



# Spatial and Temporal Body-Size Changes of Brachiopods in Relation to Varied Palaeogeographic Settings

# 7

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## 7.1 Previous Study on the Permian–Triassic Body Sizes and Potential Insights into the Palaeoenvironments

The so-called Lilliput effect refers to a macroevolutionary phenomenon where the surviving animals in the aftermath of a mass extinction tend to be smaller on average than their pre-extinction relatives (Urbanek 1993; Fraiser and Bottjer 2004; Payne 2005; Twitchett 2007; Keller and Abramovich 2009; Zhang et al. 2016). This observation clearly highlights the importance of animal body-size changes in the study of mass extinctions. Body size is a key character of any organism and profoundly affects its biology and ecology (Jablonski 1996). Body size is often controlled by environmental factors, including oxygen fluctuations (Savrda and Bottjer 1986; Payne et al. 2008, 2013), food availability (Hallam 1965; Rheault and Rice 1996; Twitchett 2007; He et al. 2010)

and temperature changes (Hunt et al. 2010; Sheridan and Bickford 2011; Edeline et al. 2013), as well as substrate conditions. As many of these factors vary with water depth, the relationship between body size and bathymetry (i.e., spatial body-size changes in this book) is crucial for the study on body-size changes (Anderson 1971; Thiel 1975; Peck and Harper 2010; Shi et al. 2016). For example, the study of spatial body-size changes is useful for examining which factor (or factors) played a more important role in controlling the differences of body sizes, thereby providing insights into the evolution of palaeoenvironments through time. Meanwhile, the study of size changes through past extinction times (i.e., temporal body-size changes in this book) is also of particular importance in understanding the biotic responses to global-scale climatic and environmental evolution (Twitchett 2007; He et al. 2010, 2015).

Numerous researches have been undertaken on the Permian–Triassic body-size changes of conodonts, brachiopods, siliceous sponges, ostracods or foraminifers in South China (He et al. 2007, 2010, 2015, 2016, 2017; Peng et al. 2007; Luo et al. 2008; Song et al. 2011; Liu et al. 2013; Chu et al. 2016; Zhang et al. 2016). Most of these studies have focused on the patterns of body-size changes of individual taxa across time and their possible underlying control mechanisms, and a few (e.g., He et al. 2010; Liu et al. 2013) have addressed the relationship between size changes in relation to primary productivity and redox

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palaeoproxies in the context of palaeobathymetry. Most recently, based on a global dataset of Changhsingian brachiopod orders, Shi et al. (2016) examined the relationship of Changhsingian brachiopod body-size changes in relation to the onshore–offshore–basin gradient.

## 7.2 Latest Permian Body-Size Changes in Relation to Varied Palaeogeographic Settings

The palaeogeographic settings of South China are already described in Chap. 2 and the age correlations in Chap. 4. Detailed descriptions of the methodology used for the measurement of body sizes and their analyses including significance testing are given in Chap. 5.

Here we present a summary of body-size changes of latest Permian brachiopods across different bathymetrically controlled palaeoenvironmental settings within the South China basin, extracted from our recent study (He et al. 2017). In this book, we adopted two most commonly found Changhsingian chonetid brachiopod species, *Fusichonetes pygmaea* and *Fusichonetes quadrata* (These two species had been referred to as *Tethyochonetes pygmaea* and *Tethyochonetes quadrata*, respectively, see Wu et al. 2017 for details), from five different sections, which together constituted an approximately-defined basin-wide bathymetric gradient spanning the shallow-water clastic shelf, shallow-water carbonate platform and ramp, and deep-water siliceous basinal settings (see Fig. 7.1; analysis of palaeo-water depths see Chap. 3). The studied five sections include Huangzhishan, Zhongzhai, Daoduishan, Majiashan and Rencunping.

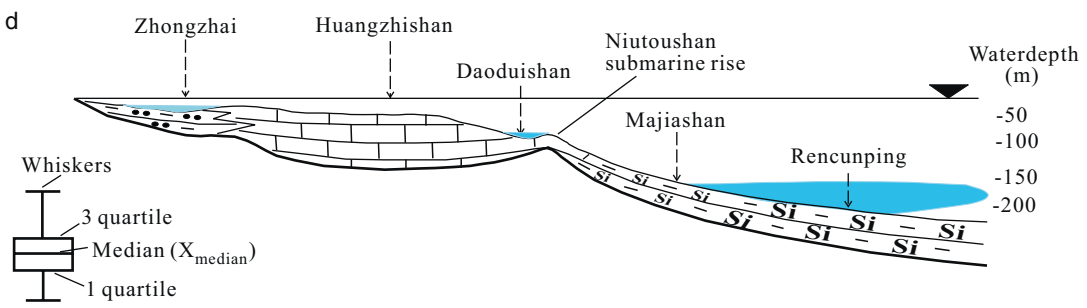
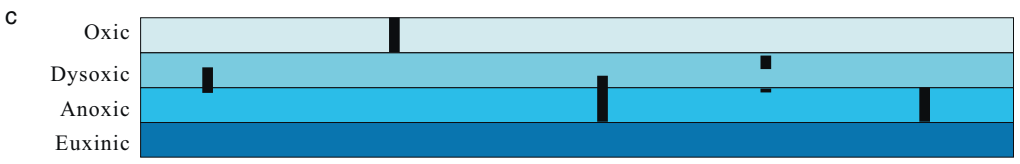
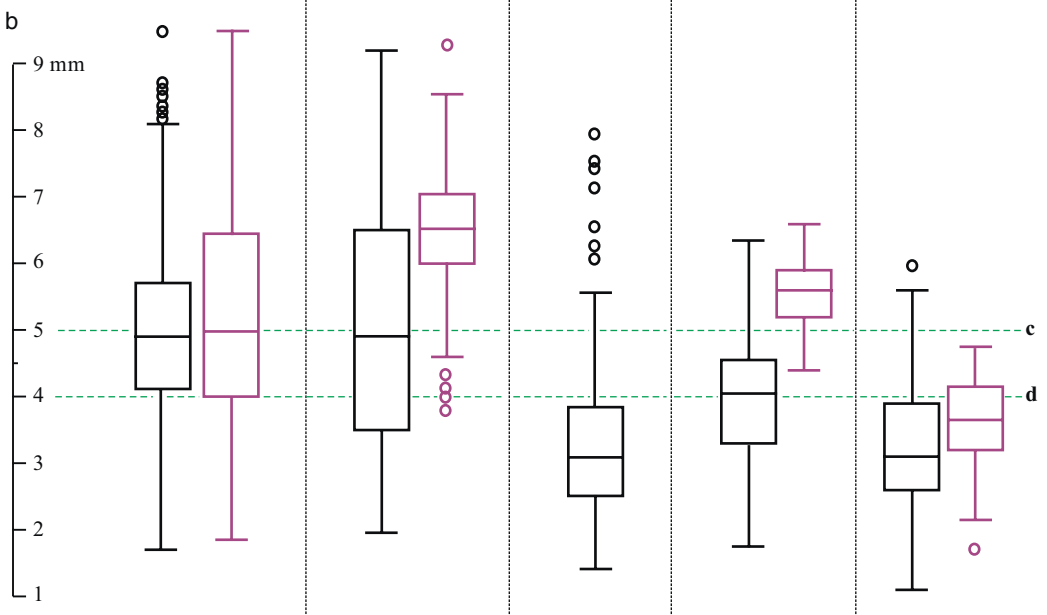
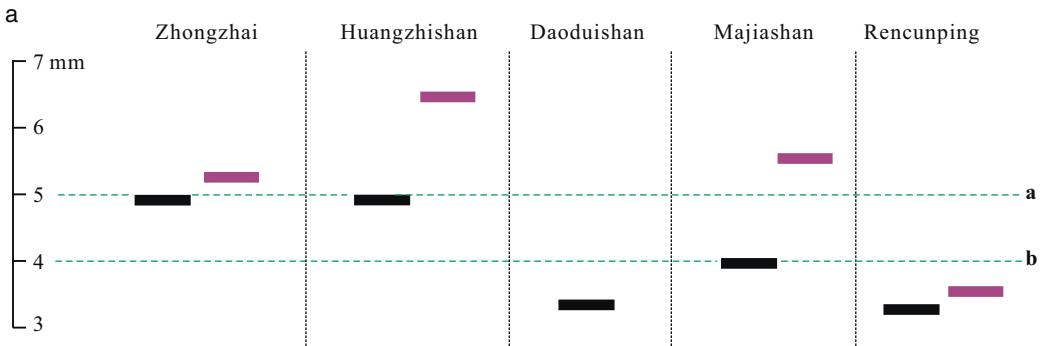
For the study of body sizes, values of  $X_{\text{mean}}$  and  $X_{\text{median}}$  were adopted (the definition and reason for selected as parameters sees Chap. 5). The  $X_{\text{mean}}$  shows that the body sizes at Zhongzhai and Huangzhishan are both close to or greater than 5 mm (see Line a in Fig. 7.1a) whereas the same size metric for the Daoduishan, Majiashan and Rencunping sections are all smaller than 4 mm (see Line b in Fig. 7.1a) except for *F. quadrata* at Majiashan whose  $X_{\text{mean}}$  reached larger than 5 mm (Fig. 7.1a).

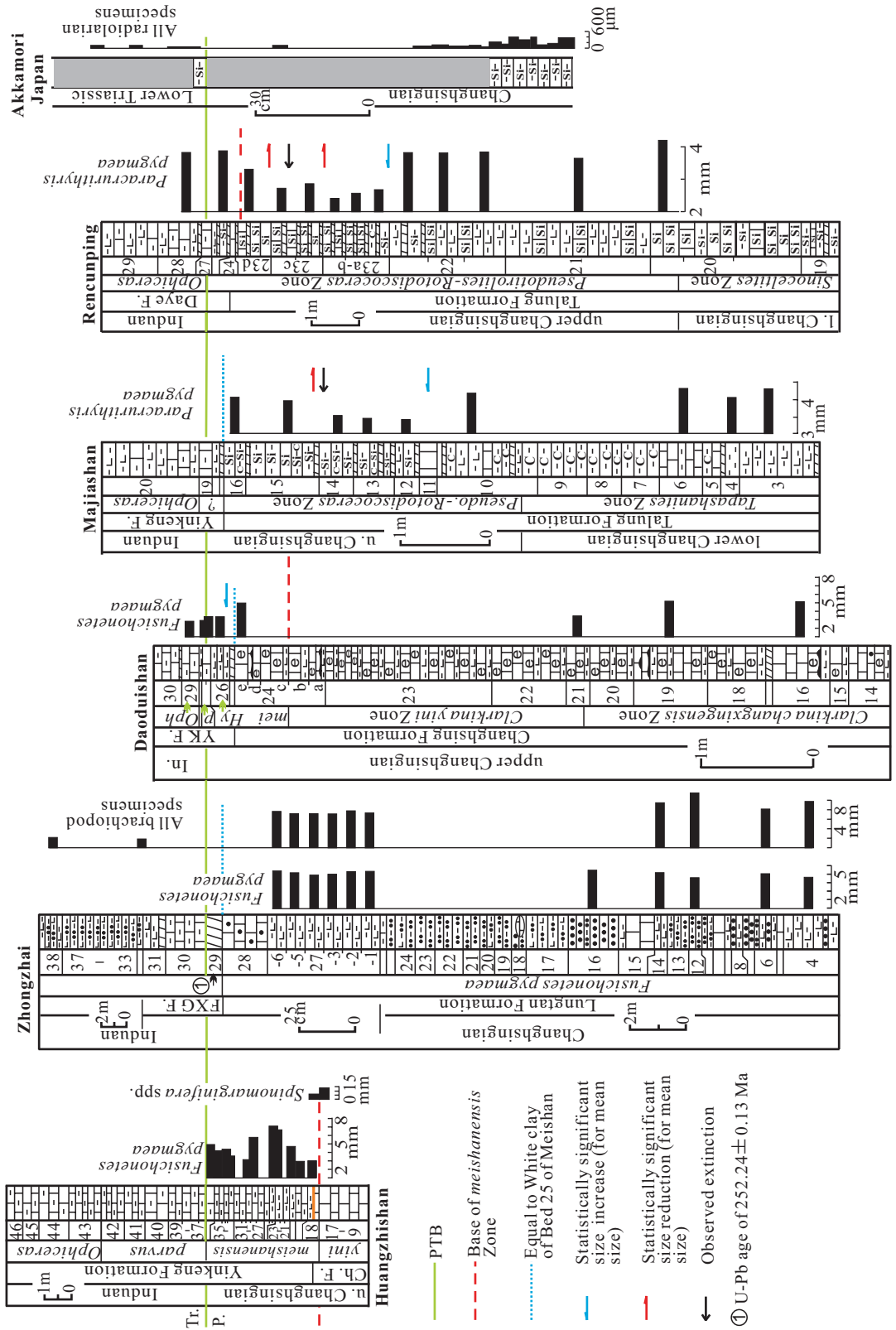
Additionally, the  $X_{\text{median}}$  shows that the median body sizes at Huangzhishan and Zhongzhai are close to or larger than 5.0 mm (see Line c in Fig. 7.1b). By contrast, the median sizes of brachiopods for the other three deeper-water sections are all close to or smaller than 4.0 mm (see Line d in Fig. 7.1b) with the exception of *F. quadrata* at Majiashan whose  $X_{\text{median}}$  attained larger than 5 mm (Fig. 7.1b). A Mann–Whitney (M–W) test revealed that the difference in median sizes between the two groups of sections (i.e., the Huangzhishan and Zhongzhai as a group representing shallow-water settings while the Daoduishan, Majiashan and Rencunping together representing a group of deeper-water settings) is statistically significant ( $P < 0.05$ , see Table 5.1), although the difference of medians for *F. quadrata* is not significant between Zhongzhai and Majiashan sections ( $P = 0.3622$ , see Table 5.1).

Overall, the analysis on body sizes for both species by using different size parameters ( $X_{\text{mean}}$  and  $X_{\text{median}}$ ) among the studied sections revealed that body sizes at Huangzhishan and Zhongzhai are significantly larger than their counterparts in the Daoduishan, Majiashan and Rencunping sections, with the only exception of *F. quadrata* at Majiashan (see explanation in Chap. 8).

**Fig. 7.1** Body-size differences of *F. pygmaea* (black) and *F. quadrata* (purple) in the five studied sections and their comparison with varied palaeo-bathymetry and redox conditions (revised after He et al. 2017). (a) Body size ( $X_{\text{mean}}$ ); (b) Body size ( $X_{\text{median}}$ ); (c) Redox conditions at the studied

sections; (d) Sketch diagram showing the palaeogeographic settings and palaeo-bathymetry of the studied sections. Note: The division for redox condition in Fig. 7.1c is based on the study of pyrite framboids (see Chap. 8). The estimation for palaeo-bathymetry in Fig. 7.1d sees Chap. 3





**Fig. 7.2** Body-size distribution of varied taxa at the studied sections (revised after He et al. 2017). Widths of thick black bars indicate the size values of brachiopods at Huangzhishan, Zhongzhai, Daoduishan, Majiashan and Rencunping sections of South China or to the size values of radiolarians at the Akkamori of Japan. Meanings of size data: for *Fusichonetes pygmaea* at Huangzhishan refer to the mean size across all specimens in *F. pygmaea* (see He et al. 2017), for *Spinomarginifera* spp. at Huangzhishan refer to the mean size across all specimens in *Spinomarginifera* spp. (see Chen et al. 2009), for *Fusichonetes pygmaea* at Zhongzhai refer to the mean size across all specimens in *F. pygmaea* (see He et al. 2017), for all brachiopod specimens at Zhongzhai refer to the arithmetic mean size (shell width) of all brachiopod species (see Zhang

et al. 2016), for *Fusichonetes pygmaea* at Daoduishan represent the mean size across all specimens in *F. pygmaea* (see He et al. 2016), for *Paracrurithyris pygmaea* at Majiashan and Rencunping represent the mean size across all specimens in *P. pygmaea* (see He et al. 2015), and for radiolarians at Akkamori of Japan represent the maximum shell diameter among all specimens (see Takahashi et al. 2009). Biostratigraphy of Huangzhishan, Majiashan and Rencunping after He et al. 2015; U–Pb age of Zhongzhai after Shen et al. 2011; biostratigraphy of Daoduishan after He et al. 2016. Note for abbreviations: u.- upper, l.- lower, FXG- Feixianguan, In.- Induan, YK- Yinkeng, *mei-Clarkina meishanensis* Zone, *Hy-Hypophiceras*, *p-Hindeodus parvus* Zone, *Oph-Ophiceras* Zone, other abbreviations for words see captions of Figs. 6.1 and 6.2

### 7.3 Temporal Body-Size Changes Through the Permian–Triassic Transition in Varied Palaeogeographic Settings

The studied species for the body-size changes include *Paracrurithyris pygmaea* from the Rencunping and Majiashan sections and *Fusichonetes pygmaea* from the Daoduishan section, with mean size as the studied parameter (see Chap. 5). The reasons for these two species were chosen for study is given in Chap. 5. In addition, body sizes of *Fusichonetes pygmaea* and *Spinomarginifera* spp. from Huangzhishan, *Fusichonetes pygmaea* and all brachiopod specimens from Zhongzhai and all radiolarian specimens from Akkamori of Japan, have also been analyzed for comparison, although their temporal changes could not be tested for significance because of scarcity of specimens (*Fusichonetes pygmaea*) or difference in taxonomy level (e.g., *Spinomarginifera* spp. being at the genus level, all radiolarian specimens being at subclass level).

The analyses revealed the following patterns (Fig. 7.2): *Paracrurithyris pygmaea* at Rencunping significantly reduced its size from Beds 22-3 to 23a and then significantly increased its size from Beds 23b-2 to 23c-1 and again from Beds 23c-2 to 23d-24; *Paracrurithyris pygmaea* at Majiashan shrank from Beds 10–12, followed by a significant increase from Beds 14–15. Thus, it is clear that the mean size of brachiopods from the deep-water Rencunping and Majiashan sections began to decline significantly (in a statistical sense) from the middle *Pseudotiroilites*–*Rotodiscoceras* Zone (≈middle *Clarkina yini* Zone) (Fig. 7.2). In contrast, significant size reduction of brachiopods in the shallower water environment of Daoduishan (shallower, compared to Rencunping and Majiashan) began in the top part of the *C. meishanensis* Zone (Fig. 7.2). As for the compared faunas, the size reduction of radiolarian specimens from the deep-water Akkamori section of Japan (pelagic environment) apparently began to take place far below the PTB, namely earlier than the faunas in the shallow-water settings of South China. The size reduction of *Spinomarginifera*

spp. at the shallow-water Huangzhishan took place at the base of *C. meishanensis* Zone and size reduction of *Fusichonetes pygmaea* at this section took place in the upper part of *C. meishanensis* Zone, both later than their counterparts of deep-water environments. At the shallow-water Zhongzhai section, although the mean body size of *Fusichonetes pygmaea* did not appear to have changed significantly, but the body sizes of all brachiopod specimens through the section demonstrate a reduction trend in the Early Triassic (e.g., Beds 32 and 38), and the reduction occurred later than brachiopods living in deep-water environments. In summary, it is evident that size reduction in deep-water environments occurred earlier than in shallow-water environments (Fig. 7.2). This pattern is consistent with the temporal trend of the brachiopod diversity evolution in that the decline of deep-water brachiopod species diversity commenced earlier than in shallow-water settings (the reason and analysis see Chap. 8).

In addition, body sizes of most species which tentatively survived the PTB, attained or demonstrated a reduction trend. For example, *Paryphella orbicularis* and *Chaohochonetes triangusinuata* (= ?*Tethyochonetes* sp. of He et al. 2010) at Majiashan reduced their body sizes immediately below the PTB and attained smaller sizes in the Early Triassic. A similar pattern of body-size changes for *Paryphella orbicularis* (= *Paryphella triquetra* of He et al. 2016) has been recorded at Daoduishan. These cases are typical of the Lilliput effect.

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