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1 **Editor summary:**

2

3 Analysing more than 1000 genera of four major orders of brachiopods spanning the Permian to Quaternary, the authors find that despite low levels of taxonomic
4 richness after the Permian-Triassic mass extinction, brachiopods continued to innovate morphologically, indicative of high evolutionary adaptability.

5

6 **Peer review information:**

7

8 Nature Ecology & Evolution thanks Philip Novack-Gottshall, Judith Sclafani and Pedro Monarrez for their contribution to the peer review
9 of this work.

10

11

12 **Inventory of Supporting Information**

13

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15

16 **Corresponding author name(s):** Zhong-Qiang Chen

17 **1. Extended Data**

18

Figure or Table #	Figure/Table title	Filename	Figure/Table Legend
Please group Extended Data items by type, in sequential order. Total number of items (Figs. + Tables) must not exceed 10.	One sentence only	Whole original file name including extension. i.e.: Smith_ED_Fig1.jpg	If you are citing a reference for the first time in these legends, please include all new references in the main text Methods References section, and carry on the numbering from the main References section of the paper. If your paper does not have a Methods section, include all new references at the end of the main Reference list.
Extended Data Fig. 1	Diversity of taxa in the revised occurrence database and diversity of taxa included in the morphological analysis.	Extended_Data_Fig. 1.jpg	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 ($p < 0.05$; two-sided).
Extended Data Fig. 2	Disparity and diversity of four orders through time.	Extended_Data_Fig. 2.jpg	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. 3	Morphospace occupation of the order Terebratulida through time.	Extended_Data_Fig. 3.jpg	Morphospaces are constructed by the first two axes (PC01 and PC02). The number in labels indicates the percentage of variances explained by the axis.
Extended Data Fig. 4	Morphospace occupation of the order Rhynchonellida through time.	Extended_Data_Fig. 4.jpg	Morphospaces are constructed by the first two axes (PC01 and PC02). The number in labels indicates the percentage of variances explained by the axis.
Extended Data Fig. 5	Morphospace occupation of the order Spiriferinida through time.	Extended_Data_Fig. 5.jpg	Morphospaces are constructed by the first two axes (PC01 and PC02). The number in labels indicates the percentage of variances explained by the axis.
Extended Data Fig. 6	Morphospace occupation of the order Athyridida through time.	Extended_Data_Fig. 6.jpg	Morphospaces are constructed by the first two axes (PC01 and PC02). The number in labels indicates the percentage of variances explained by the axis.
Extended Data Fig. 7	Percentage variance explained by each axis of the PCOA of morphological data.	Extended_Data_Fig. 7.jpg	NULL.
Extended Data Fig. 8	Morphospace centroid spaces of the four orders with bin	Extended_Data_Fig. 8.jpg	a , Terebratulida; b , Rhynchonellida; c , Spiriferinida; d , Athyridida.

	names labelled.		
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19 *Do not insert additional rows - total number of Extended Data items must not exceed 10.*

20

21 **1. Supplementary Information:**

22 **A. PDF Files**

23

Item	Present?	Filename	A brief, numerical description of file contents. i.e.: <i>Supplementary Figures 1-4, Supplementary Discussion, and Supplementary Tables 1-4.</i>
		Whole original file name including extension. i.e.: Smith_SI.pdf. The extension must be .pdf	
Supplementary Information	Yes	Supp_info.pdf	Supplementary Text and Supplementary Figures 1-3.
Reporting Summary	Yes	nr-reporting-summary-Guo.pdf	

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26

27 **Morphological innovation did not drive diversification in Mesozoic–**
28 **Cenozoic brachiopods**

29

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38

39 **Abstract**

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

56 the depauperate nature of modern-day brachiopods.

57

58 **Introduction**

59 Biologists and palaeobiologists often refer to ‘success’ in evolution, by which they
60 mean the achievement by a clade of high species richness, high abundance, and great
61 breadth of morphological-functional adaptation. Among modern organisms,
62 mammals, birds, molluscs, and angiosperms might be said to be successful against all
63 those metrics. On the other hand, turtles, crocodylians, brachiopods, and ginkgos
64 might be said to be less successful because of currently lower species numbers, lower
65 global abundance, and more restricted functional and ecological diversities. In
66 comparing so-called ‘successful’ and ‘unsuccessful’ clades, comparative studies often
67 select pairs of close relatives, such as crocodylians and birds, that shared a single
68 common ancestor, in this case some 252 million years ago (Ma) in the Triassic and
69 ask why birds today comprise more than 10,000 species, and yet their sister clade,
70 crocodylians, include ~25 extant species^{1–3}. Among marine organisms, brachiopods
71 and bivalves, are often taken as a pairing^{4–10}, not because they shared a close common
72 ancestor but because of many shared anatomical and functional features⁴. The classic
73 story has been that brachiopods dominated seabeds until the Permian-Triassic mass
74 extinction (PTME), ~252 Ma, and then bivalves took over in the Triassic¹¹. This has
75 frequently been explained by substantial loss of ecospace by brachiopods to bivalves^{4,}
76 ^{6, 7, 9}, and the current marginal role of brachiopods in world oceans seems to bear this
77 out. But is this true?

78 The Phylum Brachiopoda originated in the Cambrian, survived the ‘Big Five’
79 mass extinctions^{12, 13}, and persists in today’s oceans¹⁴. They were the most abundant
80 benthic invertebrates occupying most habitats in oceans before the Mesozoic. After
81 the PTME, brachiopods lost diversity dominance and became marginal components of
82 marine communities in Mesozoic–Cenozoic (Meso–Cenozoic) oceans^{15–19} (Fig. 1).
83 The remarkable switch from brachiopods to bivalves across the PTME, and the
84 permanent reduction in diversity of Meso–Cenozoic brachiopods, have long intrigued
85 palaeobiologists and biologists^{4–7, 9, 10, 20–23}. However, most previous studies

86 interpreted this switch in terms of taxonomic diversity alone and assumed that
87 brachiopods lost out in some way in competition with bivalves. A consequence of
88 such a view would be that post-Permian functional diversity of brachiopods,
89 represented by morphospace occupation, should be much reduced or show little
90 evidence of innovation and novel adaptation, suggesting that brachiopods were
91 squeezed into a reduced number of perhaps marginal niches by the success of the
92 bivalves in and after the Triassic.

93 Morphological disparity, which describes the diversity of morphology in a clade
94 (i.e., ‘morphological diversity’), is an important complement to taxonomic diversity to
95 depict the evolutionary dynamics of organisms²⁴. Although the two metrics may be
96 coupled or decoupled through time^{25–32}, it is often seen that morphological innovation
97 brings functional innovation and ecological opportunities to animals, paving the way
98 for the upcoming taxonomic diversification^{33–36}. In the history of the Earth, many
99 clades rapidly accumulated great diversity at the beginning of their evolutionary
100 history or swiftly recovered after mass extinctions, along with the expansion of their
101 morphological range (i.e., the early burst model)^{27, 37}. However, there are also some
102 clades whose diversity never returned to pre-extinction levels such as the post-
103 Permian brachiopods, and whether their apparent lack of success was limited by their
104 morphological disparity remains unknown.

105 Although discussed for a long time, the evolution of brachiopod morphology is
106 poorly understood³⁸. Previous studies on brachiopod disparity generally focused on
107 one of the relatively small articulate^{39–41} or inarticulate orders^{42, 43}. Ciampaglio³⁸ first
108 investigated the Phanerozoic disparity of articulate brachiopods and unravelled a
109 partially recovered and volatile disparity among post-Permian taxa, but the numbers
110 of taxa sampled and the characters analysed were rather small.

111 Here we compile a large, comprehensive morphological dataset and analyse
112 disparity over the ~300 Myr (Permian–Quaternary) history of >1000 genera belonging
113 to four major orders of Meso–Cenozoic brachiopods (Terebratulida, Rhynchonellida,
114 Spiriferinida, and Athyridida) (Extended Data Fig. 1). Their total genus richness
115 accounts for more than 95% of all post-Permian brachiopods, thus providing a nearly

116 complete picture of morphological evolution of the entire phylum. This study aims to
117 provide new insights into several questions. First, we employed two disparity metrics,
118 sum of variances (SOV) and sum of ranges (SOR) to quantitatively measure overall
119 morphological variations of the Meso–Cenozoic brachiopods and to assess their
120 coupling or decoupling relationships with diversity measures represented by genus
121 richness. Second, we examine how the PTME, Triassic–Jurassic mass extinction
122 (TJME), and Cretaceous–Paleogene mass extinction (KPgME) and their recovery
123 processes regulated morphological evolution of the post-Permian brachiopods.
124 Finally, co-variation of disparity, biodiversity, and morphospace occupation offers
125 new insights into the drivers responsible for the depauperate nature of present-day
126 brachiopods.

127

128 **Results**

129 **Disparity and diversity through time**

130 The Terebratulida, characterised by a loop in the shell, is the largest order (in terms of
131 taxonomic diversity) among post-Permian brachiopods and is also the most diverse
132 brachiopod clade in today's oceans⁴⁴. Our analyses reveal that terebratulide disparity
133 (SOV) shows an overall increasing trend from the Permian to Quaternary, and that
134 this is decoupled from the overall diversity of the order, which has peaks and troughs,
135 without a clear upward trajectory.

136 Terebratulide disparity and diversity fluctuated through time (Fig. 2a). Disparity
137 (SOV) shows major drops occurring in the Early Triassic, Middle Jurassic, early Late
138 Cretaceous, and Paleocene. After each decline and in the Middle–Late Triassic, Late
139 Jurassic, late Late Cretaceous, and Eocene, SOV rebounded rapidly to the pre-drop
140 levels or even higher. The SOV is rather low in the Middle Jurassic, but this low value
141 is not caused by the small morphological range, but rather the rapid diversification of
142 the Superfamily Lobidothyridoidea⁴⁴. Although the members of this superfamily
143 possess diverse external characters, their internal morphologies show little variance
144 (from a macroscopic perspective of the entire order), and these forms therefore gather

145 in a small region in the upper-left corner of the morphospace, pointing to a low SOV
146 value (Fig. 3a). Similarly, terebratulide SOR also exhibits a generally increasing trend
147 (Extended Data Fig. 2) although the trend is more subtle. The broad confidence
148 intervals (due to small sample size after rarefaction) make the significance difficult to
149 confirm. After the PTME and TJME, terebratulide diversity surged to a very high
150 level in the Middle Jurassic, and then returned to the Permian level during the Late
151 Cretaceous. The Cenozoic witnessed a steady increase in diversity, but present-day
152 diversity never returned to the mid-Jurassic level.

153 The crura-bearing Rhynchonellida is the second-largest order among the Meso–
154 Cenozoic brachiopods. Their disparity (SOV) showed an overall increasing trend
155 from the Triassic to Jurassic, and then declined in the Early Cretaceous. From the Late
156 Cretaceous to Quaternary, a clear trend was not exhibited, and the confidence
157 intervals were very wide (Fig. 2b). The evolution of SOV contrasts markedly with
158 diversity, which massively decreased following the Jurassic, and remained constantly
159 low to the present day, where this order is just a small subset of living brachiopods.
160 More specifically, the rhynchonellide SOV peaked in the Early–Middle Permian, Late
161 Triassic, Late Jurassic–earliest Cretaceous, and Late Cretaceous, and dropped in the
162 Late Permian, Middle Jurassic, early–middle Cretaceous and Paleocene. The SOR of
163 this order shows a similar trend to the SOV (Extended Data Fig. 2), except for even
164 lower values from the mid-Cretaceous to the present day.

165 The Spiriferinida, an order comprising spire-bearing and punctate taxa, includes
166 far fewer genera than the first two orders, yet it is one of the major components of
167 Triassic brachiopod faunas. Their taxonomic diversity, and SOV and SOR disparities
168 all were severely affected by the PTME (Fig. 2c; Extended Data Fig. 2), but rapidly
169 rebounded and finally reached the pre-extinction value in the Middle to Late Triassic.
170 Diversity declined rapidly in the Rhaetian, before a further hit by the TJME. Disparity
171 also followed this trend and gradually declined to a lower level. In Early Jurassic,
172 these three metrics did not recover until this order was wiped out in the Toarcian⁴⁵.

173 The Athyridida is another spire-bearing group that became extinct at the Toarcian
174 Oceanic Anoxic Event (Early Jurassic) along with Spiriferinida^{45, 46}. Athyridide SOV

175 was almost unchanged across through the Permian-Triassic transition despite a
176 notable drop in diversity. Their SOV rose through the Triassic, sharply declined after
177 the TJME, and then remained at low levels towards the final demise of this order in
178 Early Jurassic (Fig. 2d). SOR shared a similar pattern to SOV, that is, a high value in
179 the Permian and Triassic and an extremely low value in the Jurassic (Extended Data
180 Fig. 2). After the PTME, athyridide diversity did not recover until the Carnian of Late
181 Triassic when it surged significantly, followed by major drops in the Rhaetian (late
182 Late Triassic) and TJME, and then rather low levels in the Jurassic (Fig. 2d).

183

184 **Morphospace occupation through time**

185 The shifts of morphospace occupation in brachiopod genera can be directly observed
186 in the morphospace (Fig. 3; Extended Data Figs. 3–6). However, for some datasets,
187 the first few morphospace axes explain only a low proportion of variance and a great
188 amount of information is hidden on the other axes (Extended Data Fig. 7). Therefore,
189 we also constructed a ‘morphospace centroid space’ to complement our visualisation
190 of the results (see Methods for extended description) (Fig. 4; Extended Data Fig. 8),
191 where the distribution of time bins in the centroid space displays the similarity of
192 morphological composition in different bins. Overall, temporal trends of morphospace
193 occupation show continued innovation through time despite reductions in diversity at
194 major extinction events.

195 Terebratulides are unevenly distributed in morphospace (Fig. 3a). The
196 morphospace areas occupied by short-looped and inner-hinge-plate-lacking taxa and
197 by long-looped taxa have higher density, while other areas are less crowded (Fig. 3a).
198 From the Triassic to Jurassic, taxa in these two areas diversified greatly, while those in
199 the upper-central area gradually disappeared. Taxonomically, this pattern reflects the
200 diversification of two major descendants of the Dielasmatoidea (i.e., the short-looped
201 Loboidothyridoidea and long-looped superfamilies such as Zeillerioidea and
202 Laqueoidea) and the extinction of the Dielasmatoidea itself⁴⁴. The Jurassic to
203 Cenozoic occupation trend is characterised by the invasion of morphospace areas
204 occurring in the lower part of the plot, which is occupied by taxa having a septal pillar

205 and lacking hinge plates. The centroid space of Terebratulida shows that the centroids
206 are widely separated in the Permian, Triassic, and Jurassic–Cenozoic intervals,
207 indicating different morphological compositions (Fig. 4a). The Jurassic and Cenozoic
208 centroids are also separated, but they are bridged by the Cretaceous ones, implying
209 that morphology of terebratulides has gradually changed to the current form since the
210 Jurassic. The greatest shift in centroids of morphospace occupation occurred in the
211 Early Triassic (Fig. 4b). Although the sample size is low in the Early Triassic, this
212 shift is significant according to the result of the PERMANOVA test ($p < 0.05$)
213 (Supplementary Information). Moreover, the greater distances of centroid spaces
214 occur in the aftermaths of all three mass extinctions (Fig. 4b), implying that mass
215 extinctions may have triggered distinct shifts in centroids and altered morphological
216 compositions of terebratulides.

217 For rhynchonellides, variations of morphospace occupation indicate that the
218 previous areas were lost when new areas were explored. For instance, the Triassic–
219 Jurassic septalium-bearing taxa fully exploited the middle-right area and the Jurassic–
220 Cenozoic septifal taxa developed more in the left half region in the morphospace (Fig.
221 3b). Meanwhile, the lower part of the space (camarophorium-bearing taxa and hinge-
222 plates-fused taxa) was unoccupied after the Permian, and the right areas were
223 gradually lost from Cretaceous to Cenozoic. The centroid space of this order shows
224 that the Permian centroids are clearly distinguished from those of other periods (Fig.
225 4c). From the Triassic to Cenozoic, the centroid moved along the first principal
226 coordinate axis, indicating a gradual transformation from Triassic morphologies to
227 present-day ones, strengthened by shifts in the centroid. The most prominent shift in
228 the centroid occurs in the Early Triassic despite rather high values also occurring in
229 the Paleocene and Eocene, which, however, could be not reliable due to the limited
230 sample size (Fig. 4d; Supplementary Information).

231 The Spiriferinida broadened morphospace and occupied new areas in the
232 Triassic⁴¹, while the previous morphospace occupied by the Permian superfamily
233 Syringothyridoidea disappeared forever (Fig. 3c). In contrast, the Early–Middle
234 Triassic athyridides re-thrived in the areas previously occupied by the Permian

235 elements of the same order, and then greatly expanded to the upper-left corner by
236 evolving concavoconvex forms in the Koninckinidina (Fig. 3d). Both spiriferinides
237 and athyridides did not invade new morphospace in the Jurassic, and the Jurassic
238 morphospaces are only a subset of their Triassic ones (Fig. 3c, d). Their morphospace
239 centroids are separated from each other in the Permian, Triassic, and Jurassic (Fig. 4e,
240 g). The Spiriferinida shows a distinct centroid shift after the PTME (the Early Triassic
241 shift is doubtful due to the small sample size) (Fig. 4f), while the Athyridida shows a
242 larger centroid shift after the TJME (Fig. 4h).

243

244 **Discussion**

245 **Effect of mass extinctions on brachiopod morphology**

246 Of the three Mesozoic mass extinctions, the PTME not only depleted diversity, but
247 also regulated the distribution of morphospace (Figs. 1, 3, 4), and thus re-shaped
248 brachiopod macroevolution^{14, 17, 18}. The Paleozoic orders (Productida, Spiriferida,
249 Orthotetida, Orthida, and Dictyonellida) were not analysed in this study, but it is
250 obvious that these high-level groups and the associated morphologies were
251 permanently eliminated by the PTME. It is noteworthy that although morphological
252 compositions of the four surviving orders were altered by this mass extinction, their
253 disparity values showed less long-term effect from the PTME. The disparity and
254 diversity of both the Spiriferinida and Athyridida recovered to pre-extinction levels in
255 the Triassic, and morphological innovations in Rhynchonellida and Terebratulida
256 emerged and their disparities returned to pre-extinction levels in the early Mesozoic.
257 In contrast, the TJME had little effect on the Rhynchonellida and Terebratulida, which
258 both proliferated after the crisis. The other two orders (Spiriferinida and Athyridida)
259 suffered severe impacts from the Late Triassic events and TJME and fell into the state
260 of ‘dead clade walking’^{47, 48} in both diversity and disparity, before their disappearance
261 in the Early Jurassic. The TJME therefore had more prolonged impact on disparities
262 of Spiriferinida and Athyridida than the PTME. The KPgME did not significantly re-
263 shape morphological evolution of terebratulides and rhynchonellides. It only

264 accelerated the transition of morphological composition from the Cretaceous ones to
265 the modern ones (Figs. 3, 4).

266 In addition to these mass extinctions, other environmental events (e.g., oceanic
267 anoxia events in the Jurassic and Cretaceous) also caused diversity perturbations of
268 brachiopods^{49, 50}. However, they did not show significant effects on the morphological
269 evolution of the four orders studied (Figs. 3, 4). A more detailed study in finer time
270 bins might reveal their influences.

271

272 **Morphological innovation in post-Permian brachiopods**

273 Variations of the SOV, SOR, and morphospace occupation show that these four orders
274 exhibit four different morphological evolution patterns. The Terebratulida has steadily
275 broadened new morphospace areas since the Triassic, and only a small part of the pre-
276 occupied areas was lost. In contrast, the Rhynchonellida explored new morphospace
277 in the Triassic and Jurassic, and frequently retreated from some previously occupied
278 areas. The Spiriferinida rapidly diversified in morphology in the Triassic and took
279 over a great part of the morphospace of the Paleozoic Order Spiriferida, as
280 demonstrated by Guo et al.⁴¹, while the Triassic athyridides largely inherited their
281 Permian precursors' morphologies except for a major step of innovation introduced by
282 the new Suborder Koninckinidina (Fig. 3).

283 Disparity analyses of many animal clades show pervasive early high disparity,
284 that is animal clades tend to reach their maximum disparity relatively early in their
285 evolutionary histories^{27, 37}. The pre-Permian taxa of the four orders were not analysed
286 in this study, but according to the number of higher-level groups (i.e., suborders,
287 superfamilies)⁵¹, such an early burst was not observed in at least three of these four
288 Meso–Cenozoic orders. The Terebratulida and Spiriferinida reached their highest
289 disparities in the Cenozoic and Late Triassic, respectively. The Athyridida, typical of
290 Paleozoic orders, had high diversity in the Paleozoic, but the survival of two
291 suborders through the PTME and the emergence of a new suborder in the Triassic
292 possibly elevated its disparity to a higher level. Rhynchonellides, originating in the
293 Ordovician, were much more diverse in the Devonian than in the Mesozoic and

294 evolved into several superfamilies at that time. Because we did not study the
295 Devonian taxa, a direct comparison is not yet possible. In terms of the entire Phylum
296 Brachiopoda, the maximum disparity occurred in the late Paleozoic³⁸, about midway
297 through its evolutionary history. As a result, early high disparity was possibly not very
298 pervasive in brachiopods.

299 Each of the four orders displayed its own pattern of morphological evolution, but
300 they all explored new morphospace areas. Rigorous statistical analysis of morphology
301 and associated environments is difficult due to the lack of data for many genera, but
302 there are several examples showing adaptations of post-Permian brachiopods to new
303 environments (Fig. 5). For instance, the Athyridida had the most significant
304 innovation in the emergence of the Koninckinidina, members of which are readily
305 distinguished by having unique concavoconvex shells that are similar to the Paleozoic
306 strophomenatans, indicating an infaunal lifestyle adapted to soft substrates⁵² (Fig. 5b).
307 The Spiriferinida possessed highly varied shell outlines and delthyrium covers during
308 the Triassic, implying different ways to stabilize the shell bodies⁴¹ (Fig. 5b). The
309 rhynchonellides also exhibit co-evolution between morphology and environments⁵⁰,
310 ⁵³: the ribbed and raducal group often inhabits epicontinental seas, while the smooth
311 and weakly ornamented taxa with arcuiform and septifal crura prefer to dwell in
312 epiocceanic or deeper environments⁵⁰. Together with smooth rhynchonellides,
313 terebratulides inhabiting deeper habitats also tend to be smooth-shelled and possess a
314 unisulcate anterior commissure^{54, 55} (Fig. 5c). Another important morphological
315 change of the Terebratulida is the retention of a septal pillar (Fig. 3a), like those in the
316 Platidioidea, Kraussinoidea, and Megathyridoidea. In present-day oceans, many
317 megathyridoids live in cryptic habitats, such as shallow-water caves or undersides of
318 coral colonies⁵⁶ (Fig. 5a), and it was assumed that the low metabolic rates and low-
319 energy lifestyles help these micromorphic brachiopods to survive in such nutrition-
320 poor environments⁵⁷.

321 All lines of evidence indicate that after undergoing an evolutionary bottleneck at
322 the PTME, post-Permian brachiopods struggled to expand into new morphospaces,
323 especially the vacated ecospace of the early Triassic, like the behaviours of molluscs

324 and other elements of the ‘modern evolutionary fauna’^{58–60}.

325 Gould and Calloway⁵ hypothesized that brachiopods possess relatively less
326 flexibility to modify their basic body plans than bivalves, probably limiting the
327 ecological success of brachiopods. Unfortunately, a direct comparison between these
328 two clades is not yet possible due to unavailability of the long-term disparity
329 evolution trend of bivalves. However, the rise of a new brachiopod order, the
330 Thecideida (not included in our analysis due to incomplete fossil record) in the Late
331 Triassic, possibly does not support this hypothesis. Members of Thecideida have
332 small size, a well-developed ventral interarea with pseudodeltidium, a lidlike dorsal
333 valve, and a ventral cicatrix allowing for the cemented lifestyle. Internally, thecideides
334 possess a prominent cardinal process, a pair of well-developed inner socket ridges, a
335 variously developed median septum, and pair(s) of brachial lobes. These
336 morphological features are so unique that only few characters are shared with other
337 orders, making their phylogenetic relationships with other brachiopods
338 controversial^{61, 62}. Also debated is the systematic position of the Suborder
339 Koninckinidina, although they are currently assigned to the Athyridida⁶³. These
340 higher-level innovations provide further evidence for the evolvability in the post-
341 Permian brachiopods.

342

343 **Decoupling between morphospace and diversity evolutions**

344 Both morphospace occupation and diversity evolution trends of brachiopods clearly
345 demonstrate a decoupling of the two. Apparently, morphospace increase often did not
346 drive significant diversification of Meso–Cenozoic brachiopods (Figs. 2, 3). We
347 propose that two kinds of mechanisms that are related to the extinction and the
348 origination process, respectively, account for such decoupled evolution between
349 morphospace and diversity. Firstly, as essential components of the ‘Paleozoic
350 evolutionary fauna’⁶⁴, brachiopods intrinsically had a higher extinction rate than the
351 ‘modern evolutionary fauna’ such as bivalves^{9, 10, 65}. Brachiopods were affected by
352 various-scale extinction events more severely than molluscs, and many clades failed
353 to survive to the present-day. In contrast, most bivalve families are extant, meaning

354 that their statistical risk of extinction is less than that of brachiopods through time⁶⁶.
355 For instance, the Spiriferinida and Athyridida successfully recovered in the Triassic,
356 but they experienced a high extinction rate in the Late Triassic and TJME⁴⁵, and
357 finally became extinct in a relatively small extinction event, the Toarcian Oceanic
358 Anoxic Event. The Jurassic radiation of long-flanged deltidiform terebratulides
359 (Superfamily Loboidothyridoidea) and raducal rhynchonellides (superfamilies
360 Rhynchonelloidea and Hemithiridoidea) are good examples of adaptive radiation⁶⁷.
361 These forms were abundant and widely distributed in various settings in the Middle
362 Jurassic⁵³, making this the highest level after the PTME for diversity of the entire
363 phylum (Figs. 1, 3). However, the rather high extinction rate in the Middle–Late
364 Jurassic¹⁰ resulted in a drop in their diversity. The vast majority of families did not
365 survive into the Cenozoic, and thus contributed little to the subsequent diversification
366 of brachiopods. Why brachiopods are prone to extinction has been debated for a long
367 time. Some researchers suggested that the fixed lophophore of both athyridides and
368 spiriferinides is less advantageous during environmental stresses^{45, 68}. However, some
369 spire-bearers (e.g., Athyridida, Spiriferida) were very successful in the late Paleozoic
370 after a great number of extinctions. Moreover, the rhynchonellides and terebratulides
371 without a fixed lophophore also experienced a high extinction rate in the Middle–Late
372 Jurassic. Other hypotheses have been proposed, such as the diversification of
373 predators and competition with bivalves, but they cannot fully explain the observed
374 patterns¹⁰.

375 Limited origination of some new brachiopod forms is probably another cause for
376 failure in diversification of post-Permian brachiopods. For instance, three new
377 terebratulid superfamilies having a septal pillar in adults (Platidioidea, Kraussinoidea,
378 and Megathyridoidea) occurred in the Cretaceous and Cenozoic, evidently broadening
379 morphospace occupation (Fig. 3a). Each superfamily, however, contains <10 genera
380 (including fossil and living forms)⁴⁴, indicating a rather low origination efficiency of
381 these new high-level classification units. Moreover, the morphologically unique
382 Suborder Koninckinidina includes only nine genera⁶³; the new Order Thecideida,
383 through an ~240-Myr evolution, only has about 40 genera⁶². The taxonomic numbers

384 of these two new high-level classification units of Meso–Cenozoic brachiopods are
385 much lower than their Paleozoic morphological and ecological analogues (e.g.,
386 Productida and Strophomenida). In other words, adaptive radiation was not observed
387 in these brachiopod clades, reinforcing that morphological innovation is independent
388 of ecological opportunities and evolutionary success^{69, 70}.

389

390 **Study limitations**

391 In this paper, we analysed four major orders of brachiopods. Three other Meso–
392 Cenozoic orders, including the articulate Thecideida and inarticulate Lingulida and
393 Craniida were not considered. Their ecological lifestyles are distinguished from the
394 four analysed orders, but their fossil record is patchy and discontinuous, hampering a
395 thorough study of morphological evolution. The Thecideida has highly varied internal
396 structures⁶², and the shell morphology of the Lingulida is much more complicated
397 than previously thought^{71–73}. These orders probably have different trends in
398 morphological evolution from the four studied orders, thereby increasing the
399 complexity of the evolution of the entire phylum.

400 Morphology closely relates to ecology of brachiopods. However, as mentioned
401 above, morphological disparity is not equivalent to ecological disparity and
402 anatomical innovation does not always bring ecological breakthroughs^{36, 70}. Unlike
403 other animal clades with multiple body parts, the shell of brachiopods is relatively
404 simple. All structures must work coherently to ensure a normal life for a brachiopod.
405 As a result, it is difficult to disentangle the function of a certain trait, and functions of
406 many characters are speculative. If the connections among morphology, function, and
407 environment were better known, future independent analyses of ecological disparity
408 and morphological disparity^{36, 74} might provide a deeper understanding of the waxing
409 and waning of brachiopod diversity in Meso–Cenozoic oceans.

410

411 **Concluding remarks**

412 Although brachiopod diversity remained low and did not show great fluctuations in
413 the Mesozoic and Cenozoic, morphological evolution shows a far more dynamic

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

428 Overall, the morphological evolution of the four orders displayed very different
429 patterns across the three mass extinctions in the studied interval: an extinction event
430 may be morphologically selective (e.g., TJME on athyridides) or nearly non-selective
431 (e.g., PTME on athyridides, KPgME on terebratulides) and the long-term impacts on
432 disparity values may be weak (e.g., PTME on the four orders) or strong (e.g., TJME
433 on athyridides and spiriferinides), demonstrating the great heterogeneity among
434 lineages and extinction events. This study highlights the importance of investigating
435 morphological evolution as well as species (or generic) richness in order to
436 understand the evolutionary history of a clade.

437

438

439 **Methods**

440 **Fossil datasets**

441 This study aims to investigate the morphological evolution and diversity decline of
442 Meso–Cenozoic brachiopods, thus the orders restricted to the Paleozoic (e.g.,

443 Productida, Orthotetida, Orthida, Spiriferida, and Dictyonellida) were not considered.
444 In the Mesozoic and Cenozoic, articulate brachiopods consist of five orders:
445 Terebratulida, Rhynchonellida, Spiriferinida, Athyridida, and Thecideida. Thecideida
446 has a very rare fossil record and was not included in the compiled comparative dataset
447 for this study. Inarticulate brachiopods (orders Lingulida and Craniida) are quite
448 distinct ecologically and anatomically. However, they have a very low diversity after
449 the Paleozoic and their fossil records are discontinuous, preventing a complete and
450 detailed analysis. Therefore, this study focused on the evolution of four orders:
451 Terebratulida, Rhynchonellida, Spiriferinida, and Athyridida, representing
452 together >95% of total genus richness of all Meso–Cenozoic brachiopods; the study
453 of these four groups is sufficient to understand the Meso–Cenozoic decline of
454 brachiopods.

455 Fossil occurrences of Terebratulida, Rhynchonellida, Spiriferinida, and
456 Athyridida from the Permian to Recent (~298.89–0 Ma) were downloaded from the
457 Paleobiology Database on 29/3/2024. All analyses herein were carried out at the
458 genus level. The data cleaning and revision procedure followed Guo et al.¹⁰. Simply,
459 (1) the name of each genus was examined, and only valid names were retained; (2) the
460 temporal duration of each genus was checked, and doubtful records, namely those
461 outside the stratigraphical range in well-curated datasets such as *Treatise on*
462 *Invertebrate Palaeontology*⁵¹ and Sepkoski's compendium¹⁶, were discarded; (3) the
463 ages of taxonomic occurrences were updated according to the Geological Time Scale
464 2020⁷⁵, using the *fossilbrush* R package⁷⁶; occurrences with a high temporal
465 uncertainty (>10 Myr) but not from an international stage were removed. In addition,
466 the new Permian–Jurassic occurrences added by Guo et al.¹⁰ were kept. Occurrences
467 of 134 genera included in the *Treatise* but absent in PBDB were also added to the
468 final dataset compiled here.

469 Presence/absence tables of taxa from the Permian to the present-day were made
470 based on the fossil occurrence data. To ensure a roughly equal duration for each time
471 bin, we divided the Permian–Quaternary time span into 30 intervals: P1, Asselian–
472 Sakmarian; P2, Artinskian; P3, Kungurian; P4, Roadian–Capitanian; P5,

473 Wuchiapingian–Changhsingian; T1, Induan–Olenekian; T2, Anisian–Ladinian; T3,
474 Carnian; T4, Norian; T5, Rhaetian; J1, Hettangian–Sinemurian; J2, Pliensbachian; J3,
475 Toarcian; J4, Aalenian–Bathonian; J5, Callovian–Oxfordian; J6, Kimmeridgian–
476 Tithonian; K1, Berriasian–Valanginian; K2, Hauterivian–Barremian; K3, Aptian; K4,
477 Albian; K5, Cenomanian–Turonian; K6, Coniacian–Santonian; K7, Campanian; K8,
478 Maastrichtian; Cz1, Paleocene; Cz2, Ypresian–Lutetian; Cz3, Bartonian–Priabonian;
479 Cz4, Rupelian–Chattian; Cz5, Aquitanian–Serravallian; Cz6, Tortonian–Holocene.
480 Except for some bins with very long durations such as Norian (T4), others have a span
481 close to 10 Myr. The ‘range-through’ method was employed to infill the
482 presence/absence tables of genera, and diversity was calculated based on generic
483 richness counts following their stratigraphical ranges. Thus, Carboniferous records
484 were also employed to extend the ranges of some Permian taxa. To eliminate the
485 effect of ‘the Pull of the Recent’⁷⁷, the present-day records of fossil taxa were not
486 considered, and living genera without fossil records were also ignored.

487

488 **Morphological datasets**

489 The four orders are very different in both external and internal morphologies.
490 Therefore, we analysed morphological disparity of each order separately and devised
491 specific character lists for each order (see Supplementary Information). The characters
492 of Spiriferinida were modified from those of Guo et al.⁴¹. Nevertheless, only external
493 characters were included in Guo et al.’s dataset, so the internal structures of this order
494 were added in the new dataset analysed in this study. The characters of
495 Rhynchonellida were selected and emended based on Schreiber et al.⁷⁸ and Guo et
496 al.⁷⁹. The characters of Terebratulida and Athyridida were inspired by Carlson and
497 Fitzgerald⁸⁰ and Alvarez and Rong⁶³, respectively.

498 In contrast to previous studies on brachiopod disparity³⁸, almost all major
499 external (e.g., outline, convexity, umbo features, ornamentation) and internal (e.g.,
500 dental plates, hinge plates, loop supporting structure) characters of shells that are
501 commonly described in systematic studies were compiled in the dataset. Soft-body-
502 related features were omitted because they are rarely known in fossil taxa.

503 Cladistically non-informative characters (i.e., autapomorphies, traits only appearing in
504 one taxon) were included to comprehensively describe the morphological variation
505 and retain unique innovations⁸¹. Characters are continuous (e.g., shell width relative
506 to shell length) or discrete, with the discrete characters being either ordered (e.g.,
507 position of ventral foramen) or unordered (e.g., type of anterior commissure). Some
508 nested relationships are present in the characters (e.g., the ‘orientation of dental plates’
509 is dependent on the ‘presence/absence of dental plates’), so characters were
510 subdivided into ‘primary’ and ‘secondary’ categories, which would have implications
511 during the calculation of the distance matrices and stop secondary characters re-
512 ranking the pairwise dissimilarities based on primary ones⁸². In total, 128, 81, 48, and
513 59 characters were coded for Terebratulida, Rhynchonellida, Spiriferinida, and
514 Athyridida, respectively. Detailed descriptions of characters are provided in the
515 Supplementary Information.

516 The character states of each genus were coded based on the adult morphology of
517 its type species. If the type species was not perfectly known, another species under the
518 same genus was selected. Ontogeny is vital in studying the evolution of brachiopods,
519 and it is used as a key diagnosis in the higher-level classification units (e.g., the
520 complex loop development in Lobidothyridoidea vs. the simple loop development in
521 Terebratuloidea⁴⁴). Nevertheless, ontogenetic variation is only known in a very small
522 fraction of taxa⁴⁴. Therefore, only the morphology of adults was considered in this
523 study. Continuous characters were measured on one specimen of the type species, in
524 most cases, the one shown in the *Treatise*. One may argue that such measurements are
525 highly variable within one genus or one species (e.g., the interarea height of
526 *Liospiriferina* species). However, owing to the long time interval and wide taxonomic
527 scope of our study, normally, greater differences appear between than within genera
528 (e.g., the low interarea of *Liospiriferina* compared with the high interarea of
529 *Cisnerospira*).

530

531 **Disparity analysis**

532 The morphological datasets were employed to calculate pairwise dissimilarity

533 matrices using the Maximum Observable Rescaled Distance metric⁸³. The alpha value
534 applied to balance the contribution of primary characters and secondary characters
535 was set to 0.5 as recommended⁸². Recent studies have shown that missing data can
536 affect the position of taxa in morphospace^{84, 85}. Therefore, prior to the calculation of
537 the distance matrices, taxa with more than 20% or 30% (20% for terebratulides and
538 rhynchonellides; 30% for spiriferinides and athyridides) unknown characters (marked
539 by question mark ‘?’) were discarded from the dataset. For terebratulides, taxa whose
540 loop type is not revealed were also deleted because the loop structures have many
541 morphological characters and these include the most important criteria for the
542 classification of terebratulides. In the end, less than 10.5% genera in these orders were
543 discarded, and 529, 332, 104, and 54 genera were retained in the terebratulid,
544 rhynchonellide, spiriferinide, and athyridide datasets, respectively (Supplementary
545 Information). The diversity trajectories of the reduced datasets significantly correlate
546 with that of the raw datasets (both raw and detrended diversities; Pearson’s $r > 0.98$, p
547 < 0.05 ; Extended Data Fig. 1). The dissimilarity matrices were arcsine square root
548 transformed to make sure that the distances were normally distributed⁸³. To construct
549 morphospaces, principal coordinates analysis (PCOA) was applied to the transformed
550 dissimilarity matrix using the *pcoa* function of the *ape* R package⁸⁶. A Cailliez
551 correction⁸⁷ was also employed to deal with negative eigenvalues, at the expense of
552 reducing the reported variance expressed by each axis⁸⁸.

553 There are multiple ways to evaluate the distribution of taxa in a morphospace
554 and generate within-bin disparity time series, and each measurement has its
555 advantages and disadvantages^{89, 90}. We employed two popular metrics, the sum of
556 variances (SOV) and sum of ranges (SOR), to demonstrate the evolutionary trends of
557 morphological disparity. SOV describes the density of taxa within the occupied
558 morphospace area, while SOR reflects the total range of the area occupied. SOR has
559 some obvious drawbacks. It is sensitive to, and usually positively correlates with,
560 sample size. Thus, rarefaction analysis is needed to compare the SOR of two
561 samples⁹¹, which may result in very wide confidence intervals if the sample size is
562 low. Moreover, SOR cannot reflect variation in the central part of the morphospace

563 (e.g., unoccupied central ‘holes’) and it is easily biased by taxa located in marginal
564 areas of morphospace and outliers^{89, 90}. In contrast, SOV is insensitive to sample size
565 and outliers; therefore, it is widely used by many researchers although it may be
566 biased by taxonomic over-splitting or clumping. In this paper, we prefer to use the
567 SOV as an overall indicator of disparity. SOR was calculated as a complementary
568 index (Extended Data Fig. 2). Both SOV and SOR were calculated from PCO scores
569 of all axes. For each time bin, the median value and 95% confidence intervals were
570 calculated based on 1000 bootstrap replications⁹². For SOR, because of its sensitivity
571 to sample size, the number of taxa was rarefied to the lowest diversity of all time bins
572 in the terebratulide and rhynchonellide analyses, and to the median diversity of all
573 time bins in the spiriferinide and athyridide analyses. All disparity calculations were
574 accomplished by the *dispRity*⁹³ and *vegan*⁹⁴ R packages.

575

576 **Morphospace occupation**

577 Differing from density (SOV) and size (SOR), the position of taxa in morphospace is
578 another important aspect of morphological analysis⁹⁰. The distribution of taxa in
579 morphospace and variations in morphospace occupation are usually displayed directly
580 in the form of biplots of the major axes (Fig. 2; Extended Data Figs. 3–6). However,
581 when the first few PCO axes only explain a low percentage of the overall variation
582 (such as the rhynchonellide morphospace in this study; Extended Data Fig. 7), only a
583 small proportion of total variation can be observed directly on the morphospace
584 visualisation and a great fraction of variation is hidden on other axes.

585 Here we employed a centroid-related metric to evaluate the movement of
586 morphospace occupation. The ‘position of centroid’ is an easy way to describe the
587 position of taxa, which has been widely used by other researchers^{31, 74}. Normally, the
588 distribution of taxa in the morphospace may be non-normal and complex, and
589 therefore, some variation in morphospace cannot be indicated by shifts in centroid.
590 However, the centroid is easy to calculate and to compare between different time bins,
591 and more importantly, it can reflect asymmetrical variation in occupation, which is
592 related to selective extinction or origination³¹. A major advantage of reporting

593 centroid-related metrics is that centroids can be calculated using all PCO axes, not just
594 the first two or three⁷⁴. In contrast, a direct observation of morphospace (usually
595 constructed from the first two or three axes) cannot show information on other axes,
596 and this cannot be ignored when the first few axes explain such a low proportion of
597 the variance. Therefore, the centroid-related metric is a valuable complement to the
598 morphospace.

599 For every order, we first partitioned the morphospace according to
600 presence/absence table of taxa, and calculated the position of the centroid of all time
601 bins using all PCO axes. Next, Euclidean distances between centroids in different
602 time bins were calculated. This calculation generated a distance matrix of all time
603 bins; the distances between centroids of two adjacent bins were extracted as the ‘shifts
604 in centroid’. Finally, we use the PCOA (equivalent to principal component analysis
605 because the Euclidean distance was used) to visualise this distance matrix (i.e., the
606 ‘centroid space’). No further calculation was performed on the centroid space.

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

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

615

616 **Data availability**

617 Occurrence data were downloaded from the Paleobiology Database
618 (<https://paleobiodb.org/>). The added Permian–Jurassic fossil occurrences were from
619 Guo et al.¹⁰. All occurrence data and character matrices analysed are available in
620 Zenodo (<https://doi.org/10.5281/zenodo.11559129>)⁹⁵.

621

622 **Code availability**

623 All R scripts used to conduct the analyses are available in Zenodo
624 (<https://doi.org/10.5281/zenodo.11559129>)⁹⁵.

625

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633

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635 morphological data. Z.G. and T.L.S. performed the analysis. All authors discussed the
636 results. Z.G. drafted the paper with substantial input from all authors.

637

638 **Competing interests** The authors declare no competing interests.

639

640 **Figure Captions**

641 **Fig. 1. Diversity of Permian–Quaternary brachiopods.** The four orders analysed in
642 this study comprise the majority of the post-Permian brachiopod diversity.

643 Abbreviations: P Permian, Tr Triassic, J Jurassic, Ear. Jura. Early Jurassic, K
644 Cretaceous, Pg Paleogene, Ng Neogene, PTME Permian-Triassic mass extinction,
645 TJME Triassic-Jurassic mass extinction, KPgME Cretaceous-Paleogene mass
646 extinction.

647

648 **Fig. 2. Disparity and diversity of four brachiopod orders through time.** Disparity
649 is measured by sum of variances (SOV). The solid lines represent median value of the
650 bootstrapped disparity. The envelopes indicate 95% confidence intervals (0.025 and
651 0.975 quantiles of bootstrapped values). Diversity (number of genera) is represented
652 by dashed lines. **a**, Terebratulida; **b**, Rhynchonellida; **c**, Spiriferinida; **d**, Athyridida.

653 Abbreviations: P Permian, Tr Triassic, J Jurassic, Ear. Jura. Early Jurassic, K
654 Cretaceous, Pg Paleogene, Ng Neogene, PTME Permian-Triassic mass extinction,
655 TJME Triassic-Jurassic mass extinction, KPgME Cretaceous-Paleogene mass
656 extinction.

657

658 **Fig. 3. Morphospace occupation of the four brachiopod orders through time. a,**
659 **Terebratulida; b, Rhynchonellida; c, Spiriferinida; d, Athyridida.** Morphospaces are
660 constructed by the first two axes (PCO1 and PCO2). The number in labels indicates
661 the percentage of variances explained by the axis. The black cubes in **c** and **d**
662 represent Jurassic taxa. The cartoons (from left to right) in **a** represent long-looped,
663 deltidform-looped and inner-hinge-plates-lacking, ring-like-looped, septal-pillar-
664 bearing and loop-incomplete, and septal-pillar-bearing and loop-floor-fused
665 terebratulides, respectively. Those in **b** represent hinge-plates-fused, camarophorium-
666 bearing, septalium-bearing-raducal, and septifal rhynchonellides, respectively. Those
667 in **c** represent spiriferiform and median-septum-lacking, reticulariiform, and
668 cyrtiniform spiriferinides, respectively. Those in **d** represent multicostate-punctate,
669 concavoconvex, and bivoncx athyridides, respectively. Morphospace occupation
670 variation in finer time bins see Extended Data Figs. 3–6.

671

672 **Fig. 4. Morphospace centroid spaces and shifts in centroid position of four**
673 **brachiopod orders. a, b, Terebratulida; c, d, Rhynchonellida; e, f, Spiriferinida; g, h,**
674 **Athyridida.** Centroid spaces (**a, c, e, g**) are visualisations (using PCOA) of the
675 distance matrix of centroids in morphospace, and are constructed from the first two
676 axes (PCO1 and PCO2). Numbers in axis labels indicate the percentage of variance
677 explained. The grey arrows indicate the trend of centroid movement in the centroid
678 space. Shifts in centroid (**b, d, f, h**) indicate distance between centroids of one bin and
679 its previous bin in the morphospace. In the plots of centroid space, the size of a dot is
680 related to the diversity in that time bin. In the plots of centroid shifts, the size of a dot
681 is proportional to the lower value of diversity in that bin and diversity in its previous
682 bin (e.g., the size is proportional to 20 if diversities in that bin and its previous bin are

683 30 and 20, respectively). The larger the dot, the more reliable the shift because of
684 larger sample size. The red lines represent mass extinctions. Abbreviations of time bin
685 names see Methods. See Extended Data Fig. 8 for centroid spaces with bin names
686 labelled.

687

688 **Fig. 5. Reconstructions of some post-Permian brachiopods, showing adaptations**
689 **to certain environments. a**, small-sized terebratulides and tiny rhynchonellides
690 living in shallow-water caves; **b**, concavoconvex athyridides and spiriferinides with
691 high interarea adapted to soft substrates; **c**, smooth and weakly ornamented
692 rhynchonellides and terebratulides living in deep environments. Drawn by S.Y. Shi.

693

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