

1 Permian–Triassic evolution of the Bivalvia: extinction-recovery patterns  
2 linked to ecologic and taxonomic selectivity

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10

11 Abstract

12 The Bivalvia is an important benthic clade that was relatively less affected than  
13 other benthos during the Permian–Triassic (P–Tr) biotic crisis, reporting losses of  
14 85%, 64%, and 32% at the species, genus and family levels, respectively. This clade  
15 proliferated immediately after the P–Tr mass extinction (PTME) to become one of the  
16 key elements of the ‘Modern Evolutionary Fauna’ following the P–Tr ‘Great Dying’.  
17 Global bivalve occurrence data demonstrate that the initial recovery started in the  
18 Griesbachian, a substage immediately after the PTME, and are characterized by  
19 relatively high origination and low extinction rates. Thus, unlike other fossil groups,  
20 bivalves did not significantly engage in the survival interval. The initial Griesbachian  
21 recovery is followed by a stepwise recovery during the Dienerian to Spathian. Then, a  
22 remarkably rapid radiation occurred in the Anisian, indicated by extremely high  
23 proportional origination and extinction rates. Infaunalization has long been considered  
24 the most significant adaptation during the Mesozoic Marine Revolution (MMR),  
25 which was thought to have commenced in the Early–Middle Triassic. However, the  
26 proportion of infauna in communities remained virtually unchanged before and after  
27 the P–Tr biotic crisis; additionally there was no significant difference in proportional  
28 extinction/origination rates between infaunal and epifaunal taxa at the genus and  
29 family levels through the entire P–Tr transition, implying the absence of ecological

30 selectivity, a conclusion that differs from some previous studies. Therefore, if  
31 escalating predatory pressure indeed played a crucial role in driving the initial phases  
32 of the MMR, infaunalization was not marked prior to the Ladinian. Alternatively,  
33 infaunalization may have played a minor role in facilitating the MMR during the  
34 entire era. If so, changes in the physical and chemical environment ('Court Jester'  
35 model) (i.e. amelioration of marine environments in late Early Triassic), rather than  
36 biotic processes ('Red Queen' model), may be crucial for the origination and initial  
37 phases of the MMR during the early Mesozoic.

38

39 *Keywords: mass extinction; biotic recovery; infaunalization; Mesozoic Marine*  
40 *Revolution; macroevolution*

41

## 42 **1. Introduction**

43

44 Of the 'Big Five' mass extinctions, the Permian–Triassic (P–Tr) biotic crisis  
45 resulted in the largest drop in biodiversity and the most devastating ecosystem  
46 collapse during the Phanerozoic (Sepkoski, 1981, 1984). Global biodiversity data  
47 show that various fossil groups behaved differently during and after the PTME. Some  
48 clades like brachiopods and corals that suffered substantially during the biotic crisis  
49 recovered much later than some other groups (Hallam and Wignall, 1997; Erwin,  
50 1998; Chen et al., 2005a, b); others such as ammonoids (Brayard et al., 2009),  
51 foraminiferans (Song et al., 2011), and ophiuroid echinoderms (Chen and McNamara,  
52 2006) rebounded earlier after the P–Tr crisis. The distinctive responses to the PTME  
53 and its aftermath may be due to the different roles that various clades played within  
54 the trophic structure of the marine ecosystem (Chen and Benton, 2012). The biotic  
55 groups within the low-level trophic structure may have garnered relatively less  
56 attention from the PTME, and thus rebounded earlier than the meso-consumers or  
57 predators (Chen and Benton, 2012). Alternatively, physiologic adaptation in some key  
58 groups may have developed resistance to environmental devastation such as  
59 widespread anoxia, ocean acidification, and extreme hot seawater temperatures (Knoll

60 et al., 2007; Payne and Clapham, 2012); such resistance may be accountable for the  
61 biodiversity variations within the various groups over the P–Tr transition. Thus, both  
62 the physiology and ecological function of organisms provide some clues for  
63 unraveling the causes of the PTME and its protracted recovery (Knoll et al., 2007).  
64 Nevertheless, to date, debate still continues on whether the physical and chemical  
65 environment (‘Court Jester’ model) or biotic processes (‘Red Queen’ model) have  
66 driven biotic macroevolution over this critical interval (Benton, 2009; Chen and  
67 Benton, 2012).

68         Like many other clades, the Bivalvia underwent its greatest macroevolutionary  
69 turnover during the P–Tr transition (Erwin, 1994, 2006; Hallam and Wignall, 1997).  
70 They were subordinate in Permian communities, but became the most numerically  
71 abundant shelly fossils in the Griesbachian, the first substage following the PTME.  
72 Bivalves, together with other molluscs (i.e. ammonoids and gastropods), successfully  
73 usurped brachiopod dominance in marine shelly communities through the P–Tr  
74 transition (Thayer, 1985; Fraiser and Bottjer, 2007; Chen et al., 2010). This is possibly  
75 because they are less sensitive to anoxia (Taylor and Brand, 1975; Bayne and  
76 Livingstone, 1977; Wang and Widdows, 1993a, b; Diaz and Rosenberg, 1995; Sobral  
77 and Widdows, 1997; MacDonald et al., 1998; Ballanti et al., 2012).

78         Another feature of the PTME is the switch from brachiopod-dominated  
79 Paleozoic Evolutionary Fauna (EF) to mollusc-dominated Modern EF in marine  
80 ecosystems (Gould and Calloway, 1980; Sepkoski, 1981, 1984; Bambach et al., 2002;  
81 Fraiser and Bottjer, 2007; Alroy, 2010; Chen et al., 2010). The marine ecosystem has  
82 undergone an unprecedented, far-reaching transformation in the aftermath of the  
83 PTME that is mainly responsible for the marine ecosystem we have today. The term  
84 “restructuring” is more appropriate than “rebound” or “recovery” to describe the  
85 turnover in the biosphere (Dineen et al., 2014).

86         Previous studies show that the Bivalvia only suffered moderate disruption  
87 during the PTME based on variation in taxonomic richness and extinction rates  
88 (Nakazawa and Runnegar, 1973; Yin, 1985, 1987; Li, 1995; Fang, 2004; Huang et al.,  
89 2014). They underwent a gradual and stepwise recovery after the PTME (McRoberts,

90 2001). However, these observations were based mainly on changes in taxonomic  
91 richness without consideration of other important proxies, like proportional extinction  
92 and origination rates, as well as ecological selectivity through this critical interval.  
93 The updated, global database for the bivalves mitigates sampling bias and Lazarus  
94 effects that would largely obscure the real changing pattern of biodiversity. In addition,  
95 bivalve lifestyles are categorized into five types: infaunal motile, infaunal  
96 slow-moving, semi-infaunal motile, epifaunal stationary and low-level epifaunal  
97 stationary modes (Li, 1995; Komatsu et al., 2008; Huang et al., 2014). They represent  
98 various physiologic types associated with different habitats and climatic regimes. The  
99 proportional extinction and origination rates of the various physiologic groups may  
100 provide some insight into the environmental and climatic extremes associated with the  
101 PTME and subsequent events.

102 Infaunalization was supposedly prevalent amongst Early Mesozoic bivalves  
103 (McRoberts, 2001) by the fact that the proportion of the infauna was higher, possibly  
104 much higher than that of the epifauna (Vermeij, 1977; Thayer, 1979). Although the  
105 origination rates of the epifauna and infauna showed no significant differences, the  
106 epifauna had much higher extinction rates than that of the infauna during the same  
107 interval (McRoberts, 2001). Here, we probe the extinction and recovery patterns of  
108 the Bivalvia and their ecologic selectivity over the P–Tr transition by re-examining  
109 the global dataset derived from the Paleobiology Database with emphasis on the  
110 variations in taxonomic richness, and proportional extinction and origination rates at  
111 the species, genus and family levels, respectively. Infaunalization through the entire  
112 Early Triassic is also assessed on the basis of proportions of infauna/epifauna in the  
113 aftermath of the PTME, testing the possible driving force of the MMR in the early  
114 Mesozoic.

115

## 116 **2. Materials and methods**

117

118 All bivalve occurrences from the Changhsingian (highest Permian), Lower  
119 Triassic substages to the Anisian (Middle Triassic) analyzed in this study are sourced

120 from Paleobiology Database [[http://fossilworks.org/bridge.pl? a=displayBasic](http://fossilworks.org/bridge.pl?a=displayBasic)  
121 *DownloadForm*] and were downloaded in May, 2014. To enhance the resolution of  
122 the geological timescale, the Induan and Olenekian were subdivided into the  
123 Griesbachian and Dienerian, the Smithian and Spathian substages, respectively. Thus,  
124 a total of six time bins (Changhsingian, Griesbachian, Dienerian, Smithian, Spathian,  
125 and Anisian) are employed to calculate biodiversity (taxonomic richness) and  
126 proportional extinction and origination rates. Species, genus, and family richness of  
127 each time bin were taken into account in examining biodiversity variations from the  
128 Changhsingian to Anisian. All genera have formal taxonomic names. And species of  
129 uncertain taxonomic status (i.e., Genus sp.) were included, in agreement with some of  
130 previous studies (Chen et al., 2011; Huang et al., 2014), but they were counted only  
131 once within each named genus in order to minimize taxonomic bias. The species  
132 qualified with terms like “cf.” or “aff.” are also included in this study. However,  
133 sample intensities are clearly variable across different geological periods, thus,  
134 rarefaction analysis (Raup, 1975) computed by the palaeontological software package  
135 PAST (Hammer et al., 2001) was implemented to test taxonomic bias (e.g., Chen et al.,  
136 2010, Chen et al., 2011). It is common to plot specimen counts against the numbers of  
137 a defined taxonomic rank (i.e. numbers of species or genera) in rarefaction analysis.  
138 Nevertheless, information on specimen counts is not available in the Paleobiology  
139 Database. Therefore, the rarefaction of occurrences against genera (Fig. 1A) and two  
140 adjacent taxonomic ranks plotted against each other (Fig. 1B) were both used herein.  
141 Concerning the latter, it is noteworthy that rarefaction analysis between two adjacent  
142 ranks (i.e. species/genus or genus/family) is likely to decrease or obscure the  
143 difference between diversity curves with relatively high confidence limits (i.e. 95%  
144 confidence limit) (Shen et al., 2000). Therefore, the rarefaction analysis of species  
145 richness against family richness is employed to determine sampling quality (Fig. 1B).  
146 Moreover, a confidence limit (95%) was used to examine the robustness of rarefaction  
147 curves. To better understand the taxonomic selectivity of bivalves through the P–Tr  
148 transition, all orders of this clade were investigated using biodiversity at different  
149 taxonomic levels.

150 To unravel the true extinction and recovery patterns of the Bivalvia over the  
151 P–Tr transition, we also calculated the proportional extinction and origination rates  
152 (Harper and Gallagher, 2001; Bambach et al., 2004) in each time bin, from the  
153 Changhsingian to Anisian at the species, genus, and family levels, respectively,  
154 according to the equations below:

155 Proportional Extinction rate =  $N_{\text{extin}}/N_0 \times 100\%$ ,

156 Proportional Origination rate =  $N_{\text{orig}}/N_0 \times 100\%$ ,

157 where  $N_0$  represents the number of all taxa during certain stage (substage),  $N_{\text{extin}}/N_{\text{orig}}$   
158 represents the number of extinction/origination taxa over the same interval,  
159 respectively. The 95% confidence interval of sample sizes was shown using the  
160 “Wilson Score Interval” method programmed in R software. Moreover, a Z-test was  
161 performed to examine the significance of the differences in extinction/origination rate  
162 between the next two time bins, which may provide some insights into the actual  
163 evolutionary patterns of the Bivalvia.

164 To shed light on the ecologic selectivity over the P–Tr transition, both  
165 taxonomic richness and proportional extinction/origination rates were employed to  
166 analyze the different physiological groups of bivalves at species, genus, and family  
167 levels, respectively. However, several physiological groups have a very small number  
168 of taxa in some time bins, which can bias understanding of true ecologic selectivity.  
169 Thus, we subdivided, collectively, the bivalves into two ecologic types: infaunal and  
170 epifaunal lifestyles. The former includes infaunal motile, infaunal slow-moving, and  
171 semi-infaunal motile, while the latter comprises epifaunal stationary and low-level  
172 epifaunal stationary. Their proportional extinction/origination rates were re-calculated.  
173 A Z-test was applied not only to test the significance of differences in richness  
174 between two adjacent time bins but also to examine the significance of proportional  
175 extinction/origination rates differences between the two ecologic groups (i.e. infauna  
176 and epifauna).

177

### 178 **3. Results**

179

180 *3.1 The timing and patterns of extinction-recovery of bivalves*

181

182 *3.1.1 Biodiversity changes*

183 Compared with some typical Paleozoic-type clades (i.e. brachiopods, crinoids,  
184 and rugose corals), bivalves underwent a less marked biodiversity turnover over the  
185 P–Tr boundary. Pre-extinction Changhsingian bivalves are very diverse, including 368  
186 species, 118 genera, and 47 families. Their biodiversity declined by ~56%, 62%, and  
187 43% at the species, genus, and family levels, respectively in the PTME, and only 162  
188 species, 45 genera and 27 families occur in the Griesbachian (Fig. 2).

189 Another apparent decline in biodiversity occurred throughout part or all of the  
190 Griesbachian, with drops of ~69%, 42%, and 22% species, genera, and families,  
191 respectively. Surprisingly, the Dienerian witnessed the lowest taxonomic richness  
192 within all Early Triassic time bins, having only 50 species, 26 genera, and 21 families  
193 (Fig. 2).

194 The Smithian saw the first increase in richness at all taxonomic levels after the  
195 PTME, with a surge of 128%, 69%, and 43%, to levels of 144 species, 44 genera, and  
196 30 families in this time bin (Fig. 2). Biodiversity further increased through time, with  
197 172 species, 73 genera and 36 families present in the Spathian (Fig. 2).

198 Biodiversity continued to rise to a peak in the Anisian, up to, surprisingly, 424  
199 species, 123 genera, and 57 families (Fig. 2), with increases of 146%, 68%, and 58%,  
200 respectively from the last time bin. Such a pronounced increase in biodiversity signals  
201 a major radiation of this clade following the P–Tr biotic crisis (Komatsu et al., 2004).

202 The P–Tr biodiversity change apparently exhibits a persistent decline from the  
203 latest Permian (i.e. Changhsingian) up to the Dienerian, with the first proliferation in  
204 the Smithian and a stepwise recovery through the Smithian to Anisian when this clade  
205 dramatically diversified. However, both sampling bias and the Lazarus effect in terms  
206 of biodiversity may, to some extent, obscure the true pattern. Therefore, when the  
207 initial recovery of this group occurred remains unknown.

208

209 *3.1.2 Taxonomic selectivity*

210 The Changhsingian assemblage is very diverse and includes 16 orders (Fig. 3;  
211 Table S1). The Pectinida is the most diverse group, containing 162 species accounting  
212 for 44% of total taxa, followed by the Ostreida, Myalinida, Trigoniida, and Cardiida  
213 (Fig. 3; Table S1). The remaining orders include only a small number of species.

214 Intriguingly, all the orders survived the PTME although they behaved  
215 distinctively during the crisis and its aftermath. The Pholadida, Solemyida,  
216 Modiomorphida, and Arcida vanished in the Griesbachian, but re-appeared in the late  
217 Early Triassic, probably indicating a Lazarus effect (Jablonski, 1996; Wignall and  
218 Benton, 1999; Twitchett, 2000; Fara, 2001; Rickards and Wright, 2002). The  
219 Pholadomyida (with a decline of 92% species), Carditida (92%), Nuculanida (86%),  
220 and Pterioida (86%) all suffered dramatic biodiversity drops in the PTME. In contrast,  
221 the Ostreida experienced only a moderate to minor reduction in biodiversity across the  
222 P–Tr boundary, with a decrease of ~31% species. The Griesbachian bivalves show  
223 almost no difference from the Changhsingian assemblage in terms of the  
224 compositions of the major groups. The Pectinida is the predominant group,  
225 accounting for 56% of total species, followed by the Ostreida, Myalinida, and  
226 Trigoniida (Fig. 3; Table S1).

227 The Dienerian witnessed an apparent depletion in biodiversity relative to the  
228 Griesbachian. Of these, six groups (i.e., the Arcida, Lucinina, Modiomorphida,  
229 Pterioida, Mytilida, Nuculida, and Solemyida) disappeared in this interval, but  
230 re-appeared in the late Early Triassic, signaling a Lazarus effect. Like the  
231 Griesbachian assemblage, the Dienerian faunas are also dominated by the Pectinida  
232 representing ~38% of total species. However, the importance of three groups, the  
233 Myalinida, Ostreida, and Trigoniida (Fig. 3; Table S1) is almost equivalent, at least in  
234 terms of richness.

235 Biodiversity proliferated during the Smithian. The fauna was dominated by the  
236 Pectinida, followed by the Ostreida, Trigoniida and Myalinida (Fig. 3; Table S1).  
237 Apart from those major groups, diversification of other groups also characterized this  
238 substage, like the Nuculanida, Ostreida, and Pectinida. The Spathian bivalves  
239 experienced a minor increase in biodiversity and are dominated by the Pectinida,



240 followed by the Ostreida and Trigoniida, exhibiting a similar taxonomic composition  
241 to the Smithian assemblage. However, the Nuculanida, instead of the Myalinida,  
242 became the fourth most diverse group (Fig. 3; Table S1).

243 All orders increased in richness in the Anisian, coupled with the appearance of  
244 some new groups (i.e. the Hiattellida, Megalodontida, and Pandorida). The Ostreida  
245 replaced the Pectinida and was now the most diverse group at the species level. While  
246 the Pectinida remained the predominant group at the genus, and family levels. The  
247 Trigoniida, Mytilida, Cardiida, Carditida, and Nuculanida (Fig. 3; Table S1) are all  
248 major players that contributed to the Anisian radiation of the entire clade.

249 To sum up, the Ostreida, Trigoniida, and Mytilida performed well during the  
250 PTME and responded well to any subsequent environmental stresses; the richness of  
251 these groups rebounded in the Anisian. In contrast, the Pectinida, Myalinida, and  
252 Pholadomyida suffered from the end-Permian ‘Great Dying’. Bivalves also underwent  
253 a switch of dominance in communities from the Pectinida to the Ostreida between the  
254 Spathian and Anisian, although the presence of this turnover remains to be further  
255 examined due to the availability of only one single interval for sampling.

256

### 257 *3.1.3 Proportional extinction/origination rates*

258 Proportional origination rates are very low among the Changhsingian bivalves,  
259 exhibiting 54%, 19%, and 4%, at the species, genus, and family levels, respectively.  
260 Their proportional extinction rates at the end of the Changhsingian are moderate to  
261 high, up to 85%, 64%, 32% at the species, genus, and family levels, respectively (Fig.  
262 4; Table 1); slightly higher than previous estimates for all taxonomic levels.

263 Intriguingly, the specific origination rate is high in the Griesbachian,  
264 approaching 75%, which is significantly different from the same proxy in the  
265 Changhsingian ( $p < 0.05$ ). Conversely, the proportion extinction rates at all taxonomic  
266 levels display low to moderate levels (Fig. 4; Table 1), also clearly differing from the  
267 same proxies in the previous interval ( $p < 0.05$ ). Accordingly, the relatively high  
268 proportional origination rates, low proportional extinction rates, coupled with a high  
269 biodiversity, indicate that the initial recovery of bivalves may have occurred in the

270 Griesbachian.

271 In the Dienerian, bivalves suffered a moderate proportional extinction rate at  
272 the species level (68%) and much lower extinction rates at the genus (19%) and  
273 family (19%) levels. The proportional origination rates show similar patterns (52%,  
274 19%, 10%). It is noteworthy that the specific origination rate is significantly lower  
275 than that of the Griesbachian faunas ( $p < 0.05$ ) (Fig. 4; Table 1). Moreover, similar  
276 proportional extinction/origination rate patterns are also seen in the Smithian (Fig. 4;  
277 Table 1). The proportional origination rates in the Spathian (62%, 33%, 8%) show no  
278 difference from the same proxies in the Smithian ( $p > 0.05$ ). However, their  
279 proportional extinction rates (79%, 30%, 17%) are higher than their counterparts in  
280 the Smithian (Fig. 4; Table 1). In particular, the specific extinction rate differs clearly  
281 from that in the Smithian ( $p < 0.05$ ). Such high extinction rates suggest that many  
282 species were already extinct prior to the Anisian.

283 The Anisian saw a striking increase in proportional origination rates (83%, 52%,  
284 37%) (Fig. 4; Table 1), showing significant difference at all levels from the Spathian  
285 proxies ( $p < 0.05$ ). The Anisian bivalves are thus very different from the Spathian  
286 faunas in composition. Such a high specific origination rate indicates that speciation  
287 progressed vigorously in the Anisian, and thus contributed significantly to the  
288 radiation within this interval. Surprisingly, proportional extinction rates (75%, 37%,  
289 20%) are also elevated (Fig. 4; Table 1), indicating the rapid evolutionary rates of the  
290 bivalves at this time.

291

### 292 *3.2 Ecologic selectivity*

293

#### 294 *3.2.1 Biodiversity changes among lifestyles of bivalves*

295 Within the Changhsingian bivalve assemblages, the stationary epifauna is the  
296 most diverse, accounting for 54% of all species, followed by the motile infauna and  
297 the stationary low-level epifauna. The other two life modes of bivalves (i.e. the  
298 slow-moving infauna and motile semi-infauna) (Fig. 5; Table S2) account for  
299 relatively low percentages. All life modes survived the PTME, although the motile

300 semi-infauna disappeared during the biotic crisis but re-appeared afterwards. The  
301 stationary low-level epifauna and motile infauna declined by ~76% and 67% at species  
302 levels, respectively, ranking them as the main victims of the PTME. In contrast, the  
303 stationary epifauna experienced a lesser depletion, ~42%.

304       Following the PTME, the stationary epifauna dominated the Griesbachian,  
305 followed by the motile infauna, slow-moving infauna and the stationary low-level  
306 epifauna (Fig. 5; Table S2). Both the slow-moving infauna and stationary epifauna  
307 experienced a remarkable reduction in biodiversity through part or all of the  
308 Griesbachian, with only a very few species persisting into the Dienerian (Fig. 5; Table  
309 S2).

310       Bivalves, irrespective of their lifestyles, all underwent the first post-extinction  
311 proliferation in the Smithian. The stationary epifauna was particularly diverse,  
312 increasing 185% at the species level from the Dienerian assemblage. And the motile  
313 infauna also diversified in the same time bin (Fig. 5; Table S2). Such lifestyles  
314 extended to the Spathian. Subsequently, all bivalve life modes radiated in the Anisian  
315 when the motile semi-infauna experienced an amazing increase, ~350%, 300%, and  
316 300% at the species, genus, and family levels, respectively, followed by the stationary  
317 low-level epifauna (357%, 120%, 50%) and motile infauna (159%, 85%, 73%).

318       Accordingly, the dominance of various lifestyles in each time bin remained  
319 almost unchanged from the Changhsingian to Anisian; any changes in the ecological  
320 preferences of the bivalves were not obvious before and after the PTME.

321

### 322 *3.2.2 Proportions of extinction/origination rates among lifestyles*

323       On the basis of proportional extinction/origination rates, the extinction-recovery  
324 patterns vary amongst different life modes through the P–Tr transition (Fig. 6; Table  
325 S2). However, there is worthy of note that the motile infauna and stationary epifauna  
326 dominated the bivalve assemblages in all time bins and other life modes (e.g., the  
327 stationary low-level epifauna, slow-moving infauna, and motile semi-infauna) usually  
328 consist of a very small number of species. Such small numbers of taxa may bias the  
329 selectivity patterns if each life mode is calculated separately. Accordingly, all bivalves

330 have been re-categorized into two simple lifestyles: the infauna and epifauna.

331

### 332 3.2.2.1 *Infauna*

333 The Changhsingian infaunal bivalves suffered very high extinction rates, up to  
334 87%, 65%, and 32% at the species, genus, and family levels, respectively during the  
335 PTME (Fig. 7; Table 2). In the Griesbachian, this lifestyle group displayed rather high  
336 proportional origination rates at the species level, up to 70% and relatively low  
337 extinction rates (Fig. 7; Table 2). Surprisingly, 74% of species in the Dienerian  
338 infauna are newcomers.

339 Infaunal bivalves exhibit similar proportional extinction/origination rates  
340 between the Smithian and Spathian. Their proportional origination rates increased  
341 markedly in the Anisian, surging from 59%, 33%, and 6% in the Spathian to 82%,  
342 54%, and 39% at the species, genus, and family levels, respectively (Fig. 7; Table 2).  
343 Both specific and familial origination rates are significantly different ( $p < 0.05$ ) from  
344 the same proxies in the Spathian. The elevated origination rates, coupled with high  
345 extinction rates in Spathian, suggest rapid speciation and turnover during the Anisian.

346

### 347 3.2.2.2 *Epifauna*

348 Like the infaunal elements, the Changhsingian epifaunal bivalves also suffered  
349 high proportional extinction rates, up to 85%, 61%, and 21% at the species, genus,  
350 and family levels, respectively during the P–T ‘Great Dying’. In the Griesbachian, the  
351 epifauna experienced much higher ( $p < 0.05$ ) origination rates at the species level, and  
352 lower extinction rates, particularly in the species and genus levels ( $p < 0.05$ ) than those  
353 in the Changhsingian (Fig. 7; Table 2). As a consequence, the composition of  
354 epifaunal assemblages changed significantly across the P–Tr boundary.

355 The epifaunal group experienced relatively low proportional extinction rates  
356 (48%, 8%, 0%) and origination rates (33%, 8%, 0%) in the Dienerian (Fig. 7; Table 2).  
357 Importantly the specific origination rate differs significantly ( $p < 0.05$ ), from that in the  
358 Griesbachian. While, in the Smithian, the epifaunal taxa possessed high proportional  
359 origination rates at the species level, differing significantly ( $p < 0.05$ ) from the

360 counterparts in the Dienerian. In contrast, their extinction rates (65%, 15%, 6%)  
361 exhibit a minor increase (Fig. 7; Table 2) with no significant difference ( $p>0.05$ ) from  
362 Dienerian proxies. The proportional extinction/origination rates of the epifaunal taxa  
363 overall show no significant change from the Smithian to Spathian.

364 In the Anisian, epifaunal bivalves exhibit similar patterns in terms of  
365 proportional extinction/origination rate to those of the infaunal group, marked by high  
366 origination rates (85%, 50%, 30%), differing significantly ( $p<0.05$ ) from those of the  
367 Spathian at the species level, and high extinction rates (73%, 31%, 15%) (Fig. 7;  
368 Table 2), showing no significant difference ( $p>0.05$ ) from the counterparts in the  
369 Spathian. The high origination rates, coupled with high extinction rates in Spathian,  
370 indicate species turnover within the epifauna during the Anisian.

371

### 372 *3.2.2.3 Comparison between the infauna and epifauna*

373 A Z-test was employed to examine the significance of differences with respect  
374 to proportional extinction/origination rates between the infauna and epifauna through  
375 the P–Tr transition. At the species level, the Griesbachian witnessed a significant  
376 ( $p<0.05$ ) higher extinction rate within the epifauna when compared with that within  
377 the infaunal group. The epifauna had significant ( $p<0.05$ ) higher origination rates in  
378 the Changhsingian and Smithian, but much ( $p<0.05$ ) lower origination rates in the  
379 Dienerian, than the other group. No significant difference ( $p>0.05$ ) is observed at the  
380 genus and family levels within any time bin from the Changhsingian to Anisian.

381

## 382 **4. Discussion**

383

### 384 *4.1 The extinction-recovery patterns of the P–Tr bivalves*

385

386 The fossil record from South China suggests that bivalves experienced a  
387 single-phase mass extinction across the P–Tr boundary (Huang et al., 2014). The  
388 PTME therefore is considered as a mono-episode biotic crisis in this study. When  
389 compared to other clades (i.e. brachiopods, corals, and echinoids) (Wang and

390 Sugiyama, 2000; Twitchett and Oji, 2005; Chen et al., 2005a, b; Chen and McNamara,  
391 2006), bivalves suffered a lesser, typically moderate extinction, indicated by the  
392 proportional extinction rate at the genus level during the P–Tr ‘Great Dying’  
393 (Nakazawa and Runnegar, 1973; Yin, 1985, 1987; Li, 1995; Fang, 2004; Huang et al.,  
394 2014). The newly updated global dataset also strengthens this view as bivalves  
395 suffered an extinction rate of 64% at the genus level associated with 85% and 32% at  
396 the species and family levels, respectively. The structure of the marine ecosystem,  
397 however, had undergone the greatest turnover over the P–Tr boundary, featured by the  
398 switch of the predominant composition from the Paleozoic EF to the Modern EF,  
399 coincident with changes in the lifestyles and physiology of both the survivors and  
400 newcomers (Raup, 1979; Sepkoski, 1981; Bambach et al., 2002; Wagner et al., 2006;  
401 Leighton et al., 2013).

402         The general picture of global biodiversity shows that bivalves underwent a  
403 stepwise depletion in biodiversity through the Changhsingian–Dienerian interval. The  
404 lowest biodiversity occurred in the Dienerian, implying that extinction might  
405 continuously occur through part or all of the Griesbachian, except for the PTME (Fig.  
406 2). However, taxonomic bias may obscure the real evolutionary patterns of bivalves.  
407 Thus, more rigorous analyses are required combined with the other important proxies,  
408 such as the proportional extinction/origination rates (Harper and Gallagher, 2001;  
409 Bambach et al., 2004).

410         As stated above, bivalves experienced very high origination rates and relatively  
411 low extinction rates in the Griesbachian (Fig. 4; Table 1), when the Paleozoic-type (i.e.  
412 bivalve species appeared prior to the P–Tr biocrisis) accounted for only ~25% (Table  
413 S3). Previously, marine benthic communities were believed to be dominated by  
414 survivors from the Permian and several progenitors such as *Claraia* and the  
415 *Eumorphotis* in the Early Triassic (Hallam and Wignall, 1997; Komatsu et al., 2008),  
416 and did not diversify until early Middle Triassic (Chen, 2004; Komatsu et al., 2004,  
417 2010). In fact progenitor taxa (i.e., species of *Claraia* and *Eumorphotis*) occupy 42%  
418 of all species and 46% of all newcomers in the Griesbachian, even with the possible  
419 over-splitting of *Claraia* (Table S4). Thus, the majority of the Griesbachian taxa are

420 non-progenitors.

421 Bivalves suffered a rather high origination rate, coincident with relatively low  
422 proportional extinction rates in the Griesbachian (Fig. 4; Table 1). The high  
423 biodiversity therefore is possibly driven by the presence of many newcomers  
424 associated with rapid speciation. The combination of a relatively high biodiversity,  
425 high origination rate, and low extinction rate indicates that an initial recovery of  
426 bivalves occurred in the Griesbachian, reinforced by the presence of the diverse  
427 bivalve communities of the lowest Triassic carbonates of Guangxi, South China  
428 (Hautmann et al., 2011) and the Lower Triassic Werfen Formation, northern Italy  
429 (Hofmann et al., 2015).

430 The rather low extinction rate in the Griesbachian (Fig. 4; Table 1) rejects the  
431 possibility of a biotic extinction between the Griesbachian and Dienerian. The lowest  
432 biodiversity in the Dienerian (Fig. 2) is probably biased by a Lazarus effect (Jablonski,  
433 1996), a phenomenon commonly present in major mass extinction episodes and that  
434 also occurs in other time intervals (attributed to the incompleteness of fossil record)  
435 (Wignall and Benton, 1999; Twitchett, 2000; Fara, 2001; Rickards and Wright, 2002).  
436 Thus, the bivalve assemblage in each time bin is taxonomically categorized into  
437 newcomers, survivors from the preceding time bin, and survivors persisting from  
438 earlier time bins (Table S5). The numbers of Lazarus taxa in each sampling time bin  
439 from the Griesbachian to Spathian (Table S6) were also counted. Both proxies  
440 indicate that the Dienerian and Smithian richness have been significantly biased by  
441 the Lazarus effect. Griesbachian bivalves had a low extinction rate, many disappeared  
442 in Dienerian, but re-appeared afterwards. The Dienerian biodiversity therefore  
443 remained low.

444 Similarly, a high origination rate, concurrent with an elevated biodiversity in  
445 the Smithian (Figs 2, 4; Table 1), indicates the proliferation of this group in the  
446 Smithian. And the rather low extinction rate in the Smithian (Fig. 4; Table 1) implies  
447 that the faunal composition of assemblages remained nearly unchanged between the  
448 Smithian and Spathian. Moreover, another evolutionary revolution of bivalves  
449 occurred probably in the Anisian, Middle Triassic. Although bivalves exhibited a high

450 extinction rate in the Spathian, they reached their highest biodiversity, incorporating  
451 markedly elevated origination rate in the Anisian (Fig. 2, 4; Table 1). Consequently,  
452 the dramatic increase in biodiversity was contributed by the appearance of new taxa  
453 (Table 1), which also suggests a rapid speciation at that time. In addition, faunal  
454 compositions greatly changed from the Smithian to Anisian. The Paleozoic EF  
455 occupied 13% of all species and 45% of all genera in the Smithian assemblages, while  
456 the percentage declined to 5% and 29% at the species and genus levels, respectively  
457 in the Anisian bivalves (Table S3). All the lines of evidence indicate the bivalve  
458 radiation took place in the Anisian, as suggested in earlier studies (Komatsu et al.,  
459 2004, 2010; Ros and Echevarría, 2011; Ros et al., 2011; Chen and Benton, 2012).

460

#### 461 *4.2 Ecologic selectivity between the infauna and epifauna*

462

463 The data from South China display a lack of ecologic selectivity among  
464 bivalves through the P–Tr biotic crisis (Huang et al., 2014). The proportional  
465 extinction rates calculated from the new global dataset show no significant differences  
466 ( $p>0.05$ ) between the infaunal and epifaunal lifestyles by the end of the Permian (Fig.  
467 7; Table 2).

468 Infaunalization, particularly involving bivalves, was thought to be prevalent in  
469 Mesozoic oceans (Vermeij, 1977; Thayer, 1979). The epifaunal taxa exhibit higher  
470 extinction rates than those of the infauna, while the origination rates between the two  
471 groups show no significant difference at the genus level through the entire Triassic  
472 (McRoberts, 2001). Our study suggests, however, that the epifauna exhibits a  
473 significantly higher biodiversity than the infauna in any given time bins after the  
474 PTME (Fig. 5; Table S2). The proportions of the representative infaunal (i.e. the  
475 Cardiida) and epifaunal taxa (i.e. the Pectinida) exhibit neither increasing nor  
476 decreasing trends throughout the P–Tr transition (Table S7A). In addition, the  
477 proportion of all infaunal taxa within all the benthic communities is also calculated,  
478 which remains almost unchanged before and after the PTME (i.e. the Changhsingian  
479 and Anisian) (Table S7B), although infaunal bivalves may proliferate locally in



480 particular habitats in the Anisian (i.e. storm- and wave-dominated shelf, Komatsu et  
481 al., 2010). Latest study also suggests that the roles are minor played by mass  
482 extinctions, including PTME into ecospace utilization of the bivalves, despite their  
483 impacts on biodiversity (Mondal and Harries, 2016). Our observation is in agreement  
484 with the previous view that the elevated infaunalization among bivalves did not occur  
485 before the latest Triassic (Ros and Echevarría, 2011; Ros et al., 2011). More  
486 importantly, no significant difference ( $p>0.05$ ) is shown in proportional  
487 extinction/origination rates at the genus level between the infaunal and epifaunal  
488 groups in any time bins, at least prior to the Ladinian. Nevertheless, the proportional  
489 extinction/origination rates are occasionally different between the two lifestyle  
490 bivalves at the species level. For instance, the epifauna had a higher specific  
491 extinction rate than the infauna in the Griesbachian (Fig. 7; Table 2). This is probably  
492 due to the disappearance of both *Claraia* and *Eumorphotis* (25 out of 68 species  
493 disappeared). Anyway, in view of generic proportional extinction/origination rates, no  
494 significant ecological preference can be observed in any given time bins prior to the  
495 Ladinian (Fig. 7).

496

#### 497 *4.3. Driving force of the Mesozoic Marine Revolution*

498

499 The Mesozoic Marine Revolution (MMR) is considered to be one of the key  
500 Phanerozoic radiations, marked by the final establishment of the Modern EF in  
501 marine ecosystems. The MMR is generally thought to be driven by escalating  
502 interactions between organisms, especially the substantial increase in the intensity of  
503 predation (Vermeij, 1977; Roy, 1994; McRoberts, 2001; Kerr and Kelley, 2015). Such  
504 biotic interactions could drive adaptations, including efficient escape and defence  
505 strategies. However, crucial is the ability to take advantage of new ecospace such as  
506 infaunal habitats, free from surface-dwelling predators (Vermeij, 1977; Signor and  
507 Brett, 1984; Harper and Skelton, 1993; Roy, 1994; McRoberts, 2001). Growing  
508 evidence shows that the MMR may have originated in Early-Middle Triassic  
509 (McRoberts, 2001; Baumiller et al., 2010; Gorzelak et al., 2012; Brachaniec et al.,

510 2015). If escalating predation pressure indeed played a critical role in initially driving  
511 the MMR, infaunalization then would not be prevalent before the Ladinian,  
512 inconsistent with the earlier estimates (McRoberts, 2001). Though a  
513 three-dimensional, relatively vacant (Sheehan, 1996) and stable ecospace provided an  
514 unrivalled opportunity for the infaunal bivalves to diversify, high origination rates  
515 within the epifauna might be expected while they faced environmental stresses such  
516 as fluctuating seawater temperature, salinity, and energy flow as well as potential  
517 competition among organisms. There is, however, no significant difference in  
518 proportional extinction/origination rates between the epifauna and infauna, at least,  
519 before the Ladinian. Thus, the MMR marked by the elevated infaunalization of  
520 bivalves may not be evident until latest Triassic (Ros and Echevarría, 2011; Ros et al.,  
521 2011). Alternatively, the infaunalization may not have been involved in the initial  
522 evolution of the MMR. Hautmann et al. (2015) also suggested that the interspecific  
523 interactions were very weak in the intermediate aftermath of the greatest biotic crisis,  
524 occurring at a timescale much longer than at background timescales. As a result,  
525 physical factors such as amelioration of marine environments in the late Early Triassic  
526 (Hofmann et al., 2013, 2015; Zhang et al., 2015) may have driven the origination and  
527 early evolution of the MMR, which is reinforced by a very rare fossil record of  
528 predatory activities through the Early Triassic (McRoberts, 2001). Both intrinsic and  
529 extrinsic drivers have contributed to long-term macroevolution. Critical is an  
530 understanding the applicability and consequences of ‘Red Queen’ model (i.e.  
531 large-scale evolution is driven by interactions between organisms) in contrast to the  
532 so-called ‘Court Jester’ model (i.e. the critical driver is the physical environment)  
533 (Benton, 2009; Chen and Benton, 2012). The latter appears more relevant during the  
534 widely fluctuating environmental conditions during the earlier parts of the Triassic,  
535 setting a template for a later applicability of Red Queen interactions.

536

## 537 **5. Conclusion**

538

539 The updated global dataset shows that bivalves experienced less, typically

540 moderate extinction during the P–Tr biotic crisis. Both biodiversity and proportional  
541 extinction/origination rates indicate an initial recovery of the bivalves in the  
542 Griesbachian. Thus, no survival stage is recognized in the immediate post-extinction  
543 bivalves. The extremely low biodiversity in the Dienerian is possibly biased by a  
544 strong Lazarus effect. Bivalves underwent a stepwise recovery from the Dienerian to  
545 Anisian with the proliferation in the Smithian. The Anisian witnessed the major  
546 radiation of bivalves after the PTME, which is marked by an elevated richness and  
547 rather high origination rates. Taxonomically, the Ostreida, Trigoniida, and Mytilida  
548 may have benefited from the PTME and the associated devastation of many  
549 environments, while the other three orders, the Pectinida, Myalinida, and  
550 Pholadomyida suffered from this biotic crisis, in terms of biodiversity variations  
551 before and after PTME. No ecologic selectivity is present between the infaunal and  
552 epifaunal bivalves at the genus level in the aftermath of the PTME, evidenced by a  
553 lack of significant difference of proportional extinction/origination rates in any given  
554 time bins prior to the Ladinian. Infaunalization is one of the most efficient strategies  
555 to escape from the predatory pressure. If the MMR is indeed driven by organismal  
556 interactions, the infaunalization did not occur, at least prior to the Ladinian (Middle  
557 Triassic). Alternatively, the start of the MMR was probably not driven by biotic  
558 processes associated with escalating predation pressure (‘Red Queen’ model). Instead,  
559 environmental changes, like the amelioration of extreme physical and chemical  
560 environments (‘Court Jester’ model) in the late Early Triassic may be responsible for  
561 the origination and initial evolution of the MMR.

562

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578

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788 marine environments at the Smithian–Spathian boundary, Early Triassic.  
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791

## 792 **Figure and table captions**

793

794 Fig. 1. Rarefaction curves with 95% confidence limits for bivalves from the  
795 Changhsingian to Anisian. (A) The genus richness versus the number of occurrences.  
796 (B) family richness versus species richness.

797

798 Fig. 2. Taxonomic richness of bivalve species, genera and families through the P–Tr  
799 transition. Gr. = Griesbachian, Di. = Dienerian, Sm. = Smithian. The scale is shown.

800

801 Fig. 3. Numbers of species, genera and families of the major bivalve orders from the  
802 Changhsingian to Anisian showing taxonomic selectivity during extinction-recovery  
803 intervals. Arc. = Arcida, Modio. = Modiomorphida, Nucula. = Nuculanida, Nucu. =  
804 Nuculida, Phola. = Pholadida, Trigon. = Trigoniida, Pholado. = Pholadomyida, Myti.  
805 = Mytilida, Pteri. = Pterioida, Sole. = Solemyida, M.+P.+H. = Megalodontida +  
806 Pandorida + Hiatellida. The scale is shown.

807

808 Fig. 4. Proportional extinction (blue bar) and origination (pink bar) rates of bivalve  
809 species, genera and families from the Changhsingian to Anisian. Scale bars represent

810 95% confidence interval of sample sizes using the “Wilson score interval” method  
811 calculated with R software.

812

813 Fig. 5. Taxonomic richness at the species, genus, and family levels among different  
814 bivalve life modes from the Changhsingian to Anisian. Mo.se.-inf. = Mobile  
815 semi-infauna, Sl.-m.inf. = slow-moving infauna, Sta.low-level epi. = stationary  
816 low-level epifauna; Gr. = Griesbachian, Di. = Dienerian, Sm. = Smithian. The scale is  
817 shown.

818

819 Fig. 6. Proportional extinction and origination rates among various bivalve life modes  
820 at the species, genus, and family levels, respectively, from the Changhsingian to  
821 Anisian.

822

823 Fig. 7. Proportional extinction and origination rates between the infaunal and  
824 epifaunal bivalves at the species, genus, and family levels, respectively, from the  
825 Changhsingian to Anisian. Scale bars represent 95% confidence interval of sample  
826 sizes using the “Wilson score interval” method.

827

828 Table 1. Quantitative data on proportional extinction and origination rates of bivalve  
829 species, genera and families from the Changhsingian to Anisian. Changhs. =  
830 Changhsingian, Griesba. = Griesbachian, Diene. = Dienerian.

831

832 Table 2. Quantitative data on proportional extinction and origination rates between the  
833 infaunal and epifaunal bivalves at the species, genus and family levels, respectively,  
834 from the Changhsingian to Anisian. Changhs. = Changhsingian, Griesba. =  
835 Griesbachian, Dien. = Dienerian.

836

837 **Online Supplementary Material:**

838

839 Table S1. Quantitative data on species, genus, and family taxonomic richness among

840 all orders of bivalves from the Changhsingian to Anisian.

841

842 Table S2. Quantitative data on taxonomic richness and proportional extinction/  
843 origination rates among various bivalve life modes at the species, genus, and family  
844 levels from the Changhsingian to Anisian. Mobile semi-inf. = mobile semi-infauna,  
845 slow-m.infa. = slow-moving infauna, sta.low-level epi. = stationary low-level  
846 epifauna.

847

848 Table S3. Quantitative data showing species and genus counts of the number and  
849 percentage of the Paleozoic-type bivalves in the aftermath of the PTME. Griesba. =  
850 Griesbachian.

851

852 Table S4. Quantitative data showing counts of the number and percentage of *Claraia*  
853 and *Eumorphotis* species out of the total taxa and origination taxa in the Griesbachian  
854 and Dienerian intervals. Orig. = Origination.

855

856 Table S5. Quantitative data showing the newcomers, survivors from the preceding  
857 interval, and survivors persisting from earlier intervals. Numbers and proportions are  
858 shown herein. Griesba. = Griesbachian.

859

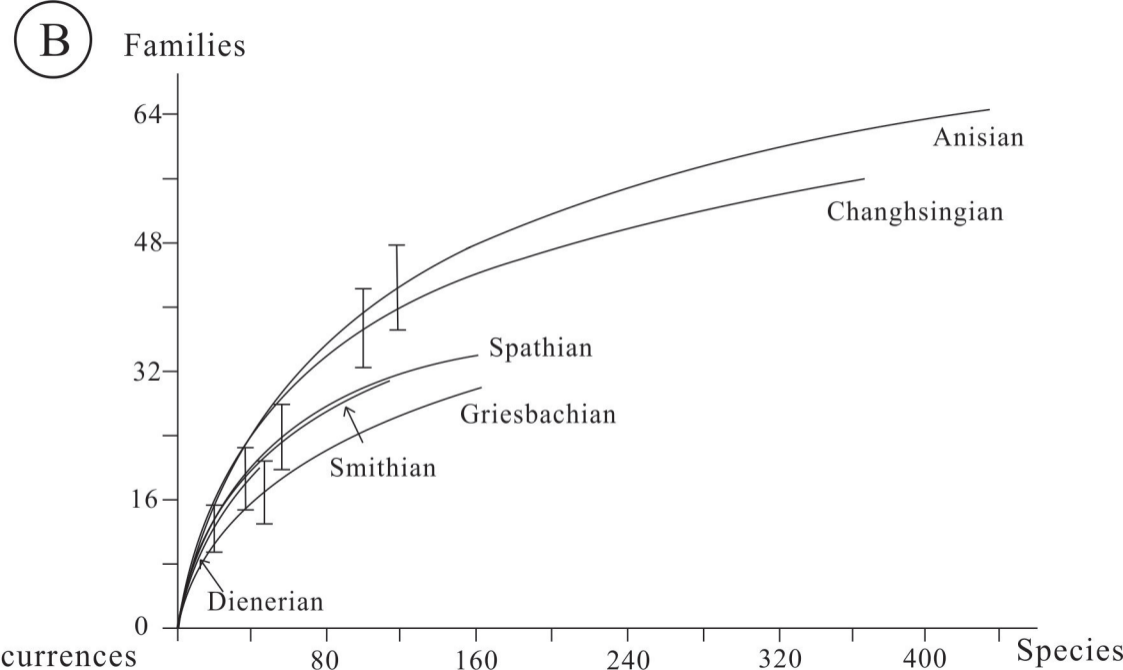
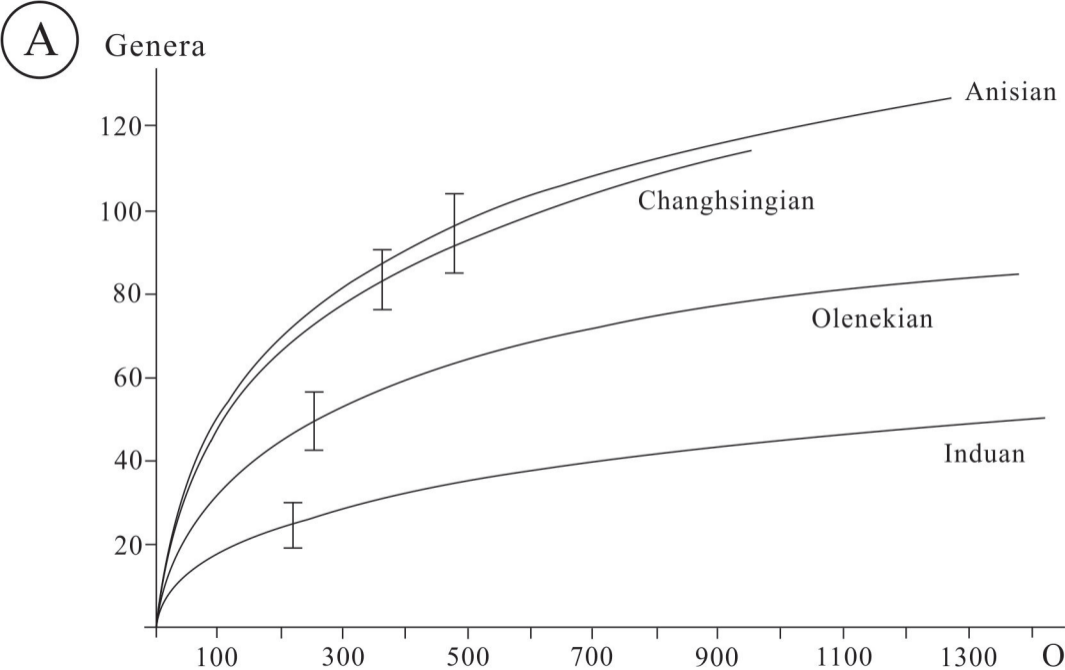
860 Table S6. Generic and specific data testing the Lazarus effect on biodiversity trends.  
861 Lazarus taxa are defined as ‘disappearance and apparent extinction of taxa that later  
862 reappear unscathed’ in fossil record. Note that the Dienerian and Smithian  
863 biodiversities were greatly influenced by the Lazarus effect. Griesba. = Griesbachian,  
864 Diene. = Dienerian, Smith. = Smithian, Spath. = Spathian.

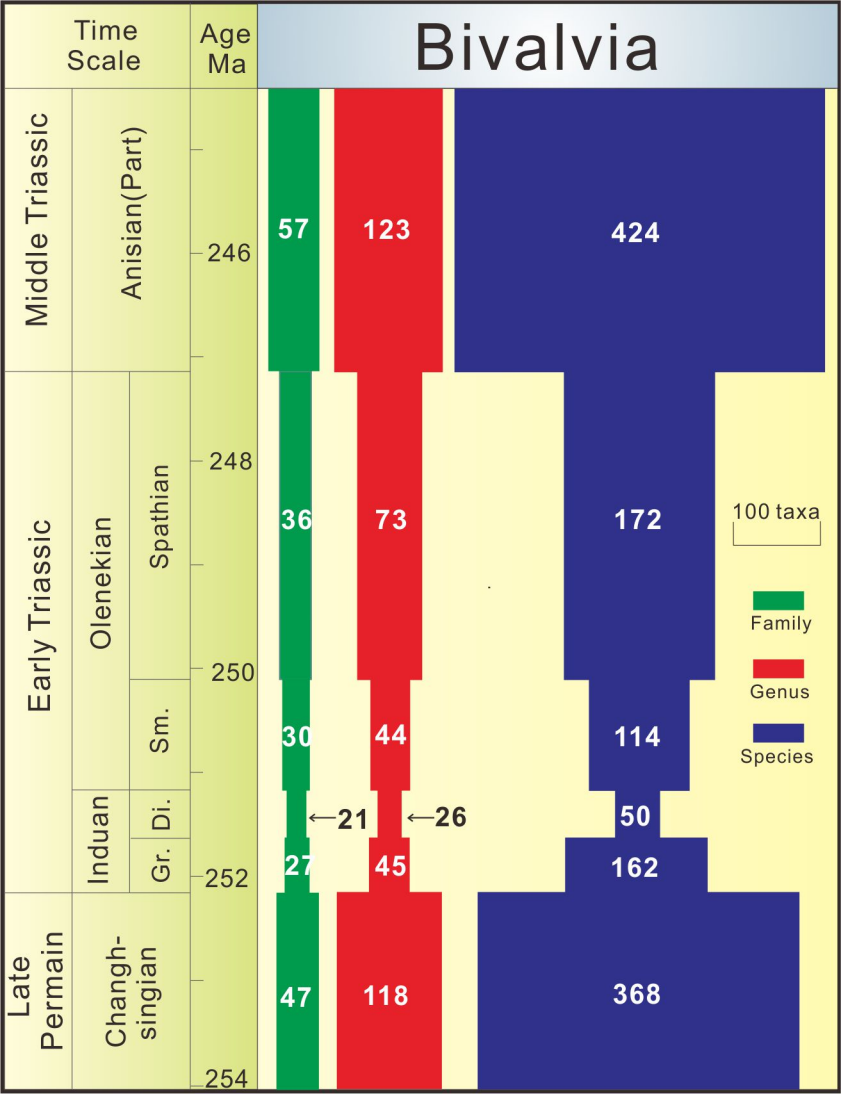
865

866 Table S7. (A) Quantitative data showing proportions of the representative infaunal  
867 (i.e. the order of Cardiida) and epifaunal taxa (i.e. the order of Pectinida) before and  
868 after the PTME. (B) Proportions of (all) the infaunal taxa (versus epifaunal taxa)  
869 within the benthic communities throughout the interval. Changhs. = Changhsingian,

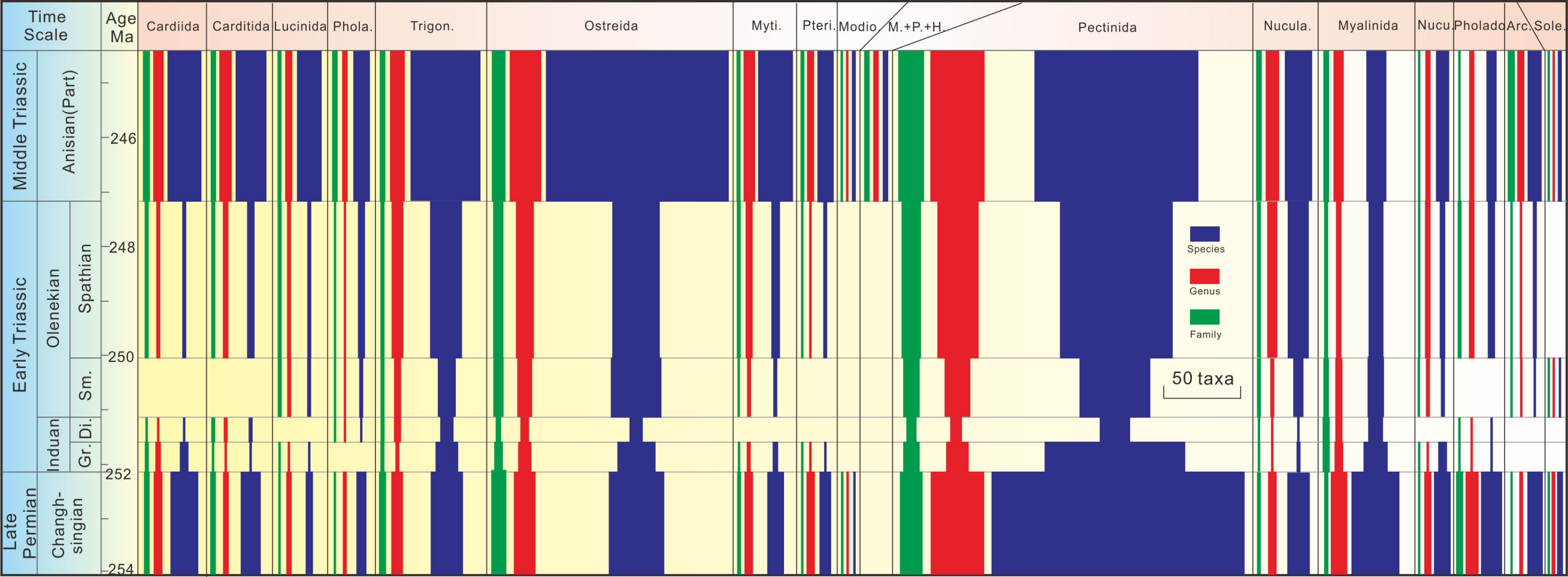
870 Griesba. = Griesbachian, Diene. = Dienerian, Smith. = Smithian, Spath. = Spathian.

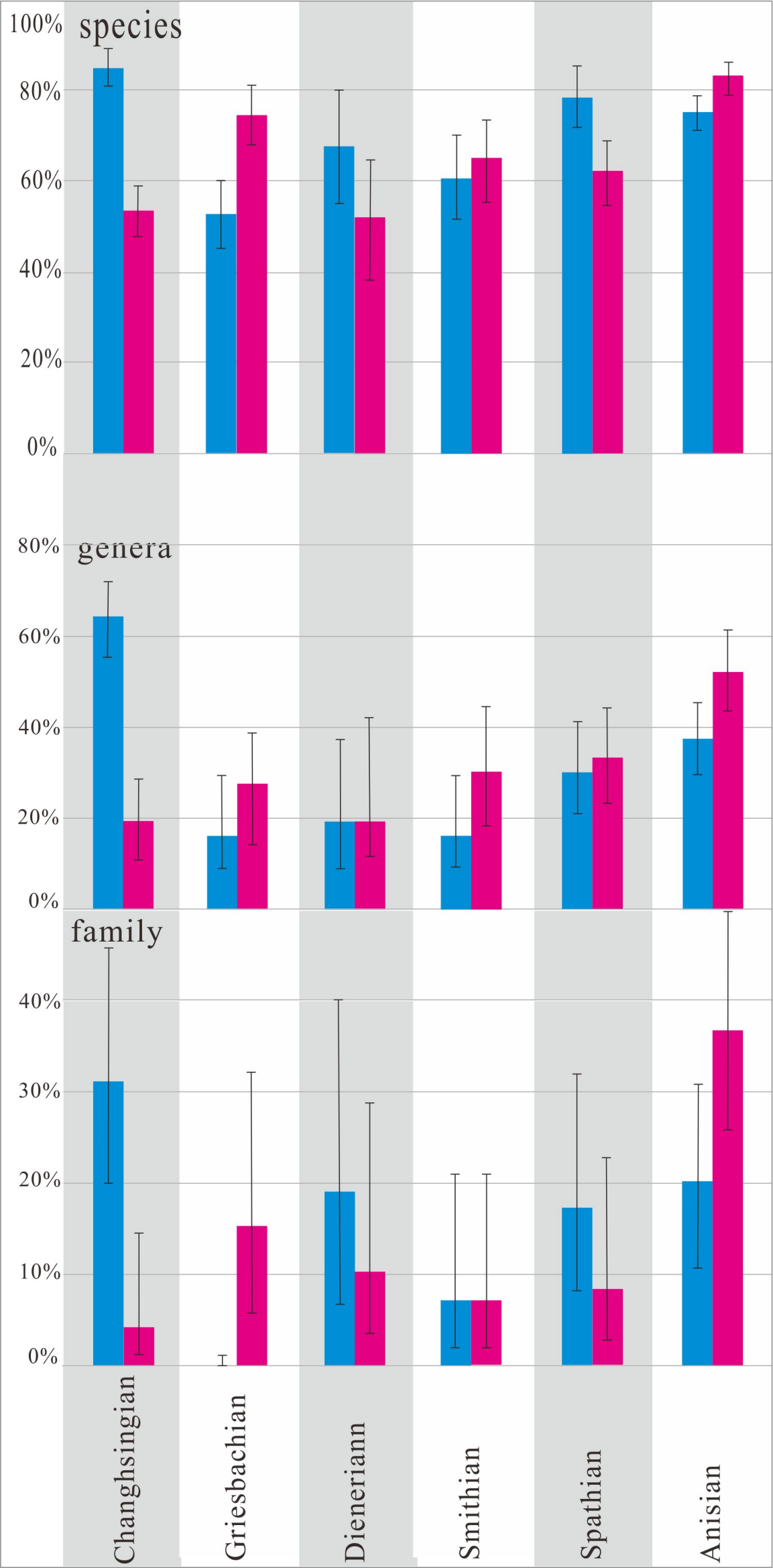
871 RI = Representative infaunal taxa, RE = Representative epifaunal taxa.











species

genera

family

Changhsingian

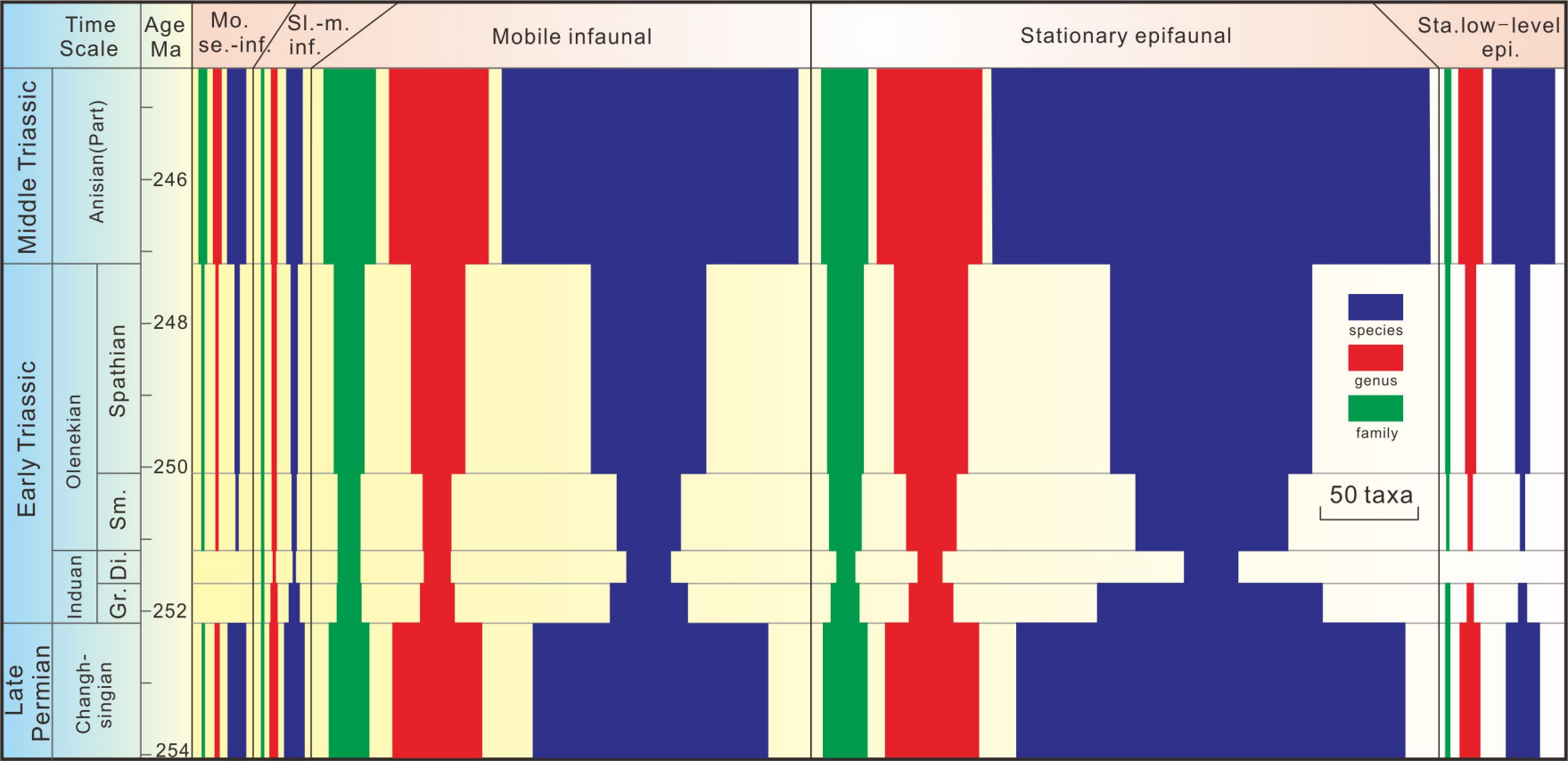
Griesbachian

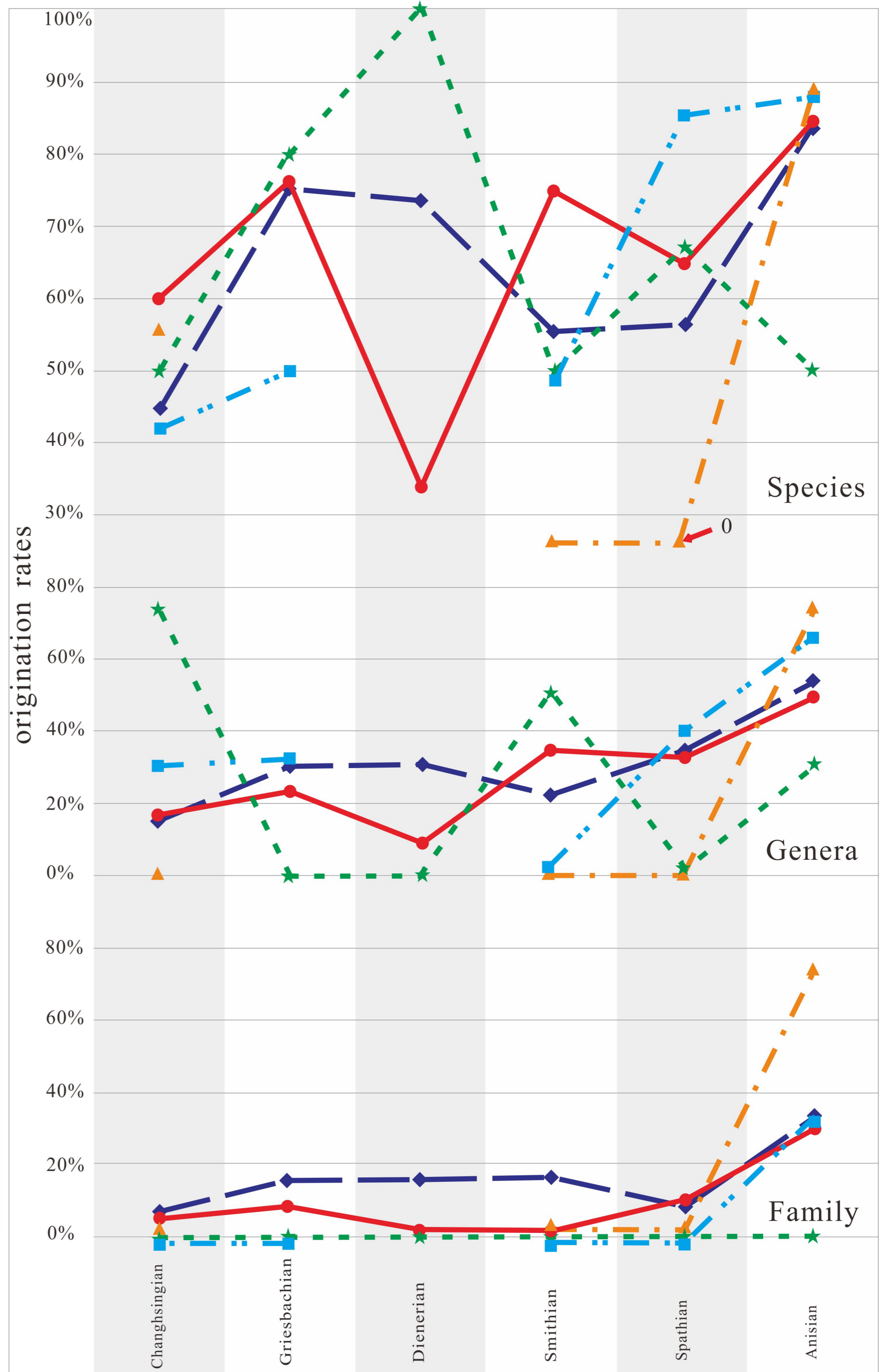
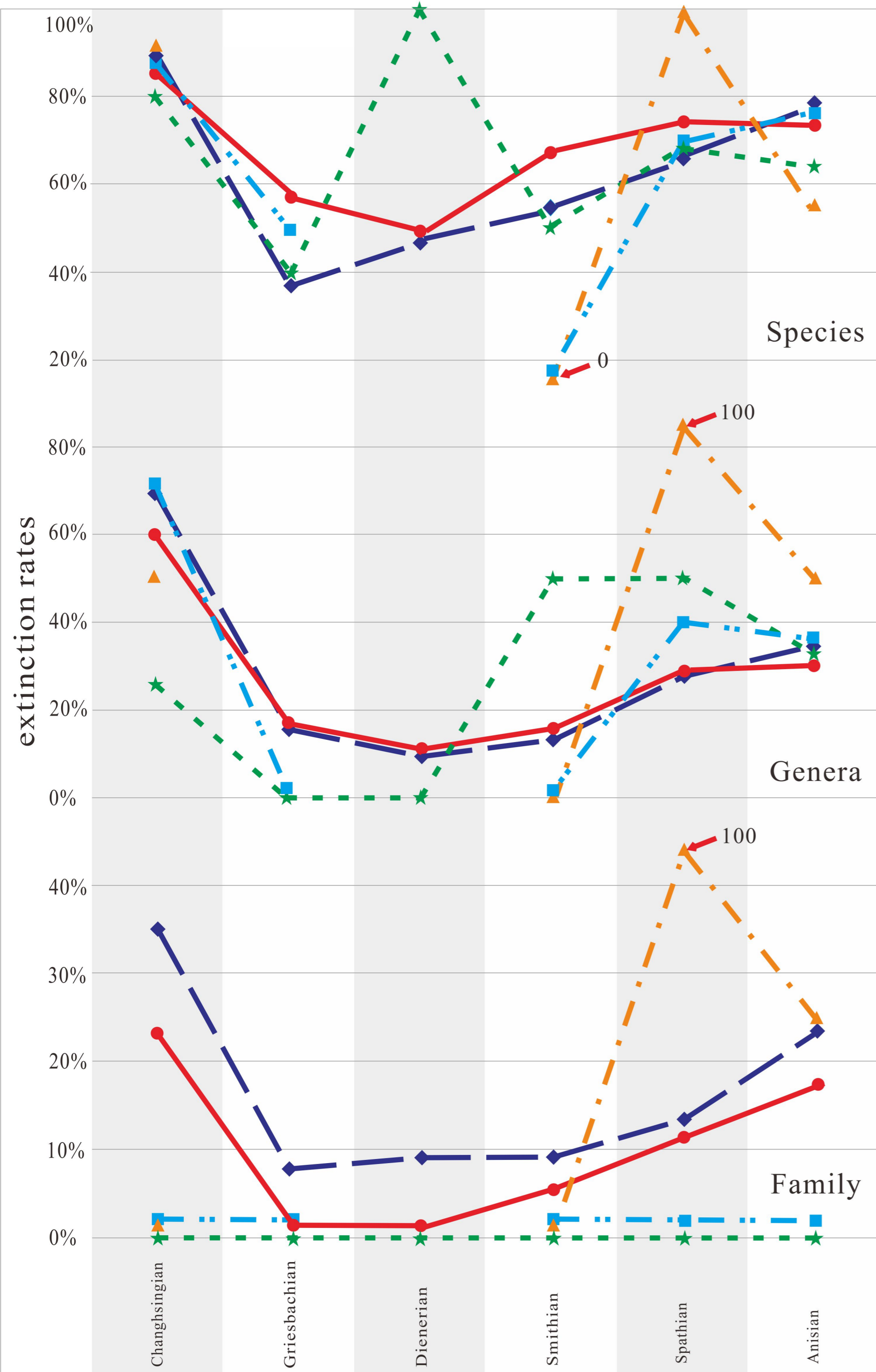
Dienerian

Smithian

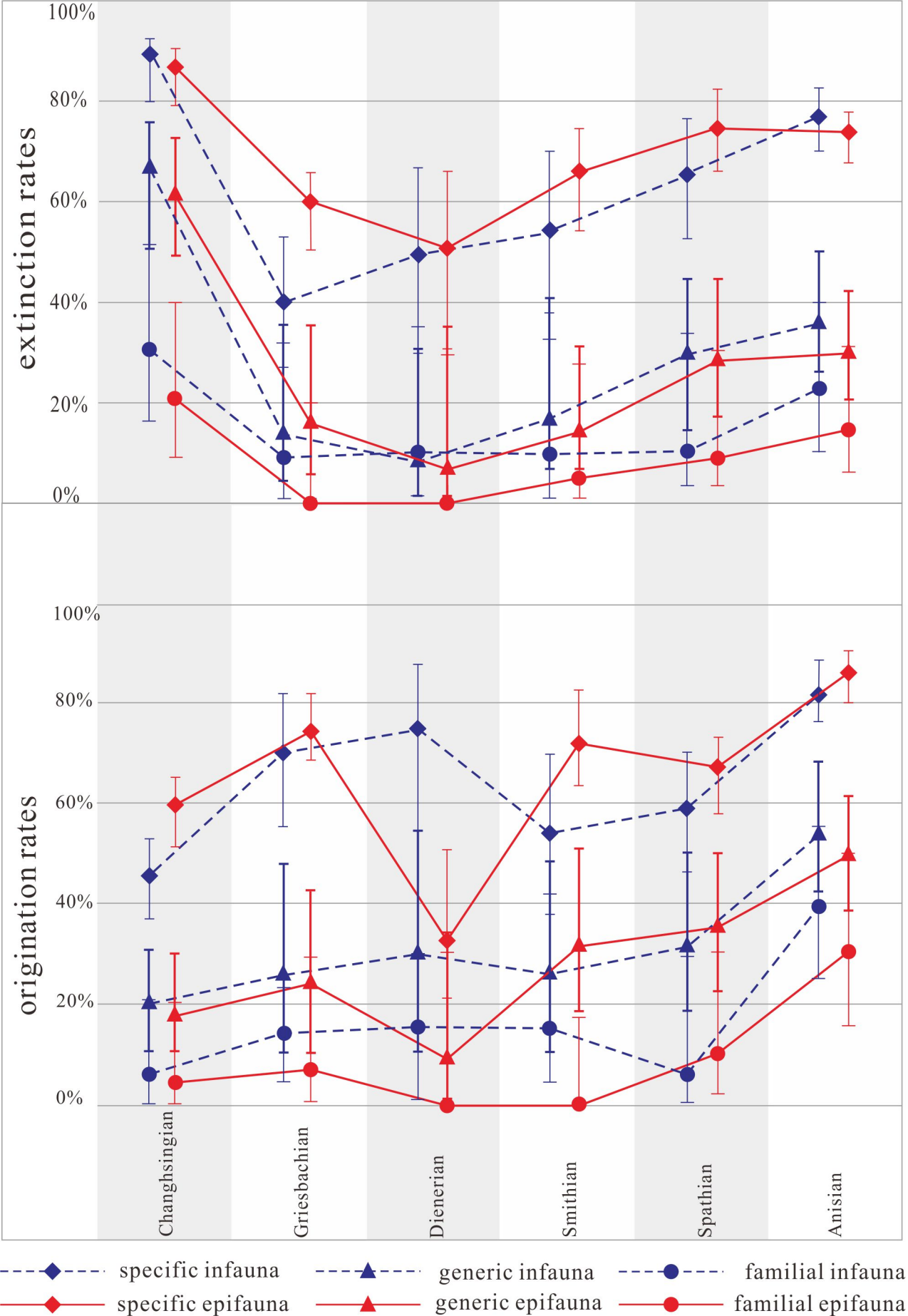
Spathian

Anisian





◆ mobile infauna  
 ● stationary epifauna  
 ▲ mobile semi-infauna  
 ★ slow-moving infauna  
 ■ stationary low-level epifauna



Intervals	Numbers of extin./new taxa			Proportional extinction rates(%)			Proportional origination rates(%)		
	Species	Genera	Family	Species	Genera	Family	Species	Genera	Family
Changhs.	314/197	76/23	15/2	85	64	32	54	19	4
Griesb.	85/121	7/11	0/4	53	16	0	75	27	15
Diene.	34/26	5/6	4/2	68	19	19	52	19	10
Smithian	70/74	7/13	2/2	61	16	7	65	30	7
Spathian	136/107	22/24	6/3	79	30	17	62	33	8
Anisian	318/351	45/64	11/21	75	37	20	83	52	37

Infaunal Intervals	Numbers of extin./new taxa			Proportional extinction rates(%)			Proportional origination rates(%)		
	Species	Genera	Family	Species	Genera	Family	Species	Genera	Family
Changhs.	120/62	33/10	7/1	87	65	32	45	20	5
Griesba.	17/31	3/5	1/2	39	15	8	70	25	15
Diene.	11/17	1/4	1/2	48	7	8	74	29	17
Smithian	19/19	3/4	1/2	54	18	8	54	24	16
Spathian	41/37	8/10	2/7	65	27	12	59	33	6
Anisian	129/137	21/31	7/12	77	37	23	82	54	39

Epifaunal Intervals	Numbers of extin./new taxa			Proportional extinction rates(%)			Proportional origination rates(%)		
	Species	Genera	Family	Species	Genera	Family	Species	Genera	Family
Changhs.	181/126	35/11	5/1	85	61	21	59	19	4
Griesba.	68/89	4/6	0/1	58	16	0	75	24	6
Diene.	13/9	1/1	0/0	48	8	0	33	8	0
Smithian	51/58	4/9	1/0	65	15	6	73	33	0
Spathian	82/72	12/15	2/2	75	29	10	66	36	10
Anisian	186/215	20/32	4/8	73	31	15	85	50	30