PTME), ~252 Ma, and then bivalves took over in the Triassic (Fraiser and Bottjer, 2007). This has frequently been explained by substantial loss of ecospace by brachiopods to bivalves (Steele-Petrović, 1979; Thayer, 1985; Sepkoski Jr, 1996; Liow et al., 2015), and the current marginal role of brachiopods in world oceans seems to bear this out. But is this true?

The Phylum Brachiopoda originated in the Cambrian, survived the ‘Big Five’ mass extinctions (Raup and Sepkoski Jr, 1982; Marshall, 2023), and persists in today’s oceans (Carlson, 2016). They were the most abundant benthic invertebrates occupying most habitats in oceans before the Mesozoic. After the PTME, brachiopods

lost diversity dominance and became marginal components of marine communities in Meso-Cenozoic oceans (Carlson, 1991; Sepkoski Jr, 2002; Chen et al., 2005b, a; Clapham et al., 2006) (Fig. 1). The remarkable switch from brachiopods to bivalves across the PTME, and the permanent reduction in diversity of Meso-Cenozoic brachiopods, have long intrigued palaeobiologists and biologists (Stanley, 1974; Steele-Petrović, 1979; Thayer, 1979; Gould and Calloway, 1980; Valentine and Jablonski, 1983; Thayer, 1985; Sepkoski Jr, 1996; Zezina, 2008; Liow et al., 2015; Guo et al., 2023). However, most previous studies interpreted this switch in terms of taxonomic diversity alone and assumed that brachiopods lost out in some way in competition with bivalves. A consequence of such a view would be that post-Permian functional diversity of brachiopods, represented by morphospace occupation, should be much reduced or show little evidence of innovation and novel adaptation, suggesting that brachiopods were squeezed into a reduced number of perhaps marginal niches by the success of the bivalves in and after the Triassic.

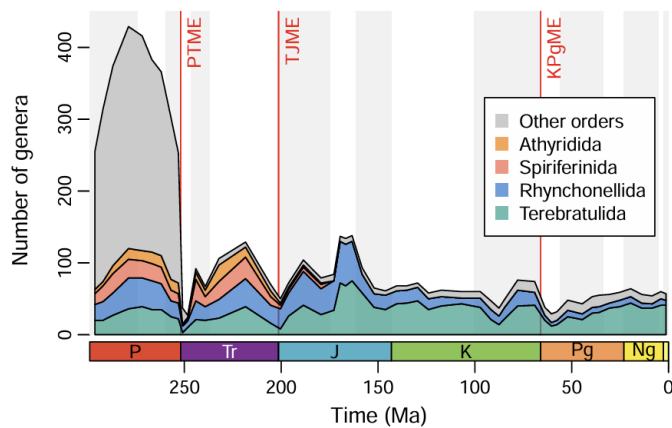


Fig. 1. Diversity of Permian–Holocene brachiopods. The four orders analysed in this study comprise the majority of the post-Permian brachiopod diversity. Abbreviations: P Permian, Tr Triassic, J Jurassic, Ear. Jura. Early Jurassic, K Cretaceous, Pg Paleogene, Ng Neogene, PTME Permian-Triassic mass extinction, TJME Triassic-Jurassic mass extinction, KPgME, Cretaceous-Paleogene mass extinction.

Morphological disparity, which describes the diversity of morphology in a clade

(i.e., ‘morphological diversity’), is an important complement to taxonomic diversity to depict the evolutionary dynamics of organisms (Erwin, 2007). Although the two metrics may be coupled or decoupled through time (Foote, 1993; Foote, 1994; Foote, 1996, 1999; Villier and Korn, 2004; Bapst et al., 2012; Korn et al., 2013; Benton et al., 2014), it is often seen that morphological innovation brings functional innovation and ecological opportunities to animals, paving the way for the upcoming taxonomic diversification (Anderson et al., 2011; Dumont et al., 2012; Stubbs and Benton, 2016; Novack-Gottshall et al., 2022). In the history of the Earth, many clades rapidly accumulated great diversity at the beginning of their evolutionary history or swiftly recovered after mass extinctions, along with the expansion of their morphological range (i.e., the early burst model) (Foote, 1994; Hughes et al., 2013). However, there are also some clades whose diversity never returned to pre-extinction levels such as the post-Permian brachiopods, and whether their apparent lack of success was limited by their morphological disparity remains unknown.

Although discussed for a long time, the evolution of brachiopod morphology remains poorly understood (Ciampaglio, 2004). Previous studies on brachiopod disparity generally focused on one of the relatively small articulate (Harper and Gallagher, 2001; Sclafani et al., 2018; Guo et al., 2020) or inarticulate orders (Smith and Bunje, 1999; Liang et al., 2023). Ciampaglio (Ciampaglio, 2004) first investigated the Phanerozoic disparity of articulate brachiopods and unravelled a partially recovered and volatile disparity among post-Permian taxa, but the numbers of taxa sampled and the characters analysed were rather small.

Here we compile a large, comprehensive morphological dataset and analyse disparity over the ~300 Myr (Permian–Holocene) history of >1000 genera belonging to four major orders of Meso-Cenozoic brachiopods (Terebratulida, Rhynchonellida, Spiriferinida, and Athyridida). Their total genus richness accounts for more than 90% of all post-Permian brachiopods, thus providing a nearly complete picture of morphological evolution of the entire phylum. This study aims to provide new insights into several questions. First, we employed two disparity metrics, sum of variances (SOV) and sum of ranges (SOR) to quantitatively measure overall

morphological variations of the Meso-Cenozoic brachiopods and to assess their coupling or decoupling relationships with diversity measures represented by genus richness. Second, we examine how the PTME, Triassic-Jurassic mass extinction (TJME) and Cretaceous-Paleogene mass extinction (KPgME) and their recovery processes regulated morphological evolution of the post-Permian brachiopods. Finally, co-variation of disparity, biodiversity, and morphospace occupation offers new insights into the drivers responsible for the depauperate nature of present-day brachiopods.

Results

Disparity and diversity in post-Permian brachiopods through time

The Terebratulida, characterised by a loop-shaped lophophore, is the largest order (in terms of taxonomic diversity) among post-Permian brachiopods and is also the most diverse brachiopod clade in today's oceans (Lee et al., 2006). Our analyses reveal that terebratulide disparity (SOV) shows an overall increasing trend from the Permian to Quaternary, and that this is decoupled from the overall diversity of the order, which has peaks and troughs, without a clear upward trajectory.

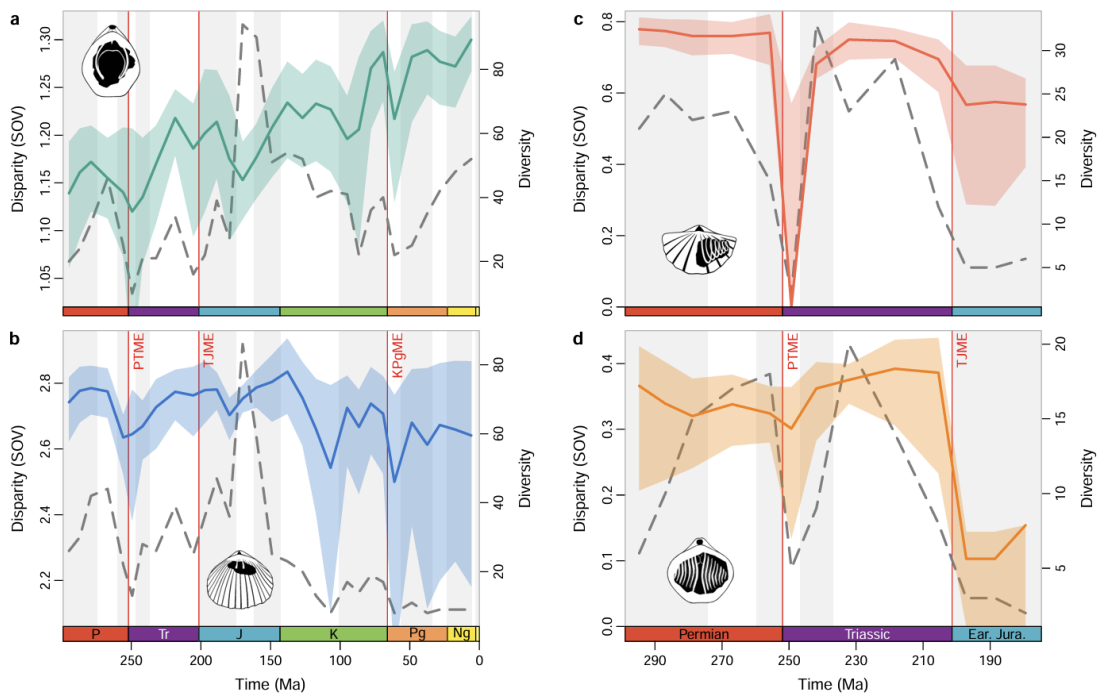


Fig. 2. Disparity and diversity of four brachiopod orders through time. Disparity is measured by sum of variances (SOV). The solid lines represent median value of the bootstrapped disparity. The envelopes indicate 95% confidence intervals (0.025 and 0.975 quantiles of bootstrapped values). Diversity (number of genera) is represented by dashed lines. **a**, Terebratulida; **b**, Rhynchonellida; **c**, Spiriferinida; **d**, Athyridida. Abbreviations: P Permian, Tr Triassic, J Jurassic, Ear. Jura. Early Jurassic, K Cretaceous, Pg Paleogene, Ng Neogene, PTME Permian-Triassic mass extinction, TJME Triassic-Jurassic mass extinction, KPgME, Cretaceous-Paleogene mass extinction.

Terebratulide disparity and diversity fluctuated through time (Fig. 2a). Disparity (SOV) shows major drops occurring in the Early Triassic, Middle Jurassic, early Late Cretaceous, and Paleocene. After each decline and in the Middle–Late Triassic, Late Jurassic, late Late Cretaceous, and Eocene, SOV rebounded rapidly to the pre-drop levels or even higher. The SOV is also rather low in the Middle Jurassic, but this low value is not caused by the small morphological range, but rather the rapid diversification of the Superfamily Loboidothyridoidea (Lee et al., 2006). Although the members of this superfamily possess diverse external characters, their internal morphologies show little variance (from a macroscopic perspective of the entire order), and these forms therefore gather in a small region in the upper-left corner of the morphospace, pointing to a low SOV value (Fig. 3a). Similarly, terebratulide SOR also exhibits a generally increasing trend (Extended Data Fig. 3) although the trend is more subtle. The broad confidence intervals (due to small sample size after rarefaction) make the significance difficult to confirm. After the PTME, terebratulide diversity surged to a very high level in the Middle Jurassic, and then returned to the Permian level during the Late Cretaceous. The Cenozoic witnessed a steady increase in diversity, but present-day diversity never returned to the mid-Jurassic level.

The crura-bearing Rhynchonellida is the second-largest order among the Mesozoic brachiopods. Their disparity (SOV) showed an overall increasing trend from Triassic to Jurassic, and then slightly declined in the mid-Cretaceous. From Late Cretaceous to Quaternary, a clear trend was not exhibited, but the confidence interval

was very wide (Fig. 2b). The evolution of SOV contrasts markedly with diversity, which massively decreased following the Jurassic, and remained constantly low to the present day, where this order is just a small subset of living brachiopods. More specifically, the rhynchonellide SOV peaked in the Early–Middle Permian, Late Triassic, Late Jurassic–earliest Cretaceous, and Late Cretaceous, and dropped in the Late Permian, Middle Jurassic, Middle Cretaceous and Paleocene. The SOR of this order shows a similar trend to the SOV (Extended Data Fig. 3), except for even lower values from the mid-Cretaceous to the present day.

The Spiriferinida, an order comprising some spire-bearing taxa, includes far fewer taxa than the first two orders, yet it is one of the major components of Triassic brachiopod faunas. Their taxonomic diversity, and SOV and SOR disparities all were severely affected by the PTME (Fig. 2c; Extended Data Fig. 3), but rapidly rebounded and finally reached the pre-extinction value in the Middle to Late Triassic. Diversity declined rapidly in the Rhaetian, before a further hit by the TJME. Disparity also followed this trend and gradually declined to a lower level. In Early Jurassic, these three metrics did not recover until this order was wiped out in the Toarcian (Vörös et al., 2016).

The Athyridida is another spire-bearing group that became extinct at the Toarcian Oceanic Anoxic Event (Early Jurassic) along with Spiriferinida (Baeza-Carratalá et al., 2015; Vörös et al., 2016). Athyridide SOV was almost unchanged across through the Permian-Triassic transition despite a notable drop in diversity. Their SOV rose through the Triassic, then sharply declined after the TJME, and then remained at low levels towards the final demise of this order in Early Jurassic (Fig. 2d). SOR shared a similar pattern to SOV, that is, a high value in the Permian and Triassic and an extremely low value in the Jurassic (Extended Data Fig. 3). After the PTME, athyridide diversity did not recover until the Carnian of Late Triassic when it surged significantly, followed by major drops in the Rhaetian (Late Triassic) and TJME, and then rather low levels in the Jurassic (Fig. 2d).

Morphospace occupation through time

The shifts of morphospace occupation in brachiopod genera can be directly observed in the morphospace (Fig. 3). However, for some datasets, the first few morphospace axes explain only a low proportion of variance and a great fraction of information is hidden on the other axes. Therefore, we also constructed a ‘morphospace centroid space’ to complement our visualization of results (see Methods) (Fig. 4), where the distribution of time bins in the centroid space displays the similarity of morphological composition in different bins. Overall, temporal trends of morphospace occupation show continued innovation through time despite reductions in diversity at major extinction events.

Terebratulides are unevenly distributed in morphospace (Fig. 3a). The morphospace areas occupied by short-looped and inner-hinge-plate-lacking taxa and by long-looped taxa have higher density, while other areas are less crowded (Fig. 3a). From the Triassic to Jurassic, taxa in these two areas diversified greatly, while those in the upper-central area gradually disappeared. Taxonomically, this pattern reflects the diversification of two major descendants of the Dielasmatoidea (i.e., the short-looped Loboidothyridoidea and long-looped superfamilies such as Zeillerioidea and Laqueoidea) and the extinction of the Dielasmatoidea itself. The Jurassic to Cenozoic occupation trend is characterised by the invasion of morphospace areas occurring in the lower part of the plot, which is occupied by taxa having a septal pillar and lacking hinge plates. The centroid space of Terebratulida shows that the centroids are widely separated in the Permian, Triassic, and Jurassic–Cenozoic intervals, indicating different morphological compositions. The Jurassic and Cenozoic centroids are also separated, but they are bridged by the Cretaceous ones, implying that morphology of present-day terebratulides has gradually changed since the Jurassic (Fig. 4a). The greatest shift in centroids of morphospace occupation occurred in the Early Triassic. Although the sample size is low in the Early Triassic, this shift is significant according to the result of the PERMANOVA test ($p < 0.05$) (Supplementary Information). Moreover, the greater distances of centroid spaces occur in the aftermaths of all three mass extinctions (Fig. 4a), implying that mass extinctions may have triggered distinct shifts in centroids and altered morphological compositions of

terebratulides.

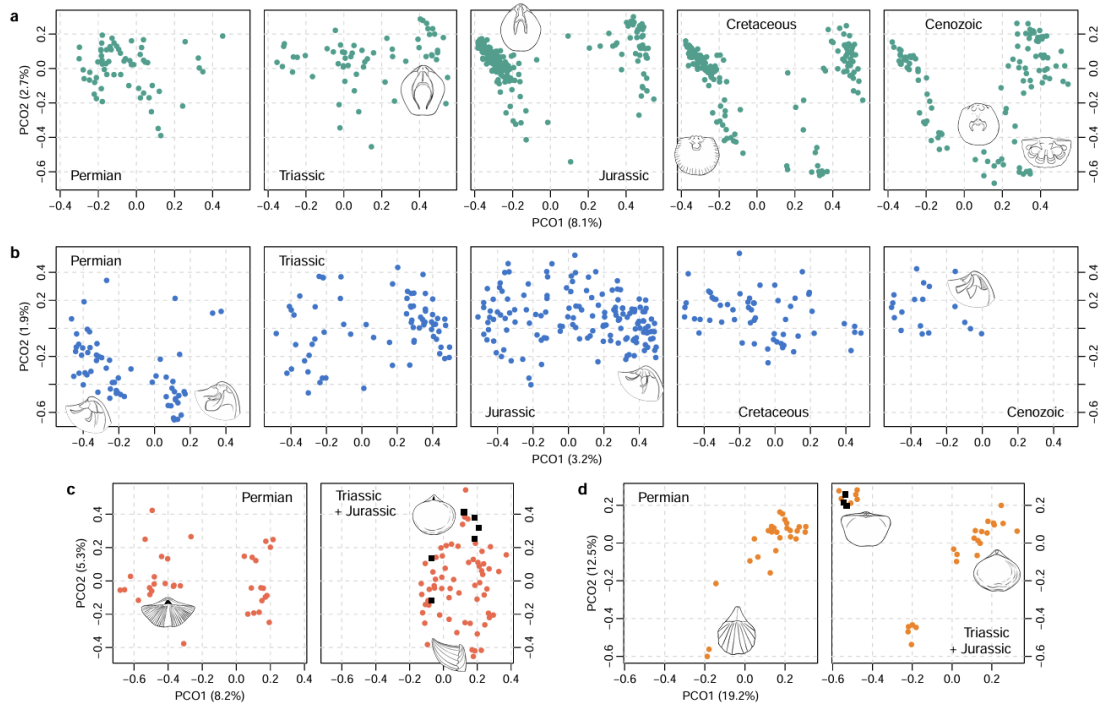


Fig. 3. Morphospace occupation of the four brachiopod orders through time. a, Terebratulida; **b,** Rhynchonellida; **c,** Spiriferinida; **d,** Athyridida. Morphospaces are constructed by the first two axes (PCO1 and PCO2). The number in labels indicates the percentage of variances explained by the axis. The black cubes in **c** and **d** represent Jurassic taxa. The cartoons (from left to right) in **a** represent long-looped, deltiform-looped and inner-hinge-plates-lacking, ring-like-looped, septal-pillar-bearing and loop-lacking, and septal-pillar-bearing and loop-floor-fused terebratulides, respectively. Those in **b** represent hinge-plates-fused, camarophorium-bearing, septalium-bearing-raducal, and septifal rhynchonellides, respectively. Those in **c** represent spiriferiform and median-septum-lacking, cyrtiniform, and reticulariiform spiriferinides, respectively. Those in **d** represent multicostate-punctate, concavoconvex, and bivoncx athyridides, respectively. Morphospace occupation variation in finer time bins see Extended Data Figs. 4–7.

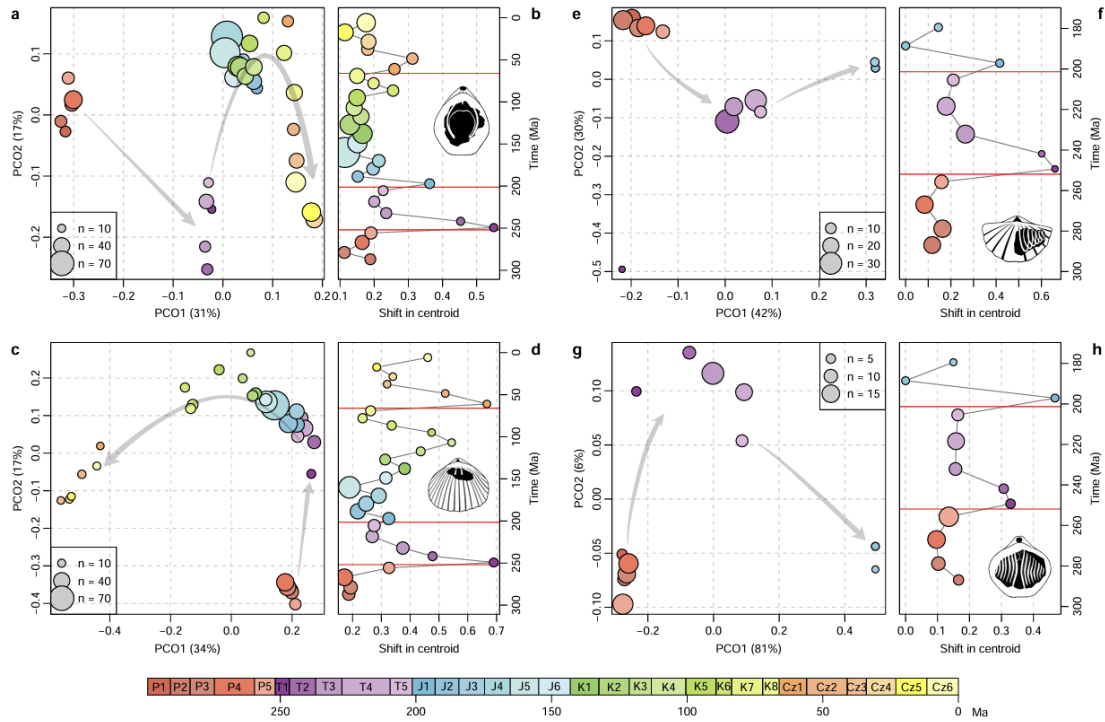


Fig. 4. Morphospace centroid spaces and shifts in centroid position of four brachiopod orders. **a, b**, Terebratulida; **c, d**, Rhynchonellida; **e, f**, Spiriferinida; **g, h**, Athyridida. Centroid spaces (**a, c, e, g**) are visualisations (using PCOA) of the distance matrix of centroids in morphospace, and are constructed from the first two axes (PCO1 and PCO2). Numbers in axis labels indicate the percentage of variance explained. The grey arrows indicate the trend of centroid movement in the centroid space. Shifts in centroid (**b, d, f, h**) indicate distance between centroids of one bin and its previous bin in the morphospace. In the plots of centroid space, the size of a dot is related to the diversity in that time bin. In the plots of centroid shifts, the size of a dot is proportional to the lower value of diversity in that bin and diversity in its previous bin (e.g., the size is proportional to 20 if diversities in that bin and its previous bin are 30 and 20, respectively). The larger the dot, the more reliable the shift because of larger sample size. The red lines represent mass extinctions. Abbreviations of time bin names see Methods. See Extended Data Fig. 8 for centroid spaces with bin names labelled.

For rhynchonellides, variations of morphospace occupation indicate that the previous areas were lost when new areas were explored. For instance, the Triassic–Jurassic septalium-bearing taxa fully exploited the middle-right area and the Jurassic–Cenozoic septifal taxa developed more in the left half region in the morphospace (Fig.

3b). Meanwhile, the lower part of the space (camarophorium-bearing taxa and hinge-plates-fused taxa) was unoccupied after the Permian, and the right areas were gradually lost from Cretaceous to Cenozoic. The centroid space of this order shows that the Permian centroids are clearly distinguished from those of other periods. From Triassic to Cenozoic, the centroid moved along the first principal coordinate axis, indicating a gradual transformation from Triassic morphologies to present-day ones, strengthened by shifts in the centroid. The most prominent shift in the centroid occurs in the Early Triassic despite rather high values also occurring in the Paleocene and Eocene, which, however, could be not reliable due to the limited sample size (Supplementary Information).

The Spiriferinida broadened morphospace and occupied new areas in the Triassic (Guo et al., 2020), while the previous morphospace occupied by the Permian superfamily Syringothyridoidea disappeared forever (Fig. 3c). In contrast, the Early–Middle Triassic athyridides re-thrived in the areas previously occupied by the Permian elements of the same order, and then greatly expanded to the upper-left corner by evolving concavoconvex forms in the Koninckinidina (Fig. 3d). Both spiriferinides and athyridids did not invade new morphospace in the Jurassic, and the Jurassic morphospaces are only a subset of their Triassic ones (Fig. 3c, d). Their morphospace centroids are separated from each other in the Permian, Triassic, and Jurassic (Fig. 4c, d). The Spiriferinida shows a distinct centroid shift after the PTME (the Early Triassic shift is doubtful due to the small sample size) (Fig. 4c), while the Athyridida shows a larger centroid shift after the TJME (Fig. 4d).

Discussion

Effect of mass extinctions on brachiopod morphology

Of the three Mesozoic mass extinctions, the PTME not only depleted diversity, but also regulated the distribution of morphospace (Figs. 1, 3, 4), and thus re-shaped brachiopod macroevolution (Chen et al., 2005a; Carlson, 2016). The Paleozoic orders (Productida, Spiriferida, Orthis, Orthida, and Dictyonellida) were not analysed in

this study, but it is obvious that these high-level groups and the associated morphologies were permanently eliminated by the PTME. It is noteworthy that although morphological compositions of the four surviving orders were altered by this mass extinction, their disparity values showed less long-term effect from the PTME. The disparity and diversity of both the Spiriferinida and Athyridida recovered to pre-extinction levels in the Triassic, and morphological innovations in Rhynchonellida and Terebratulida emerged and their disparities returned to pre-extinction levels in the early Mesozoic. In contrast, the TJME had little effect on the Rhynchonellida and Terebratulida, which both proliferated after the crisis. The other two orders suffered severe impacts from the Late Triassic events and TJME and fell into the state of ‘dead clade walking’ (Jablonski, 2002; Barnes et al., 2021) in both diversity and disparity, before their disappearance in the Early Jurassic. The TJME therefore had more prolonged impact on the Spiriferinida and Athyridida than the PTME. The KPgME did not significantly re-shape morphological evolution of terebratulides and rhynchonellides. It only accelerated the transition of morphological composition from the Cretaceous ones to the modern ones (Figs. 3, 4).

In addition to these mass extinctions, other environmental events (e.g., oceanic anoxia events in the Jurassic and Cretaceous) also caused diversity perturbations of brachiopods (Piazza et al., 2020; Baeza-Carratalá and Garcia Joral, 2020). However, they did not show significant effects on the morphological evolution of the four orders studied (Figs. 3, 4). A more detailed study in finer time bins might reveal their influence.

Morphological innovation in post-Permian brachiopods

Variations of the SOV, SOR, and morphospace occupation show that these four orders exhibit four different morphological evolution patterns. The Terebratulida steadily broadened new morphospace areas after the Triassic, and only a small part of the pre-occupied areas was lost. In contrast, the Rhynchonellida explored new morphospace in the Triassic and Jurassic, and frequently retreated from some previously occupied areas. The Spiriferinida rapidly diversified in morphology in the Triassic and took

over a great part of the morphospace of the Paleozoic Order Spiriferida, as demonstrated by Guo et al. (2020), while the Triassic athyridides largely inherited their Permian precursors' morphologies except for a major step of innovation introduced by the new Suborder Koninckinidina (Fig. 3).

Disparity analyses of many animal clades show pervasive early high disparity, that is animal clades tend to reach their maximum disparity relatively early in their evolutionary histories (Foote, 1994; Hughes et al., 2013). The pre-Permian taxa of the four orders are not analysed in this study, but according to the number of higher-level groups (i.e., suborders, superfamilies) (Kaesler and Selden, 1997-2007), such an early burst was not observed in at least three of these four Meso-Cenozoic orders. The Terebratulida and Spiriferinida reached their highest disparities in the Cenozoic and Late Triassic, respectively. The Athyridida, typical of Paleozoic orders, had high diversity in the Paleozoic, but the survival of two suborders through the PTME and the emergence of a new suborder in the Triassic elevated its disparity to a higher level. Rhynchonellides, originating in the Ordovician, were much more diverse in the Devonian than in the Mesozoic and evolved into several superfamilies at that time. Because we did not study the Devonian taxa, a direct comparison is impossible. In addition, the entire Brachiopoda had maximum disparity in the late Paleozoic (Ciampaglio, 2004). As a result, early high disparity was possibly not pervasive in brachiopods.

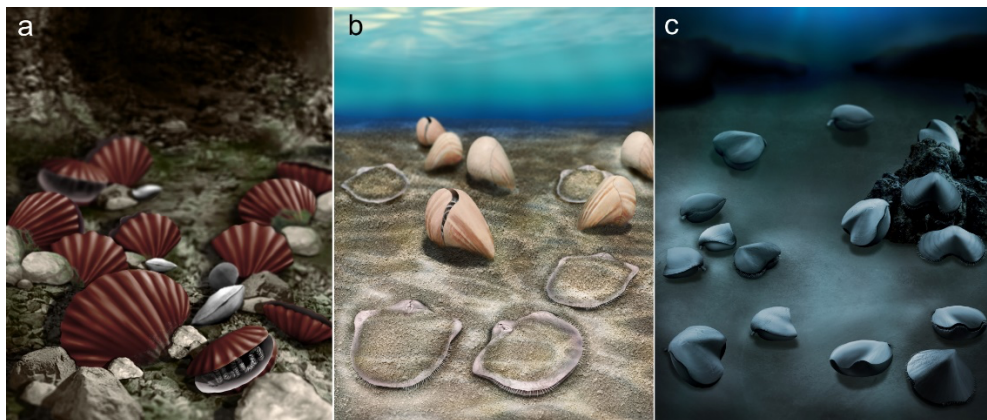


Fig. 5. Reconstructions of some post-Permian brachiopods, showing adaptations to

certain environments. a, small-sized terebratulides and tiny rhynchonellides living in shallow-water caves; **b**, concavoconvex athyridides and spiriferinides with high interarea adapted to soft substrates; **c**, smooth and usually sulcate rhynchonellides and terebratulides living in deep environments. Drawn by S.Y. Shi.

Each of the four orders displayed its own pattern of morphological evolution, but they all explored new morphospace areas. Rigorous statistical analysis of morphology and associated environments is difficult due to a lack of data for many genera, but there are several examples showing adaptations of post-Permian brachiopods to new environments (Fig. 5). For instance, the Athyridida had the most significant innovation in the emergence of the Koninckinidina, members of which are readily distinguished by having unique concavoconvex shells that are similar to the Paleozoic strophomenatans, indicating an infaunal lifestyle adapted to soft substrates (Stanley, 2020) (Fig. 5b). The Spiriferinida also possessed highly varied shell outlines and delthyrium covers during the Triassic, implying different ways to stabilize the shell bodies (Guo et al., 2020) (Fig. 5b). The rhynchonellides exhibit co-evolution between morphology and environments (Ager, 1965; Baeza-Carratalá and García Joral, 2020): the ribbed and raducal group often inhabits epicontinental seas, while the smooth and weakly ornamented taxa with arcuiform and septifal crura prefer to dwell in epi-oceanic or deeper environments (Baeza-Carratalá and García Joral, 2020). Together with these smooth rhynchonellides, terebratulides inhabiting deeper habitats also tend to be smooth-shelled and possess a unisulcate anterior commissure (Cooper, 1972; Vörös, 2005) (Fig. 5c). Another important morphological change of the Terebratulida is the retention of a septal pillar, like those in the Platidioidea, Kraussinoidea, and Megathyridoidea. In present-day oceans, many megathyridoids live in cryptic habitats, such as shallow-water caves or undersides of coral colonies (Logan, 2007) (Fig. 5a), and it was assumed that the low metabolic rates and low-energy lifestyles help these micromorphic brachiopods to survive in such nutrition-poor environments (Peck, 1992).

All lines of evidence indicate that after undergoing an evolutionary bottleneck at

the PTME, post-Permian brachiopods struggled to expand into new morphospaces, especially the vacated ecospace of the early Triassic (Ciampaglio, 2004), like the behaviours of molluscs and other elements of the modern evolutionary fauna (McGowan, 2004; Chen and Benton, 2012; Song et al., 2018).

Gould and Calloway (Gould and Calloway, 1980) hypothesized that brachiopods possess relatively less flexibility to modify their basic body plans than bivalves, probably limiting the ecological success of brachiopods. Unfortunately, a direct comparison between these two clades is not yet possible due to unavailability of the long-term disparity evolution trend of bivalves. However, the rise of a new brachiopod order, the Thecideida (not included in our analysis due to limited number of genera) in the Late Triassic, possibly does not support this hypothesis. Members of Thecideida show small size, a well-developed ventral interarea with pseudodeltidium, a lidlike dorsal valve, and a ventral cicatrix allowing for the cemented lifestyle. Internally, thecideids possess a prominent cardinal process, a pair of well-developed inner socket ridges, a variously developed median septum, and a pair of brachial lobes. These morphological features are so unique that only few characters are shared with other orders, making their phylogenetic relationships with other brachiopods controversial (Jaecks and Carlson, 2001; Baker, 2006). Also hotly debated is the systematic position of the Suborder Koninckinidina, although they are currently assigned to the Athyridida (Alvarez and Rong, 2002). These higher-level innovations provide further evidence for the evolvability in the post-Permian brachiopods.

Decoupling between morphospace and diversity evolution responsible for the depauperate nature of post-Permian brachiopods

Both morphospace occupation and diversity evolution trends of brachiopods clearly demonstrate a decoupling of the two. Apparently, morphospace increase often did not drive significant diversification of Meso-Cenozoic brachiopods (Figs. 2, 3). We propose that two kinds of mechanisms that are related to the extinction and the origination process, respectively, account for such decoupled evolution between morphospace and diversity. Firstly, as essential components of the 'Paleozoic

evolutionary fauna' (Sepkoski Jr, 1981), brachiopods intrinsically had a higher extinction rate than the 'Modern evolutionary fauna' such as bivalves (Stanley, 2007; Liow et al., 2015; Guo et al., 2023). Brachiopods were affected by various-scale extinction events more severely than molluscs, and many clades failed to survive to the present-day. In contrast, most bivalve families are extant, meaning that their statistical risk of extinction is less than that of brachiopods through time (Mondal and Harries, 2016). For instance, the Spiriferinida and Athyridida successfully recovered in the Triassic, but they experienced a high extinction rate in the Late Triassic and TJME (Vörös et al., 2016), and finally became extinct in a relatively small extinction event, the Toarcian Oceanic Anoxic Event. The Jurassic radiation of long-flanged deltiform terebratulides (Superfamily Loboidothyridoidea) and raducal rhynchonellides (superfamilies Rhynchonelloidea and Hemithiridoidea) are good examples of adaptive radiation (Losos, 2010). These forms were abundant and widely distributed in various settings in the Middle Jurassic (Ager, 1965), making this the highest level after the PTME for diversity of the entire phylum (Figs. 1, 3). However, the rather high extinction rate in the Middle–Late Jurassic (Guo et al., 2023) resulted in a drop in their diversity. The vast majority of families did not survive into the Cenozoic, and thus contributed little to the subsequent diversification of brachiopods. Why brachiopods are prone to extinction has been discussed for a long time. Some researchers suggested that the fixed lophophore of athyridides and spiriferinides is less advantageous during environmental stresses (Ager, 1987; Vörös et al., 2016). However, some spire-bearers (e.g., Athyridida, Spiriferida) were very successful in the late Paleozoic after a great number of extinctions. Moreover, the rhynchonellides and terebratulides without a fixed lophophore also experienced a high extinction rate in the Middle–Late Jurassic. Other hypotheses have been proposed, such as the diversification of predators and competition with bivalves, but they cannot explain the observed patterns (Guo et al., 2023).

Limited origination of some new brachiopod forms is probably another cause for failure in diversification of post-Permian brachiopods. For instance, three new terebratulid superfamilies having a septal pillar in adults (Platidioidea, Kraussinoidea,

and Megathyridoidea) occurred in the Cretaceous and Cenozoic, evidently broadening morphospace occupation (Fig. 3). Each superfamily, however, contains <10 genera (including fossil and living forms) (Lee et al., 2006), indicating a rather low origination efficiency of these new high-level classification units. Moreover, the morphologically unique Suborder Koninckinidina includes only nine genera; the new Order Thecideida, through an ~240-Myr evolution, only has about 40 genera. The taxonomic numbers of these two new high-level classification units of Mesozoic brachiopods are much lower than their Paleozoic morphological and ecological analogues (e.g., Productida and Strophomenida). In other words, adaptive radiation was not observed in these brachiopod clades, reinforcing that morphological innovation is independent of ecological opportunities and evolutionary success (Erwin, 2015; Jablonski, 2017).

Study limitations

In this paper, we analysed four major orders of brachiopods. Three other Mesozoic orders, including the articulate Thecideida and inarticulate Lingulida and Craniida were not considered. Their ecological lifestyles are distinguished from the four orders we studied, but their fossil record is patchy and discontinuous, hampering a thorough study of morphological evolution. The Thecideida have highly varied internal structures (Baker, 2016), and the shell morphology of the Lingulida is much more complicated than previously thought (Peng and Shi, 2008; Posenato, 2016; Bitner and Emig, 2016). These orders probably have different trends in morphological evolution from the four studied orders, thereby increasing the complexity of the evolution of the entire phylum.

Morphology closely relates to ecology of brachiopods. However, as mentioned above, morphological disparity is not equivalent to ecological disparity and anatomical innovation does not always bring ecological breakthroughs (Novack-Gottshall et al., 2022). Unlike other animal clades with multiple body parts, the shell of brachiopods is relatively simple. All structures must work coherently to ensure a

normal life for a brachiopod. As a result, it is difficult to disentangle the function of a certain trait, and functions of many characters are speculative. If the connections between morphology, function, and environment were better known, future independent analyses of ecological disparity and morphological disparity (Cole and Hopkins, 2021; Novack-Gottshall et al., 2022) might provide a deeper understanding of the waxing and waning of brachiopod diversity in Meso-Cenozoic oceans.

Concluding remarks

Although brachiopod diversity remained low and did not show great fluctuations in the Mesozoic and Cenozoic, morphological evolution shows a far more dynamic pattern. The PTME significantly altered the morphological composition of brachiopods, but the disparity of surviving groups successfully rebounded or even exceeded the pre-extinction values. All orders exploited new areas in morphospace and the Meso-Cenozoic morphology is not simply a subset of the Paleozoic one. This evidence suggests that brachiopod evolvability was not prohibited by the ‘modern evolutionary fauna’, instead, was still rather active after the PTME. Nonetheless, not all new morphological forms succeeded in diversification; some new higher-level groups did not contribute much to the diversity of the phylum. Furthermore, the high extinction rate of brachiopods resulted in shorter longevity (stratigraphical duration) of brachiopod higher-level clades relative to bivalves, preventing the accumulation of diversity. In short, morphological innovation did not save the phylum from decline. Why Meso-Cenozoic brachiopods are prone to extinction and why some post-Permian forms did not have the same opportunity to diversify as their Paleozoic morphological analogues are two questions that need further investigation.

Overall, the morphological evolution of the four orders displayed very different patterns across the three mass extinctions in the studied interval: an extinction event may be morphologically selective (e.g., TJME on athyridides) or nearly non-selective (e.g., PTME on athyridides, TJME on terebratulides) and the long-term impacts on disparity values may be weak (e.g., PTME on the four orders) or strong (e.g., TJME on athyridides and spiriferinides), demonstrating the great heterogeneity among

lineages and extinction events. This study highlights the importance of investigating morphological evolution as well as species (or generic) richness in order to understand the evolutionary history of a clade.

Methods

Fossil datasets

This study aims to investigate the morphological evolution and diversity decline of Meso-Cenozoic brachiopods, thus the orders restricted to the Paleozoic (e.g., Productida, Orthotetida, Orthida, Spiriferida, and Dictyonellida) were not considered. In the Mesozoic and Cenozoic, articulate brachiopods consist of five orders: Terebratulida, Rhynchonellida, Spiriferinida, Athyridida, and Thecideida. Thecideida has a very rare fossil record and was not included in the compiled comparative dataset for this study. Inarticulate brachiopods (orders Lingulida and Craniida) are quite distinct ecologically and anatomically. However, they have a very low diversity after the Paleozoic and their fossil records are discontinuous, preventing a complete and detailed analysis. Therefore, this study focused on the evolution of four orders: Terebratulida, Rhynchonellida, Spiriferinida, and Athyridida, representing together >90% of total genus richness of all Meso-Cenozoic brachiopods; the study of these four groups is sufficient to understand the Meso-Cenozoic decline of brachiopods.

Fossil occurrences of Terebratulida, Rhynchonellida, Spiriferinida, and Athyridida from the Permian to Recent (~298.89–0 Ma) were downloaded from the Paleobiology Database on 29/3/2024. All analyses herein were carried out at the genus level. The data cleaning and revision procedure followed Guo et al. (Guo et al., 2023). Simply, (1) the name of each genus was examined, and only valid names were retained; (2) the temporal duration of each genus was checked, and doubtful records, namely those outside the stratigraphical range in well-curated datasets such as *Treatise on Invertebrate Palaeontology* (Kaesler and Selden, 1997-2007) and

Sepkoski's compendium (Sepkoski Jr, 2002), were discarded; (3) the ages of taxonomic occurrences were updated according to the Geological Time Scale 2020 (Gradstein et al., 2020), using the *fossilbrush* R package (Flannery-Sutherland et al., 2022); occurrences with a high temporal uncertainty (>10 Myr) but not from an international stage were removed. In addition, the new Permian-Jurassic occurrences added by Guo et al. (Guo et al., 2023) were kept. Occurrences of 134 genera included in the *Treatise* but absent in PBDB were also added to the final dataset compiled here.

Presence/absence tables of taxa from the Permian to the present-day were made based on the fossil occurrence data. To ensure a roughly equal duration for each time bin, we divided the Permian-Quaternary time span into 30 intervals: P1, Asselian–Sakmarian; P2, Artinskian; P3, Kungurian; P4, Roadian–Capitanian; P5, Wuchiapingian–Changhsingian; T1, Induan–Olenekian; T2, Anisian–Ladinian; T3, Carnian; T4, Norian; T5, Rhaetian; J1, Hettangian–Sinemurian; J2, Pliensbachian; J3, Toarcian; J4, Aalenian–Bathonian; J5, Callovian–Oxfordian; J6, Kimmeridgian–Tithonian; K1, Berriasian–Valanginian; K2, Hauterivian–Barremian; K3, Aptian; K4, Albian; K5, Cenomanian–Turonian; K6, Coniacian–Santonian; K7, Campanian; K8, Maastrichtian; Cz1, Paleocene; Cz2, Ypresian–Lutetian; Cz3, Bartonian–Priabonian; Cz4, Rupelian–Chattian; Cz5, Aquitanian–Serravallian; Cz6, Tortonian–Holocene. Except for some bins with very long durations such as Norian (T4), others have a span close to 10 Myr. The ‘range-through’ method was employed to infill the presence/absence tables of genera, and diversity was calculated based on generic richness counts following their stratigraphical ranges. Thus, Carboniferous records were also employed to extend the ranges of some Permian taxa. To eliminate the effect of ‘the Pull of the Recent’ (Raup, 1979), the present-day records of fossil taxa were not considered, and living genera without fossil records were also ignored.

Morphological datasets

The four orders are very different in both external and internal morphologies. Therefore, we analysed morphological disparity of each order separately and devised specific character lists for each order (see Supplementary Information). The characters

of Spiriferinida were modified from those of Guo et al. (Guo et al., 2020).

Nevertheless, only external characters were included in Guo et al.'s dataset, so the internal structures of this order were added in the new dataset analysed in this study. The characters of Rhynchonellida were selected based on Schreiber et al. (Schreiber et al., 2013) and Guo et al. (Guo et al., 2022). The characters of Terebratulida and Athyridida were inspired by Carlson and Fitzgerald (Carlson and Fitzgerald, 2008) and Alvarez and Rong (Alvarez and Rong, 2002), respectively.

In contrast to previous studies on brachiopod disparity (Ciampaglio, 2004), almost all major external (e.g., outline, convexity, umbo features, ornamentation) and internal (e.g., dental plates, hinge plates, loop supporting structure) characters of shells that are commonly described in systematic studies were compiled in the dataset. Soft-body-related features were omitted because they are rarely known in fossil taxa. Cladistically non-informative characters (i.e., autapomorphies, traits only appearing in one taxon) were included to comprehensively describe the morphological variation and retain unique innovations (Matzke and Irmis, 2018). Characters are continuous (e.g., shell width relative to shell length) or discrete, with the discrete characters being either ordered (e.g., position of ventral foramen) or unordered (e.g., type of anterior commissure). Some nested relationships are present in the characters (e.g., the 'orientation of dental plates' is dependent on the 'presence/absence of dental plates'), so characters were subdivided into 'primary' and 'secondary' categories, which would have implications during the calculation of the distance matrices and stop secondary characters re-ranking the pairwise dissimilarities based on primary ones (Hopkins and St John, 2018). In total, 128, 81, 48, and 59 characters were coded for Terebratulida, Rhynchonellida, Spiriferinida, and Athyridida, respectively. Detailed descriptions of characters are provided in the Supplementary Information.

The character states of each genus were coded based on the adult morphology of its type species. If the type species was not perfectly known, another species under the same genus was selected. Ontogeny is vital in studying the evolution of brachiopods, and it is used as a key diagnosis in the higher-level classification units (e.g., the complex loop development in Loboidothyridoidea vs. the simple loop development in

Terebratuloidea (Lee et al., 2006)). Nevertheless, tontogenetic variation is only known in a very small fraction of taxa (Lee et al., 2006). Therefore, only the morphology of adults was considered in this study. Continuous characters were measured on one specimen of the type species, in most cases, the one shown in the *Treatise*. One may argue that such measurements are highly variable within one genus or one species (e.g., the interarea height of *Liospiriferina* species). However, owing to the long time interval and wide taxonomic scope of our study, normally, greater differences appear between than within genera (e.g., the low interarea of *Liospiriferina* compared with the high interarea of *Cisnerospira*).

Disparity analysis

The morphological datasets were employed to calculate pairwise dissimilarity matrices using the Maximum Observable Rescaled Distance metric (Lloyd, 2016). The alpha value applied to balance the contribution of primary characters and secondary characters was set to 0.5 as recommended (Hopkins and St John, 2018). Recent studies have shown that missing data can affect the position of taxa in morphospace (Flannery Sutherland et al., 2019; Gerber, 2019). Therefore, prior to the calculation of the distance matrices, taxa with more than 20–30% (20% for terebratulides and rhynchonellides; 30% for spiriferinides and athyridides) unknown characters (marked by question mark ‘?’) were discarded from the dataset. For terebratulides, taxa whose loop type is not revealed were also deleted because the loop structures have many morphological characters and these include the most important criteria for the classification of terebratulides. In the end, less than 10.5% genera in these orders were discarded, and 529, 332, 104, and 54 genera were retained in the terebratulid, rhynchonellide, spiriferinide, and athyridide datasets, respectively (Supplementary Information). The diversity trajectories of the reduced datasets significantly correlate with that of the raw datasets (both raw and detrended diversities; Pearson’s $r > 0.98$, $p < 0.05$; Extended Data Fig. 1). The dissimilarity matrices were arcsine square root transformed to make sure that the distances were normally distributed (Lloyd, 2016). To construct morphospaces, principal coordinates

analysis (PCOA) was applied to the transformed dissimilarity matrix using the *pcoa* function of the *ape* R package (Paradis and Schliep, 2019). A Cailliez correction (Cailliez, 1983) was also employed to deal with negative eigenvalues, at the expense of reducing the reported variance expressed by each axis (Nordén et al., 2018).

There are multiple ways to evaluate the distribution of taxa in a morphospace and generate within-bin disparity time series, and each measurement has its advantages and disadvantages (Ciampaglio et al., 2001; Guillerme et al., 2020). We employed two popular metrics, the sum of variances (SOV) and sum of ranges (SOR), to demonstrate the evolutionary trends of morphological disparity. SOV describes the density of taxa within the occupied morphospace area, while SOR reflects the total range of the area occupied. SOR has some obvious drawbacks. It is sensitive to, and usually positively correlates with, sample size. Thus, rarefaction analysis is needed to compare the SOR of two samples (Foote, 1992), which may result in very wide confidence intervals if the sample size is low. Moreover, SOR cannot reflect variation in the central part of the morphospace (e.g., unoccupied central ‘holes’) and it is easily biased by taxa located in marginal areas of morphospace and outliers (Ciampaglio et al., 2001; Guillerme et al., 2020). In contrast, SOV is insensitive to sample size and outliers; therefore, it is widely used by many researchers although it may be biased by taxonomic over-splitting or clumping. In this paper, we prefer to use the SOV as an overall indicator of disparity. SOR was calculated as a complementary index (Extended Data Fig. 3). Both SOV and SOR were calculated from PCO scores of all axes. For each time bin, the median value and 95% confidence intervals were calculated based on 1000 bootstrap replications (Kowalewski and Novack-Gottshall, 2010). For SOR, because of its sensitivity to sample size, the number of taxa was rarefied to the lowest diversity of all time bins in the terebratulide and rhynchonellide analyses, and to the median diversity of all time bins in the spiriferinid and athyridide analyses. All disparity calculations were accomplished by the *dispRity* (Guillerme, 2018) and *vegan* (Oksanen et al., 2022) R packages.

Morphospace occupation

Differing from density (SOV) and size (SOR), the position of taxa in morphospace is another aspect of morphological analysis (Guillerme et al., 2020). The distribution of taxa in morphospace and variations in morphospace occupation are usually displayed directly in the form of biplots of the major axes (Fig. 2; Extended Data Figs. 4–7). However, when the first few PCO axes only explain a small proportion of the overall variation (such as the rhynchonellide morphospace in this study), only a small proportion of total variation can be observed directly on the morphospace and a great fraction of variation is hidden on other axes.

Here we used a centroid-related metric to evaluate the movement of morphospace occupation. The ‘position of centroid’ is an easy way to describe the position of taxa, which has been widely used by other researchers (Korn et al., 2013; Cole and Hopkins, 2021). Normally, the distribution of taxa in the morphospace may be non-normal and complex, and therefore, some variation in morphospace cannot be indicated by shifts in centroid. However, the centroid is easy to calculate and to compare between different time bins, and more importantly, it can reflect asymmetrical variation in occupation, which is related to selective extinction or origination (Korn et al., 2013). A major advantage of reporting centroid-related metrics is that centroids can be calculated using all PCO axes, not just the first three (Cole and Hopkins, 2021). In contrast, a direct observation of morphospace (usually constructed from the first two or three axes) cannot show information on other axes, and this cannot be ignored when the first few axes explain such a low proportion of the variance. Therefore, the centroid-related metric is a valuable complement to the morphospace.

For every order, we first partitioned the morphospace according to presence/absence table of taxa, and calculated the position of the centroid of all time bins using all PCO axes. Next, Euclidean distances between centroids in different time bins were calculated. This calculation generated a distance matrix of all time bins; the distances between centroids of two adjacent bins were extracted as the ‘Shifts in centroid’. Finally, we use the PCOA (equivalent to principal component analysis because the Euclidean distance was used) to visualise this distance matrix

(i.e., the ‘Centroid space’). No further calculation was performed on the centroid space.

It should be noted that the centroid space does not directly show the morphological forms in a time bin. It clearly illustrates the relative similarities (or distances) of morphological composition (or ‘mean’ morphology) among time bins, in other words, in which bins the morphological compositions are closer to each other.

To examine whether the morphospace occupation in adjacent time bins is significantly different, we also performed the permutational multivariate ANOVA test (PERMANOVA). The analysed data are coordinates of taxa in the morphospace, and again, all PCO axes were considered.

Data availability

Occurrence data were downloaded from the Paleobiology Database (<https://paleobiodb.org/>). The added Permian–Jurassic fossil occurrences were from Guo et al. (Guo et al., 2023). All occurrence data and character matrices analysed are available in Zenodo (XXX).

Code availability

All R scripts used to conduct the analyses are available in Zenodo (XXX).

References

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Author contributions Z.-Q.C. and Z.G. designed the research. Z.G. collected morphological data. Z.G. and T.L.S. analysed the data. All authors discussed the results. Z.G. drafted the paper with substantial input from all authors.

Ethics statement

Competing interests The authors declare no competing interests.

Extended Data Fig. 1. Diversity of taxa in the revised occurrence database and diversity of taxa included in the morphological analysis. The left panel shows the comparison of raw diversity (sample size $N = 30$ for Rhynchonellida and Terebratulida; $N = 13$ for Spiriferinida and Athyridida). The right panel shows the comparison of detrended (i.e., first difference) data. Correlation parameters (Pearson's r) are indicated. All correlations are significant ($p < 0.05$).

Extended Data Fig. 2. Percentage variance explained by each axis of the PCOA of morphological data.

Extended Data Fig. 3. Disparity and diversity of four orders through time.

Disparity is measured by sum of ranges (SOR). The solid lines represent median value of the bootstrapped disparity. The envelopes indicate 95% confidence intervals (0.025 and 0.975 quantiles of bootstrapped values). Diversity (number of genera) is represented by dashed lines. **a**, Terebratulida; **b**, Rhynchonellida; **c**, Spiriferinida; **d**, Athyridida. Abbreviations as in Fig. 2.

Extended Data Fig. 4. Morphospace occupation of the order Terebratulida through time. Morphospaces are constructed by the first two axes (PCO1 and PCO2). The number in labels indicates the percentage of variances explained by the axis.

Extended Data Fig. 5. Morphospace occupation of the order Rhynchonellida through time. Morphospaces are constructed by the first two axes (PCO1 and PCO2). The number in labels indicates the percentage of variances explained by the axis.

Extended Data Fig. 6. Morphospace occupation of the order Spiriferinida

through time. Morphospaces are constructed by the first two axes (PCO1 and PCO2). The number in labels indicates the percentage of variances explained by the axis.

Extended Data Fig. 7. Morphospace occupation of the order Athyridida through time. Morphospaces are constructed by the first two axes (PCO1 and PCO2). The number in labels indicates the percentage of variances explained by the axis.

Extended Data Fig. 8. Morphospace centroid spaces of the four orders with bin names labelled. a, Terebratulida; **b,** Rhynchonellida; **c,** Spiriferinida; **d,** Athyridida.

Supplementary Information. Contents: 1. Characters of Terebratulida. 2. Characters of Rhynchonellida. 3. Characters of Spiriferinida. 4. Characters of Athyridida. 5. List of taxa present in the occurrence database but absent in the morphological analyses. 6. Results of the permutational multivariate ANOVA (PERMANOVA) test.