Palaeogeography, Palaeoclimatology, Palaeoecology 448 (2016) 85–95

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Significant pre-mass extinction animal body-size changes: Evidences from the Permian–Triassic boundary brachiopod faunas of South China

Yang Zhang [a,b,c,*], G.R. Shi [b,**], Wei-hong He [a], Hui-ting Wu [d], Yong Lei [e], Ke-xin Zhang [a], Cheng-chen Du [f,g], Ting-lu Yang [d], Ming-liang Yue [d], Yi-fan Xiao [d]

[a] State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, 388 Lumo Road, Hongshan, Wuhan 430074, China
[b] Deakin University, Geelong and School of Life and Environmental Sciences, 221 Burwood Highway, Burwood, Victoria 3125, Australia
[c] School of Earth Sciences and Resource, China University of Geosciences (Beijing), 29 Xueyuan Road, Haidian District, Beijing 100083, China
[d] Faculty of Earth Sciences, China University of Geosciences, 388 Lumo Road, Hongshan, Wuhan 430074, China
[e] Center for Protecting Geological Heritage of Shanxi Province, 3 Wangjing Road, Taiyuan 030024, China
[f] Key Laboratory of Earthquake Geodesy, Institute of Seismology, China Earthquake Administration, Wuhan 430071, China
[g] Earthquake Administration of Hubei Province, Wuhan 430071, China

ARTICLE INFO

Article history:
Received 5 June 2015
Received in revised form 11 November 2015
Accepted 23 November 2015
Available online 2 December 2015

Keywords:
Permian–Triassic boundary
Brachiopods
Extinction
Body-size change
South China

ABSTRACT

This paper has undertaken a quantitative and statistical analysis of brachiopod body-size changes through the marine Permian–Triassic boundary section at Zhongzhai, Guizhou Province, South China, and found that (1) pre-mass extinction dwarfing is evident for at least the rugosochonetid species chosen for this study; (2) *Tethyochonetes* species reduced their size earlier than that in the *Neochonetes* species; and (3) no significant size reduction occurred in the newly evolved species of these two genera. Inter-species competition for resources between *Neochonetes* species and *Tethyochonetes* species and the reduction of food supply in the upper part of the uppermost Permian is here proposed to explain these observed stratigraphic patterns of brachiopod body-size changes throughout the Zhongzhai section. In the case of the newly evolved species showing no significant body-size change, morphological innovations (adaptations) in the process of speciation are considered to have significantly enhanced these newly evolved species' flexibility and survival in coping with degrading environmental conditions.

1. Introduction

Body size is one of the key characters that can influence the biology, ecology and evolution of an organism (Calder, 1984; Jablonski, 1996; Petchey and Belgrano, 2010). In the past few decades, this topic has attracted considerable attentions from paleobiologists, as evident from a large number of papers published on the documentation and elucidation of body-size change in the fossil record. Such studies, most notably, have included foraminifers (Keller and Abramovich, 2009; Wade and Olsson, 2009; Payne et al., 2011, 2012a,b; Song et al., 2011; Rego et al., 2012; Zhang and Payne, 2012), conodonts (Luo et al., 2008), gastropods (Fraiser and Bottjer, 2004; Payne, 2005; Twitchett, 2007), bivalves (Hayami, 1997, 1998; McGowan et al., 2009; Posenato, 2009; Metcalfe et al., 2011), brachiopods (Chen et al., 2005; He et al., 2007, 2010; Peng et al., 2007; Twitchett, 2007; Novack-Gottshall and Lanier, 2008; Zhang and He, 2008; McGowan et al., 2009; Huang et al., 2010; Metcalfe et al., 2011), echinoderms (Twitchett et al., 2005), fishes (Mutter and Neuman, 2009) and tetrapods (Smith, 1995; Tverdokhlebov et al., 2002).

However, the terms used to refer to the phenomenon of body size reduction over time have been varied, and at least three variants have been commonly used: 'dwarfing', 'Lilliput effect' and 'miniaturization'. As different definitions and understandings of these terms have been adopted and used differently in the literature, causing a significant degree of confusion among researchers, it is therefore necessary to review and clarify these terms.

When Marshall and Corruccini (1978) studied the Late Quaternary dwarfed marsupial lineages from Australia, they initially defined the term 'dwarfing' simply as a decreasing trend of mean body size within a lineage over time. Hanken and Wake (1993), on the other hand, referred to 'miniaturization' as a complex combination involving size reduction and structural simplification, as well as increased variability and morphological novelty.

Independently, Urbanek (1993) coined the metaphor 'Lilliput effect', to describe the remarkable phenomenon of the occurrence of diminutive forms following an extinction event based on the research of the Late Silurian graptoloids. Urbanek (1993) further explained the Lilliput effect as 'a subnormal phenotype due to the reduction of size (stunting or dwarfing)'. Recognizing the Lilliput effect potentially as a widespread

* Correspondence to: Y. Zhang, State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, 388 Lumo Road, Hongshan, Wuhan 430074, China.
** Corresponding author.
E-mail addresses: zhangy05@163.com (Y. Zhang), grshi@deakin.edu.au (G.R. Shi).

http://dx.doi.org/10.1016/j.palaeo.2015.11.020
0031-0182/

and general post-extinction macro-evolutionary feature, Payne (2005) further proposed four potential modes for the occurrence of the post-extinction size decrease, as follows: 1) extinction of large taxa; 2) post-crisis appearance of many small taxa; 3) temporary disappearance of large taxa; and 4) within-lineage size decrease. Similarly, Harries and Knorr (2009) also suggested three possible