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Post-extinction diversification patterns of brachiopods in the early–middle Llandovery, Silurian

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ABSTRACT

Network and frequency distribution analyses of global brachiopod occurrences in the earliest Silurian (Rhuddanian–Aeronian) revealed that brachiopod recovery from the end-Ordovician mass extinction during the early–late Rhuddanian was represented mainly by the reestablishment of Late Ordovician cosmopolitan hold-over taxa. Brachiopods nearly doubled their generic diversity from Rhuddanian to Aeronian, owing to the radiation of both endemic and cosmopolitan taxa, associated with an overall post-glacial amelioration of global environment and increased habitat heterogeneity as a result of marine transgressions and expansion of epeiric seas. A drastic turnover from the Ordovician-type to Silurian-type brachiopod faunas took place in the Aeronian, several million years after the terminal Ordovician mass extinction. Compared with the orders of orthides and strophomenides that radiated and predominated in the Ordovician, the atrypides and pentamerides displayed pulses of drastic diversification from the Rhuddanian to Aeronian, mainly in tropically located paleoplates, to become the most abundant and diverse brachiopod orders in the Silurian. Atrypides recovered in the early Rhuddanian, whereas diversification of pentamerides was delayed until the Aeronian and becoming widespread in South China, Kazakhstan terranes, Baltica, Avalonia, and Laurentia.

1. Introduction

In the Phanerozoic, mass extinctions caused drastic reduction in total biodiversity worldwide (e.g. Droser et al., 1997; Hallam and Wignall, 1997; Sheehan, 2001) and left numerous ecological niches empty. Compared to these biotic crises themselves, post-extinction recovery and diversification of organisms into the vacant ecological niches tend to be just as rapid and dramatic, often resulting in major evolutionary innovations and re-shaping the patterns and trajectories of evolution of life (Gould, 2002; Jablonski, 2002).

The end-Ordovician biotic crisis was associated with a brief but intense glaciation episode in Earth history, marked by two pulses of mass extinctions (Berry and Boucot, 1973; Sheehan, 1973; Brenchley et al., 1994; Sheehan, 2001; Brenchley et al., 2003; Rong et al., 2004; Harper et al., 2014; Bond and Grasby, 2017). Following the mass extinctions, the world gradually returned to a warmer climate, and rising eustatic sea levels in the early Silurian (Brenchley et al., 1995; Harper and Rong, 1995, 2001; Sheehan, 2001). Post-glacial marine transgression created vast new habits in epicontinental seas, in which benthic faunas established and diversified, with brachiopods being one of the most abundant and diverse fossil groups.

The rate, timing, and scale of faunal turnover across the Ordovician-Silurian boundary interval, however, have been a matter of debate. Some argued that the severity of end-Ordovician mass extinction is rather modest compared to the other mass extinctions, especially the P-T and K/T events (e.g., Sheehan, 2001; Alroy, 2010), whereas others identified a drastic brachiopod faunal turnover across the Ordovician-Silurian boundary (Sepkoski, 1996). More recently, Rong et al. (2013) recognized that, at the ordinal level, the brachiopod faunal turnover across the Rhuddanian-Aeronian boundary was more significant than that across the Ordovician-Silurian boundary. The Rhuddanian-Aeronian brachiopod faunal turnover was marked by a gradual decline of the strophomenides and orthides (Ordovician-type brachiopods) and a relatively rapid proliferation of the pentamerides, atrypides and athyridides (Silurian-type brachiopods) through long-ranging ecological adaptation and competition (Rong et al., 2008, 2013). The turnover changed the taxonomic composition of brachiopods as a major group of the Palaeozoic evolutionary fauna, and demonstrated the persistence of many relict Ordovician elements following the end-Ordovician mass extinction (Baarli and Harper, 1986; Harper and Rong, 1995, 2001; Jin and Chatterton, 1997; Jin and Copper, 2000, 2010; Rong and Harper, 1999; Rong and Zhan, 2004; Rong et al., 2007, 2008;

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Huang et al., 2013; Finnegan et al., 2016). This mass extinction only delayed the ongoing replacement of the Ordovician-type by the Silurian-type brachiopods, even though typical Ordovician brachiopods continued to dominate until the late Rhuddanian (Huang et al., 2017).

In recent years, the brachiopod faunas of the early Silurian (Rhuddanian and Aeronian ages) have been reviewed (Cocks and Rong, 2008; Rong and Cocks, 2014), with a preliminary analysis of faunal evolution patterns and their palaeobiogeography for the Rhuddanian to investigate the survival of Ordovician taxa and the early evolution of Silurian taxa (Huang et al., 2012). The main objectives of this study, therefore, are to (1) investigate the rate and pattern of brachiopod diversity change at supraspecific, especially ordinal, levels after the end-Ordovician mass extinction event, based on global faunal data, including newly published information of Rhuddanian and Aeronian brachiopods using frequency distribution analysis and network analysis (Vilhena and Antonelli, 2015), and (2) explore the paleoecological and paleogeographical factors that may have influenced the shift in dominance and richness of various groups of brachiopods, such as the decline of the orthides and strophomenides, and the concomitant rise of the pentamerides and atrypides as the hallmarks of the Silurian brachiopod fauna.

2. Data and methods

2.1. Brachiopod faunal data

This study is based mainly on previously published data on brachiopod faunas worldwide, in addition to new taxonomic revisions by the authors of this study. Cocks and Rong (2008) recognized a total of 109 genera of Rhuddanian brachiopods, in which 63 genera are early Rhuddanian, and 87 genera late Rhuddanian in age. This global dataset was updated by Huang et al. (2012), resulting in 137 occurrences of 72 genera from 13 localities of the lower Rhuddanian, and 271 occurrences of 91 genera from 26 localities of the upper Rhuddanian. The information from recent studies on Rhuddanian brachiopods (e.g. reorganized data from Rubel, 2011 based on new stratigraphic information from Männik, 2014; Huang et al., 2013; Baarli, 2014 and personal communication, 2017; Copper and Jin, 2014, 2017; Copper, 2015; Nikitina et al., 2015) are also incorporated into the new database which contains 83 and 98 genera of lower and upper Rhuddanian respectively.

In their review of Aeronian brachiopods, Rong and Cocks (2014) recognized 509 occurrences of 215 genera worldwide. For this study, however, only the well-documented brachiopod faunas from South China, Avalonia, Baltica, Laurentia and Siberia are used for paleobiodiversity and paleobiogeographic analyses. Aeronian brachiopods from high-latitude Gondwana were also taken into consideration. For many Aeronian brachiopod faunas, it has not been possible to separate them into the early or late Aeronian due to biostratigraphic limitations. For this study, the new information provided for the Aeronian brachiopods of South China (Huang et al., 2016a) and northern Laurentia (Gushulak and Jin, 2017) is also incorporated.

To investigate the brachiopod diversification patterns and processes after the end-Ordovician mass extinction, the faunal data are segregated into three time slices: the early Rhuddanian (*Akidograptus ascensus* and *Parakidograptus acuminatus* biozones), late Rhuddanian (*Cystograptus vesiculosus* and *Coronograptus cyphus* biozones), and Aeronian (*Demirastrites pectinatustriangulatus* to *Stimulograptus sedgwickii* biozones) (Melchin et al., 2012; Ogg and Ogg, 2016) (Fig. 1). The age of most brachiopod in the dataset was fully discussed (Cocks and Rong, 2008; Rong and Cocks, 2014), and is applied herein. New biostratigraphic information in recent studies is also adopted for updating the dataset (e.g. Baarli, 2014; Männik, 2014). This study will focus on the broad global trend of diversification. To avoid data bias and unevenness among various localities in the three time intervals, we organized and grouped the data from various localities of the early Rhuddanian and the late Rhuddanian into six major paleoplates, and omitted data from some terranes where the data is poor or sparse. An overview of the brachiopod distribution in six major paleo-plates is shown in Table 1 and Fig. 2.

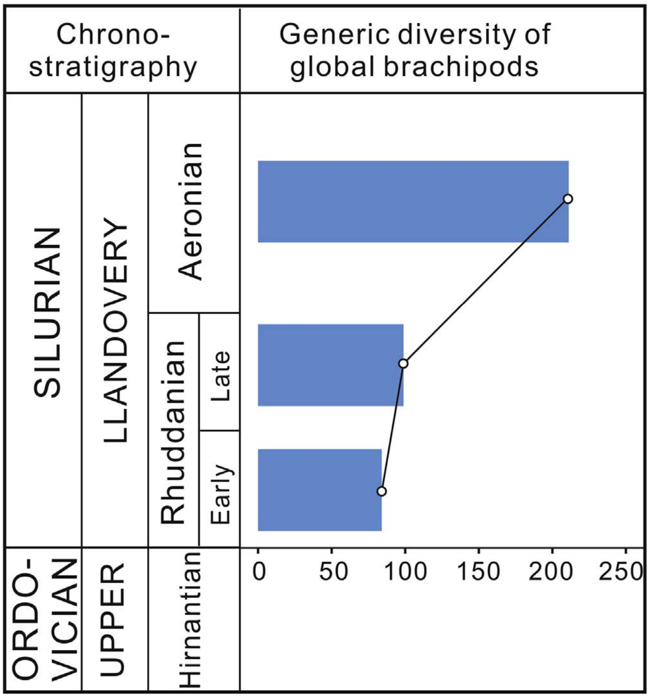

Fig. 1. Generic diversity of global brachiopods across the three time intervals after the end-Ordovician mass extinction.

Table 1
Generic diversity data of brachiopods from the six major paleoplates across the three time intervals after the end-Ordovician mass extinction.

	early Rhuddanian	late Rhuddanian	Aeronian
Laurentia	25	39	105
Avalonia	31	39	88
Baltica	36	42	95
Siberia	18	15	72
South China	34	21	58
Gondwana	–	16	52

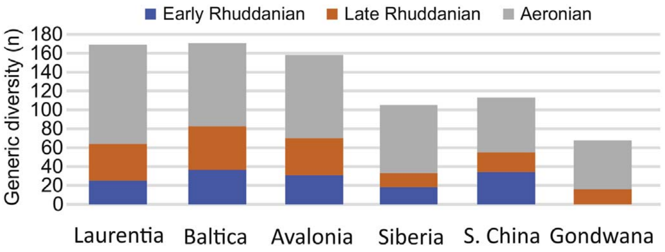

Fig. 2. Bar charts showing generic diversity of brachiopods from the six major paleoplates across the three time intervals after the end-Ordovician mass extinction.

In the Aeronian brachiopod faunal data of Rong and Cocks (2014), Gondwana was combined with some other regions. In our study, we only considered the high-latitude Gondwana brachiopod data and compared them to those of late Rhuddanian age from other regions (there is no brachiopod data of early Rhuddanian age for Gondwana). Although some data are omitted (e.g. 23 occurrences of genera from the Rhuddanian of Kazakhstan, as noted in Nikitina et al., 2015), the lost data represent only a minor portion of the total brachiopod diversity (1.8% for the early Rhuddanian, 4.4% late Rhuddanian, and 4.1% Aeronian) and, therefore, will not significantly affect the diversity