1 **Heterochrony in the evolution of the planktonic foraminifera *Trilobatus sacculifer* plexus**

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4 RRH: HETEROCHRONY IN THE *TRILOBATUS SACCULIFER* PLEXUS

5 LRH: ANIEKE BROMBACHER ET AL.

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Abstract.—Planktonic foraminifera are extremely well-suited to study evolutionary change in the fossil record due to their high-resolution deposits and global distribution. Species are typically conservative in their shell morphology with the same geometric shapes appearing repeatedly through iterative evolution, but the mechanisms behind the architectural limits on foraminiferal shell shape are still not well understood. To understand when and how these developmental constraints evolve, we study morphological change leading up to the origination of the unusually ornate species *Globigerinoidesella fistulosa*. We measured the size and circularity of over 900 specimens of *G. fistulosa,* its ancestor *Trilobatus sacculifer* and intermediate forms from a site in the Western Equatorial Pacific. Our results show that the origination of *G. fistulosa* from the *Trilobatus sacculifer* plexus involved a combination of two heterochronic expressions: earlier onset of protuberances (pre-displacement) and steeper allometric slope (acceleration) as compared to its ancestor. Our work provides a case study of the complex morphological and developmental changes required to produce unusual shell shapes and highlights the importance of developmental changes in evolutionary origination.

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Introduction

31

32   Trait variation amongst individuals provides the constituents for evolution through natural

33   selection. Since the seminal works of Gould (1977) and Alberch et al. (1979), the importance of

34   heterochrony in facilitating trait variation, and the resultant link between ontogeny and

35   phylogeny, has become increasingly appreciated in the field of evolutionary developmental

36   (palaeo)biology (Dobreva et al. 2022; Keyte and Smith 2014). Heterochrony may be broadly

37   defined as a change to the timing or rate of developmental events, relative to the same events in

38   the ancestor (e.g., McNamara (2012); see comparable definitions in Alberch et al. (1979); Gould

39   (1977); McKinney and McNamara (1991); McNamara (1986)) and is widely regarded as having

40   a central role in morphological evolution following the formalisations of Gould (1977) and

41   Alberch et al. (1979).

42

43   There are two expressions of heterochrony, termed paedomorphosis and peramorphosis (Alberch

44   et al. 1979; McNamara 1986). These are not processes, as is often erroneously assumed (see

45   discussion in McNamara (1986)), but resultant expressions of trait morphology. Paedomorphosis

46   results from a descendant morphospecies passing through fewer ontogenetic stages than its

47   ancestor so that the descendant exhibits adult characters that were juvenile characters in the

48   ancestor (Alberch et al. 1979; McNamara 1986). Conversely, peramorphosis results from the

49   descendant passing through more ontogenetic stages than its ancestor, with the descendant

50   exhibiting adult characters beyond that of the ancestor (Alberch et al. 1979; McNamara 1986).

51

52   Paedomorphosis and peramorphosis each result from three different (and opposing)

53   heterochronic expressions. Peramorphosis includes hypermorphosis (continued development past

3

54 the ancestor stage, Fig. 1A), pre-displacement (earlier onset of trait development in the

55 descendant, Fig. 1B) and acceleration (faster development in the same amount of ontogenetic

56 time as the ancestor, Fig. 1C). Paedomorphosis can result from hypomorphosis (reduced duration

57 of development, Fig. 1D), post-displacement (later onset of trait development, Fig. 1E) or

58 deceleration (slower trait development in the same amount of ontogenetic time as the ancestor,

59 Fig. 1F). Note that following Reilly et al. (1997), two of the terms, hypomorphosis and

60 deceleration, have been chosen to replace progenesis and neoteny of Alberch et al. (1979).

61

62 The fossil record is integral in studies assessing the role of heterochrony in the evolution of novel

63 forms as the traits of interest are often morphological. However, a long-acknowledged problem

64 for palaeontologists is determining the ontogenetic age of fossils. Although it is possible to infer

65 age in some groups, such as fossil bivalves (Jones and Gould 1999), trilobites (Whittington

66 1957), fish (Trueman et al. 2016), trees (Falcon-Lang 2015) and dinosaurs (Sanchez et al. 2010;

67 Sander and Klein 2005), age is a poorly constrained parameter in most fossil organisms. To this

68 end, size is often used as a proxy for age, and assessments of heterochrony are often identified

69 under the framework of "allometric heterochrony" (McKinney and McNamara 1991; McKinney

70 1986; Wei 1994). Allometry describes trait covariation with body size according to a power

71 relationship (Huxley 1932) and is therefore ideally suited to studies of heterochrony in the fossil

72 record.

73

74 Planktonic foraminifera are a perfect target group for investigations into heterochrony. They

75 have one of the best and most complete fossil records of any group (e.g., Lazarus 2011; Norris

76 2000), phylogenetic relationships between taxa are well resolved (Aze et al. 2011; Kennett and

77 Srinivasan 1983; Olsson et al. 1999; Pearson et al. 2006a; Wade et al. 2018) and every chamber

78 from the first (proloculus) to the last is retained through growth. Brummer et al. (1986) and

79 Brummer et al. (1987) proposed five ontogenetic stages (prolocular, juvenile, neanic, adult, and

80 terminal stages) in most morphospecies of planktonic foraminifera. Transitions from one

81 ontogenetic stage to the next are determined by a size threshold, rather than chamber number

82 (Brummer et al. 1986, 1987; Caromel et al. 2016; Caromel et al. 2017; Schmidt et al. 2013; Wei

83 et al. 1992) so size is a good approximation for ontogenetic age in planktonic foraminifera.

84 Finally, the concept of heterochrony could explain the apparent lack of functional morphology in

85 some foraminifera traits. Heterochrony could potentially explain the evolution of traits without

86 known functions if a particular ontogenetic stage, rather than morphology, is selected for.

87 Therefore, heterochrony presents an additional framework to study planktonic foraminifera

88 evolution.

89

90 Here we investigate if heterochrony took place during the origination of the planktonic

91 foraminifer *Globigerinoidesella fistulosa*, a species characterised by an unusually ornate, digitate

92 morphology with numerous protuberances on its final chamber(s) (Fig. 2). *Globigerinoidesella*

93 *fistulosa* evolved from the *Trilobatus sacculifer* plexus when a small subset of the *T. sacculifer*

94 population (which includes morphospecies *T. trilobus, T. immaturus* and *T. quadrilobatus,* see

95 Poole and Wade (2019) for taxonomic discussion) increased in size, developed more extreme

96 protuberances and gradually diverged into *G. fistulosa* (Chaisson and Leckie 1993; Parker 1967;

97 Poole and Wade 2019) (Fig. 2). The complex shell shape of *G. fistulosa* stands out among

98 planktonic foraminifera, which are typically limited in morphological variation to the same basic

99 shapes (Norris 1991). To understand the drivers of morphological innovation in foraminifera we

100   quantify test size and shape in *T. sacculifer* and *G. fistulosa* before and after the origination of *G.*

101   *fistulosa.* We compare our results to previously published cases of heterochrony in planktonic

102   foraminifera to assess if developmental expressions can be rewired to overcome developmental

103   constraints.

104

105   **Methods**

106   *Study species.—Globigerinoidesella fistulosa* is a short-ranging morphospecies with a

107   distinct stratigraphic range. Both its origination and extinction have been used as markers in

108   Neogene planktonic foraminiferal biostratigraphy (Wade et al. 2011). *Globigerinoidesella*

109   *fistulosa* evolved from the *Trilobatus sacculifer* plexus in the late Pliocene (King et al. 2020;

110   Raffi et al. 2020) and went extinct in the early Pleistocene, marking the Base of Subzone PT1a

111   (Raffi et al. 2020). It is assigned to the genus *Globigerinoidesella* (El-Naggar 1971) as the

112   radially elongated protuberances on the final chambers are considered a genus-level

113   characteristic (Spezzaferri et al. 2015). The phylogenetic relationships are well-constrained and

114   the morphospecies *T. sacculifer* and *G. fistulosa* are morphologically disparate (Poole and Wade

115   2019), but intermediate specimens bridge the morphological evolution (**Error! Reference**

116   **source not found.**) and remain as common as *G. fistulosa* s.s. throughout the stratigraphic range

117   of *G. fistulosa* (Poole and Wade 2019). *Trilobatus sacculifer* has a much longer stratigraphic

118   range. It evolved in the early Miocene (Kennett and Srinivasan, 1983) and persists throughout

119   the stratigraphic range of *G. fistulosa*. It is still alive today (Wade et al. 2011), occupying the

120   mixed-layer (Rebotim et al. 2017) in warm tropical oceans and harbouring some of the highest

121   concentrations of algal photosymbionts in modern planktonic foraminifera (Kucera 2007; Takagi

122   et al. 2019). Geochemical data indicates that *G. fistulosa* had the same habitat as *Trilobatus*

123   (Poole 2017).

124

125   *Material*. —Ocean Drilling Program (ODP) Site 1115 is located in the western Woodlark

126   Basin, western Pacific (9º11.382' S, 151º34.437' E) at a water depth of 1149 m (Fig. 3) (Shipboard

127   Scientific Party, 1999). Hole 1115B was chosen primarily because the *G. fistulosa* specimens are

128   abundant and well-developed. Our sampling method was to examine end-members i.e., before the

129   first occurrence of *G. fistulosa sensu stricto* (s.s.), and samples towards the end of the *G. fistulosa*

130   range. The evolution of *G. fistulosa* occurred rather gradually, to ensure maximum morphological

131   differentiation with its ancestor we chose to analyse *G. fistulosa* and contemporary specimens of

132   the *T. sacculifer* plexus from a time slice close to the top of the stratigraphic range of *G. fistulosa*.

133   Eleven pre-speciation late Pliocene samples containing solely *T. sacculifer* plexus (*T. trilobus, T.*

134   *immaturus* and *T. quadrilobatus*), were examined from 24X (216.82-224.02 mbsf). Two closely

135   spaced samples were analysed from core 10H (mean depth 88 mbsf) following the speciation (i.e.,

136   post-speciation samples) where *T. sacculifer*, *G. fistulosa* and intermediate specimens are all

137   present in each sample. Samples from 10H were pooled in order to increase the sample size and

138   statistical power. Samples were dry sieved at the 250-μm size fraction to avoid inclusion of

139   juvenile specimens. Adult specimens of both study species are much larger than 250 μm across

140   and there was no abrupt cutoff in the size data (see Results section and figures) so there was

141   minimal risk of missing smaller adult specimens. All samples were picked for all *T. sacculifer*

142   plexus and *G. fistulosa* tests, resulting in over 900 specimens. Specimens were positioned in

143   umbilical view and imaged using a camera mounted on a light microscope. Images were analysed

144   using the Image Pro Premier software (version 9.3).

145

Stratigraphy. —Chuang et al. (2018) provide an integrated stratigraphy for Site 1115,

incorporating paleomagnetic reversal events with planktonic foraminifer and calcareous

nannofossil bioevents and high-resolution oxygen isotope analysis tied to the benthic foraminifer

oxygen isotope reference curve (LR04 stack of). Unfortunately the Chuang et al. (2018)

integrated stratigraphy ends slightly younger than our studied interval. We used biostratigraphy

(Poole 2017; Chuang et al. 2018) and magnetostratigraphy (Takahashi et al. (2001), to determine

the age of the samples studied, extrapolating back in time from the tuned record of Chuang et al.

(2018) (Fig. 4, Table 1). Chuang et al. (2018) used the magnetochronology of Cande and Kent

(1995), we have refrained from updating the Site 1115 record to more recently published

magnetochronologies to keep our time scales consistent. Note, the biochronology of the Bottom

of the *Pulleniatina* L5 coiling shift in Chuang et al. (2018) is significantly older (~127 kyr) than

calibrations from other Indo-Pacific sites (Pearson et al. 2023), thus we have removed this event

from Figure 3. However, the Top of the *Pulleniatina* L5 coiling shift at 1.777±0.003 Ma is

extremely consistent with the global calibration of 1.78±0.01 Ma from multiple Indo-Pacific sites

(Pearson et al. 2023). We follow Poole and Wade (2019) and limit *G. fistulosa* s.s. to specimens

typically possessing four broad, flattened final chambers, that increase rapidly in size, with one

or more finger-like protuberances, multiple supplementary apertures and a distinct lip on the

primary aperture. Our lowest occurrence of *G. fistulosa* s.s. is thus higher than indicated by

Shipboard Scientific Party (1999) for Hole 1115B. Furthermore, we find the highest occurrence

of *G. fistulosa* at 88 mbsf (Poole 2017), which is a slightly higher level than in the Shipboard

Scientific Party (1999) and Chuang et al. (2018).

167

168   *Analysis.*—All specimens were analysed for total test area and curvature as measured from

169   two-dimensional images (Fig. 5). Test curvature is calculated as follows:

170

171
$$C = \frac{P^2}{4\pi A}$$
(1)

172

173   Here P is test perimeter (μm) and A is test area (μm^2). The equation divides specimen perimeter

174   length by surface area, as measured from the umbilical side. Lengthier perimeters score higher

175   curvature values, and thus specimens that are lobate with high numbers of protuberances such as

176   *G. fistulosa* s.s. will have higher curvature values than specimens with a more rounded test

177   periphery like *T. sacculifer* s.s.

178

179   We study allometric relationships between test size and curvature to detect the presence of

180   heterochrony during speciation. Allometry can be expressed in the classic power law equation of

181   Huxley (1932):

182

183
$$y = bx^\alpha$$
(2)

184

185   Here, α and b are constants (α is the scaling exponent coefficient), x is size, and y is the response

186   trait. When expressed in logarithmic transformed notation, the scaling relationship becomes

187   linear:

188

189
$$\log y = \log b + \alpha \log x$$
(3)

190

9

191   Here, α is the slope of the relationship and log(b) is the intercept. Both determine the type of

192   heterochrony quantitatively: unchanged slopes and intercepts indicate hyper- or hypomorphosis

193   (Fig. 1A, D), whereas a change in intercept points to pre-/post-displacement (Fig. 1B, E) and a

194   change in slope shows acceleration or deceleration (Fig. 1C, F).

195

196   Differences in slopes and intercepts among species and time slices were quantified with Linear

197   Mixed Effect models using the R package "nlme" (version 3.1.152) (Pinheiro et al. 2021; R Core

198   Team 2021). The models looks for linear trends among subsets of the data (here: species or time

199   slices) by comparing support for four different scenarios:

200

201   1) No overall trend between curvature and area with a consistent slope across species;

202   2) No overall trend between curvature and area, but varying species-specific slopes;

203   3) A relationship between curvature and area with a consistent slope across species;

204   4) A relationship between curvature and area with species-specific slopes.

205

206   Variance differences among species or time slices were assessed using the varIdent function in

207   nlme (Pinheiro and Bates 2000). The model with the lowest Akaike Information Criterion (AIC)

208   value (a measure for model parsimony) and the highest Akaike weight (a measure for relative

209   model likelihood) has the most statistical support among those models fitted.

210

211   **Results**

212   Preceding speciation, *T. sacculifer* alternates between intervals of low and high curvature,

213   whereas average size remains unchanged (Fig. 6) resulting in parallel allometric slopes with

214   different intercepts. The linear mixed effect models confirm that the size-curvature slopes remain

215   parallel throughout the pre-speciation interval (Table 2). After speciation, the intermediate

216   specimens also show comparable curves to *T. sacculifer*, but with intermediate specimens

217   showing both larger size and higher curvature than the ancestral forms (Fig. 7).

218   *Globigerinoidesella fistulosa* is larger on average than both *T. sacculifer* and intermediate forms,

219   although it should be noted that maximum size varies very little among species. Rather, the range

220   in size of both *G. fistulosa* and intermediate specimens is narrower and concentrated at the larger

221   end of the size range of *T. sacculifer*. In contrast, the range of curvature values for *G. fistulosa* is

222   much higher than both ancestral forms and increases strongly with size. This results in an

223   allometric slope significantly different from its ancestors (Table 3, Fig. 7). A visual inspection of

224   the residuals shows that they are approximately Normally distributed, satisfying the model

225   prerequisites (Supplementary figures S1 and S2).

226

227   **Discussion**

228   We study allometric relationships between test size and curvature to detect the presence of

229   heterochrony during speciation. The allometric slopes in *T. sacculifer* immediately prior to the

230   origination of *G. fistulosa* show shifts between high and low curvature (Fig. 6). The parallel

231   slopes, and similar size throughout the pre-speciation interval suggest a pattern of alternating

232   pre- and post-displacement (Fig. 1B, E). Changes in *T. sacculifer* outline shape are primarily

233   driven by variation in the shape of the sac-like final chamber (Poole and Wade 2019), suggesting

234   that in the pre-speciation interval, the *T. sacculifer* plexus alternated between more and less

235   "*fistulosa*-like" final chambers. These phases could be a plastic response to local environmental

236   change. Schmidt et al. (2016) showed that *T. sacculifer* size and shape is partly controlled by

237   temperature. The pre-speciation interval includes Marine Isotope Stage M2, an unusually

238   pronounced glacial stage by Pliocene standards (Lisiecki and Raymo 2005), which likely

239   contributed to local environmental fluctuations that may have fed through to morphological

240   changes.

241

242   Our morphometric analyses reveal an alternating pattern of low and intermediate curvature in the

243   *T. sacculifer* plexus (Fig. 6). This indicates that even before the origination of *G. fistulosa,* some

244   of the morphological variation necessary to produce the new species was already present in the

245   ancestor. However, pre-displacement was not enough to result in the unusual final morphology

246   of *G. fistulosa*. The increase in average size of intermediate specimens compared to *T. sacculifer*

247   (Fig. 7) points to hypermorphosis (Fig. 1A) on top of continued pre-displacement through higher

248   curvature at similar sizes in intermediate specimens. The final transition from intermediate

249   specimens to *G. fistulosa* is marked by a steeper allometric slope than both *T. sacculifer* and

250   intermediate specimens (Fig. 7). Additionally, *G. fistulosa* often develops protuberances on

251   multiple chambers in the final whorl (Poole and Wade 2019), which points to further pre-

252   displacement by earlier onset of protuberances and likely contributes to the observed high

253   curvature values. These results indicate that the origination of *G. fistulosa* involved a

254   combination of two peramorphic expressions: pre-displacement through earlier onset of more

255   pronounced protuberances and acceleration through a steeper allometric slope than its ancestor.

256

257   The steep allometric slope in *G. fistulosa* is likely directly related to the high number of

258   protuberances in the species. The area of the protuberances is very small compared to the total

259   test area, whereas a single protuberance can increase shell perimeter by as much as 50%. The

12

260   underfitting of the slope at the highest curvature values is likely the result of a handful of

261   specimens with multiple long protuberances which disproportionally affect the curvature values.

262

263   There are numerous described cases of heterochrony in the Cenozoic fossil record of planktonic

264   foraminifera, and both paedomorphic and peramorphic expressions have been observed in

265   quantitative and qualitative studies. For example, studies of the Paleocene-Eocene

266   *Globanomalina chapmani - Globanomalina luxorensis - Pseudohastigerina wilcoxensis* lineage

267   found evidence of pre-displacement (Speijer and Samir (1997) and hypermorphosis or

268   acceleration (Berggren et al. (1967). The Eocene transition from *G. australiformis* to

269   *Turborotalia frontosa* is interpreted as resulting from hypermorphosis (Olsson and Hemleben

270   2006; Pearson et al. 2006b). Interestingly, the subsequent *Turborotalia* lineage demonstrates a

271   regressive paedomorphic trend, which effectively reversed the former hypermorphosis

272   expression (Pearson et al. 2006b). Wei (1994) conducted a comprehensive study to calculate

273   allometric "trajectories" for assessing heterochronic modes over time in the morphological

274   evolution within species of the *Globorotalia* (*Globoconella*) *puncticulata-inflata* plexus.

275   Following the divergence of *G.* (*G.*) *puncticulata* and *G.* (*G.*) *inflata*, both morphospecies

276   underwent different modes of heterochrony (Wei 1994). In *G.* (*G.*) *puncticulata*, the change in

277   allometric trajectories suggested acceleration with later forms developing higher peripheral

278   roundness in comparison to same-sized ancestral forms (Wei 1994). In *G.* (*G.*) *inflata*, the initial

279   post-displacement trend is interpreted as a delay in the onset of the neanic ontogenetic stage and

280   probable cause of divergence between the morphospecies (Wei 1994). Interestingly, this is

281   followed by a reversing trend of pre-displacement (Wei 1994). Finally, Morard et al. (2019)

282   combined genetics and morphological measurements in modern species of the *Globigerinoides*

283   genus to explain the apparent mismatch between morphological disparity and a high degree of

284   genetic kinship. They found that relatively large morphological differences between closely

285   related species can be attained by small changes in the developmental sequence, highlighting the

286   importance of considering heterochronic expressions when studying planktonic foraminifera

287   evolution.

288

289   The peramorphic expressions of both pre-displacement and acceleration in the origination of *G.*

290   *fistulosa* bears close resemblance to the evolution of Eocene *Hantkenina*. Like *G. fistulosa*,

291   hantkeninids are bizarre-looking planktonic foraminifera characterised by tubulospines. The

292   tubulospines first developed on the final, adult chambers, before earlier trait onset in later

293   hantkeninid species (Pearson and Coxall 2014). Such a shift to earlier trait (tubulospine)

294   development in later morphospecies, such as *Hantkenina mexicana*, may therefore indicate pre-

295   displacement, although they are generally also larger than the transitional forms, pointing to

296   hypermorphosis (Pearson and Coxall 2014). To our knowledge, the hantkeninids and *G. fistulosa*

297   are the only species of planktonic foraminifera whose origination included multiple expressions

298   of heterochrony. Possibly, their extreme shapes could only be formed through multiple

299   developmental shifts, which might explain why unusual shapes such as protuberances and

300   tubulospines are so rare in planktonic foraminifera.

301

302   *Mechanisms.*—Although the aforementioned heterochronic changes explain how *G.*

303   *fistulosa* managed to reach a more extreme shape than most other planktonic foraminifera, the

304   drivers of these morphological adaptations are harder to interpret. The species' stratigraphic

305   range includes the onset of Northern Hemisphere glaciation (NHG, ~3.5 to 2.5 Ma) (Bailey et al.

306   2013; Westerhold et al. 2020). During this interval, Earth transitioned from a unipolar glacial

307   state, with large ice sheets only on Antarctica, to one that was sufficiently cool by ~2.5 Ma to

308   induce growth of large ice sheets in the Northern Hemisphere and associated rafting of icebergs

309   across the subpolar North Atlantic Ocean (Shackleton et al. 1984). The high-resolution oxygen

310   isotope record of *T. sacculifer* at Site 1115 does not indicate any dramatic change associated with

311   the extinction of *G. fistulosa* (Chuang et al. 2018). Furthermore, *G. fistulosa* was restricted to the

312   tropical oceans and its exposure to environmental change originating in the high northern

313   latitudes was therefore likely limited.

314

315   Both the *T. sacculifer* plexus and *G. fistulosa* are spinose, occupy the mixed-layer and harbour

316   algal photosymbionts. It has been shown that the acquisition of symbionts is necessary for *T.*

317   *sacculifer* to achieve maximum sizes (Bé et al. 1982). The large size of *G. fistulosa* compared to

318   *T. sacculifer* would have required even more symbionts than *T. sacculifer*, but the surface-area:

319   volume ratio in globular chambers of planktonic foraminifera, and thus space for symbionts,

320   decreases with increasing volume. The protuberances in *G. fistulosa* potentially counteract this

321   trend by increasing surface area to host more symbionts. Modern species with shells that have a

322   high surface area to volume ratio often show a higher increase in symbiont content with

323   increasing size than more spherical ones (Takagi et al. 2019), suggesting that irregular shapes are

324   beneficial to symbiont activity. This hypothesis could be tested in future studies by comparing

325   stable carbon isotopes between *G. fistulosa* and *T. sacculifer* to test for differences in symbiont

326   activity. The protuberances themselves are spinose (Poole and Wade 2019), further increasing

327   effective test size. Other digitate species such as the hantkeninids have been argued to evolve

328   elongated chambers to increase effective test size and food gathering efficiency (Coxall et al.

329   2007), which possibly further helped *G. fistulosa* to reach and maintain a large body size.

330   Finally, it should be noted that there might not be any clear evolutionary advantage of the

331   tubulospines. Much of the functional morphology of foraminifera shell shape remains unclear

332   (Caromel et al. 2014; Renaud and Schmidt 2003), and the development of some morphological

333   features may not have a specific functional response. An evolutionary advantage or fulfilment of

334   a particular function does not need to be assumed by the development of a trait, such as

335   protuberances in *G. fistulosa*.

336

337   **Conclusions**

338   The origination of the unusual test size and shape of *Globigerinoidesella fistulosa* was the result

339   of a combination of pre-displacement and acceleration of ancestral traits found in *T. sacculifer*.

340   These results imply that shifts in multiple developmental expressions are required for the

341   origination of unusual morphologies. As both ancestor and descendant species continued to

342   thrive following the origination of *G. fistulosa*, the drivers of morphological change are unlikely

343   to be environmental changes that favoured one species over the other. Our work provides a case

344   study of the complex developmental changes required to produce ornate shell shapes and

345   highlights the importance of development in the origination of unusual forms.

346

355

356   **Competing interests**

357   The authors declare no competing interests.

358

359   **Data availability statement**

360   Data is currently privately available from the Dryad repository:

361   https://datadryad.org/stash/share/ixZXllt38iDtf5EyfN7J6jvVczOwPmaXM4gYTbWbuYc. It will

362   be made publicly available upon publication of the manuscript.

363

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Figure captions

553 **Figure 1**. Schematic representations of trait development for the six types of heterochrony: a)

554 hypermorphosis, where traits develop longer in the descendent than the ancestor while the rate

555 and onset of trait development remain the same; b) pre-displacement, where the onset of

556 descendent trait development starts earlier while the rate of development remains the same; c)

557 acceleration, where the rate of trait development is higher in the descendent species while the

558 onset of development is the same as the ancestor; d) hypomorphosis, where traits stop

559 developing earlier in the descendant than the ancestor; e) post-displacement, where the onset of

560 descendant trait development starts later than in the ancestor; and f) deceleration, where the rate

561 of trait development is lower in the descendant than the ancestor.

562 **Figure 2.** (1) *Trilobatus sacculifer* (re-illustrated from Poole and Wade, 2019, Fig. 9D); (2) an

563 intermediate form between *T. sacculifer* and *Globigerinoidesella fistulosa* (re-illustrated from

564 Poole and Wade, 2019, Fig. 11L); (3) *Globigerinoidesella fistulosa* (re-illustrated from Poole

565 and Wade, 2019, Fig. 13J). All specimens from ODP Site 1115. All scale bars represent 100 μm.

566 **Figure 3**. Magneto- and bio-stratigraphy at ODP Hole 1115B. Gray shaded boxes indicate

567 intervals examined in this study for morphometric analysis. Magnetic chrons and bioevents from

568 Chuang et al. (2018), supplemented by planktonic foraminifera biostratigraphy in Poole (2017).

569 **Figure 4**. Location of ODP Site 1115 in the western Woodlark basin, equatorial Pacific.

570 **Figure 5**. Biometric and morphometric parameters measured on *Trilobatus sacculifer* and

571 *Globigerinoidesella fistulosa*.

572 **Figure 6.** *Trilobatus sacculifer* size and shape allometry in five time intervals from oldest (a) to

573 youngest (e) preceding the origination of *Globigerinoidesella fistulosa*. Blue and red arrows

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574   indicate pre- and post-displacement respectively. Most stages include several samples: stage (a)

575   contains all samples from cores 24X-06 and 24X-05, stage (b) contains all samples from core

576   24X-04, stage (c) contains samples from core 24X-03, stage (d) contains all samples from core

577   24X-02 and stage (e) contains all samples from core 24X-01. See Table 1 for full sample IDs.

578   **Figure 7**. Log size and curvature for *Trilobatus sacculifer*, intermediate and *Globigerinoidesella*

579   *fistulosa* specimens. Straight lines show linear regressions for each species (*T. sacculifer*: $R^2 =$

580   0.17, p < 0.001. Intermediate: $R^2 = 0.014$, p < 0.001. *G. fistulosa*: $R^2 = 0.29$, p < 0.001).

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Table captions

Table 1. Sample ID, depth and number of analysed specimens per sample. Abbreviations: mbsf = metres below sea-floor; n = number of specimens. The pooled sample contains specimens from sample IDs 1115B-10H-4 127-129 cm and 1115B-10H-3 104-106cm.

Table 2. Log likelihood, AIC and Akaike weights for all four analysed models of *Trilobatus sacculifer* area and curvature preceding origination of *Globigerinoidesella fistulosa.* ΔAIC represents the difference between AIC and the set's minimum AIC. The best performing model based on AIC and Akaike weight is indicated in bold.

Table 3. Log likelihood, AIC and Akaike weights for all four analysed models comparing *Trilobatus sacculifer* and intermediate specimen area and curvature. ΔAIC represents the difference between AIC and the set's minimum AIC. The best performing model based on AIC and Akaike weight is indicated in bold.