Evidence for Decoupling of Relative Abundance and Biodiversity of Marine Organisms in Initial Stage of GOBE: A Preliminary Study on Lower Ordovician Shellbeds of South China

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INTRODUCTION
Shellbeds are defined as any relatively dense accumulation of bioclasts with various amounts of sedimentary matrix (Kidwell et al., 1986). Shellbeds have various taxonomic compositions, state of preservation, and degree of post-mortem modification (Kidwell et al., 1986), controlled primarily by the evolutionary changes in ecology, diversity, and environmental distribution of bioclast-producing and bioclast-destroying organisms (Kidwell and Brenchley, 1994).

Sepkoski (1981) identified statistically three evolutionary faunas (EF) with shared ecologies and diversity histories, as well as had similar distributions and taxonomic dominance in the Phanerozoic oceans, and viewed the great Ordovician biodiversification event (GOBE sensu Webby, 2004) as an inevitable result of development of the Paleozoic EF, dominated by articulate brachiopods with important contributions from corals, ostracodes, cephalopods, echinoderms and bryozoans, and concomitant decline of the trilobite-dominated Cambrian EF (Sepkoski, 1981). Only sporadic studies have been carried out on several paleoplankton to reveal the effects of the GOBE in light of the development of shellbeds so far (Finnegan and Droser, 2008; Li and Droser, 1999; Waisfeld et al., 1999; Kidwell and Brenchley, 1994; Webby and Percival, 1983). All these studies documented a transition from the Cambrian-type shellbeds to the Paleozoic-type shellbeds, in concomitance with the replacement of the sequential evolutionary faunas. However, the process and factors controlling the temporal variations

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in shellbeds during the GOBE as well as their "taphonomic feedback" in the initial stage of the GOBE are poorly understood.

In this study, we assessed the relative abundance of diagnostic bioclasts and depict the temporal pattern of the shellbed in the Lower Ordovician fossiliferous carbonates in the Three Gorges region of South China. Such kind of study is crucial to the better understanding of the geobiological process of the GOBE, and other biodiversification events in the Phanerozoic.

**GEOLOGICAL SETTINGS**

During the Early Ordovician, the South China paleoplate was extensively covered by an epeiric sea on the Yangtze platform. In Tremadocian, extensive shallow-marine carbonates prevailed in the offshore area, with terrigenous clastics deposited in the inshore area (Zhan and Jin, 2007). From early Floian, the Middle and Lower Yangtze regions were deposited with mixed carbonate-siliciclastic sediments due to rapid sea level rise (Liu, 2006).

In this study, the Chenjiahe Section, located in northern Yichang, Hubei Province, Central China, is selected to document the temporal changes in relative abundance of bioclasts in the Early Ordovician. The studied section is 3 km north of the Huanghuachang Section (the GSSP for the base of the Middle Ordovician). The studied stratigraphical interval at Chenjiahe Section comprises the uppermost Nantsinkuan (13 m thick), Fenghsiang (43 m thick), Hunghuayuan (20 m thick), and lowermost Dawan (3 m thick) formations (Fig. 1), and is assigned to the late early Tremadocian and early Floian, based chiefly on conodonts (An, 1987). Shellbeds and other fossiliferous carbonates are well developed at the section.

**TEMPORAL VARIATIONS IN LITHOFACIES AND SHELLBEDS**

The uppermost Nantsinkuan Formation of the upper lower Tremadocian consists of thin- to medium-bedded oolitic grainstone, and subordinate skeletal packstone/grainstone (Fig. 1), which were primarily deposited in a shallow subtidal setting. The lower Fenghsiang Formation of the upper Tremadocian is characterized by the dominance of medium-bedded

**Figure 1. Temporal changes in lithofacies, relative sea level, diagnostic carbonate components, and**
shelbed intervals of the Lower Ordovician at Chenjiahe Section of northern Yichang, Hubei Province, Central China.

skeletal packstone/grainstone and upward-increasing yellowish gray shales, deposited in deep to shallow subtidal settings. The skeletal packstone interbedded with shales represents storm-generated event beds, as indicated by lenticular bedding, scoured basal contacts, and commonly graded bedding. Bryozoan-sponge reefs are well developed in the middle interval. The upper Fengsiang Formation of the upper Tremadocian is dominated by medium-bedded peloidal packstone/grainstone and subordinate skeletal packstone, as well as yellowish gray shales, deposited mostly in a deep subtidal setting. Small, low-relief Calathium-sponge-microbial reefs occur sporadically in the middle succession (Fig. 1). The Honghuayuan Formation of the uppermost Tremadocian to lower Floian is characterized by medium-bedded skeletal packstone/grainstone with subordinate Calathium-sponge-microbial and bryozoan-sponge reefs, bioturbated lime mudstone, as well as flat-pebble conglomerate, deposited in shallow to deep subtidal settings. The overlying lowermost Dawan Formation of the lower Floian is dominated by thin-bedded skeletal grainstone with abundant glauconite deposited in deep subtidal to basinal settings.

As noted above, the Lower Ordovician succession at Chenjiahe Section is characterized by diversified bioclasts, including dominant trilobites, echinoderms, articulate brachiopods, and subordinate bryozoans, lithistid sponge, receptacle lid Calathium etc.. The proportion of the selected bioclasts (trilobite, echinoderm, brachiopod, and bryozoan) as well as ooids is semi-quantitatively estimated from more than 50 thin sections from the studied strata, and is calibrated by point-counting analyses. The relative abundances of the selected bioclastics and ooids in the studied interval are represented with the width of bars (Fig. 1).

Clearly, the diagnostic bioclasts and ooids in the Lower Ordovician show a distinctive trend. The deposition of oolitic limestone was limited to the Nantsinkuan Formation with a sporadic exception in the overlying succession. Trilobites are the dominant bio-

clasts, especially in the uppermost Nantsinkuan and lower Fengsiang formations, and their relative abundance declines gradually in the younger strata, though in some cases trilobites can become the dominant bioclasts in shellbeds. Echinoderms show an inconspicuous decrease in relative abundance throughout the studied interval. Contrastively, articulate brachiopods keep the lower relative abundance in the uppermost Nantsinkuan and lower Fengsiang formations, but become the dominant components in the fossiliferous deposits in the overlying strata. Bryozoans in the lower Fengsiang Formation at Chenjiahe Section are the oldest fossil record of this phylum. The relative abundance of bryozoans in the section is commonly minor with the exception in the bryozoan-sponge reefs in the lower Fengsiang and Honghuayuan formations.

According to the temporal variations in relative abundances of diagnostic components, the Lower Ordovician of Chenjiahe can be divided into three shellbed intervals (Fig. 1). Interval 1, equivalent to the uppermost Nantsinkuan Formation, is predominated by oolitic grainstone. Shellbeds of this interval are commonly trilobite- and echinoderm-dominated. Brachiopods are minor in composition of shellbeds. Interval 2 has bioclastic proportion similar to Interval 1, with almost the disappearance of ooids, and first appearance of bryozoan, the later relatively rich at bryozoan-sponge reef sites. Interval 3 is characterized by the first appearance of brachiopod-dominated paleocommunities, and slight increase in bryozoan abundance. Echinoderms and trilobites diminish their relative abundance in this interval comparing with those in Interval 2. To sum up, the changes in the relative abundance of bioclasts in the Lower Ordovician at Chenjiahe Section show a gradual but distinct replacement of the trilobite-dominated shellbeds by the brachiopod-dominated ones in the upper Tremadocian (Interval 3).

DISCUSSION AND CONCLUSIONS

The temporal variations in the Phanerozoic shellbeds are caused by depositional, taphonomic, and/or evolutionary changes in bioclast producers (Kidwell and Brenchley, 1994). Our analysis was restricted to the taxonomic compositions of bioclasts in the Lower Ordovician fossiliferous carbonates, deposi-
ited in comparatively shallow-marine (shallow to deep subtidal) environments, the long-term, temporal trends in the Lower Ordovician shellbeds of South China should be the results of the evolutionary changes in bioclast producers rather than local depositional or taphonomic factors.

Until now, only a few published references have documented the temporal trends of the abundance of Early–Middle Ordovician taxa in shellbeds or other bioclastic carbonates in several paleoaplates. In South China, Liu (2006) reported a replacement of trilobite-dominated shellbeds by echinoderm-brachiopod-dominated shellbeds in the earliest Floian in the western inner shore area of the Yangtze platform (at Honghuayuan Section of Guizhou Province). The similar faunal turnover in the Early and Middle Ordovician has been documented from Laurentia and Gondwana paleoaplates. In the Great Basin of western North America, several classical quantitative analyses declared that an abrupt biotic transition from trilobite-dominated shellbeds to brachiopod-dominated ones happened in the Dapingian (early Middle Ordovician) (Finnegan and Droser, 2008; Li and Droser, 1999). However, such a transition had already occurred in the late Floian in Argentine Precordillera and Central Andean basin of Argentina (Waisfeld et al., 1999). Thus, the replacement of the Cambrian-type shellbeds by Paleozoic-type shellbeds occurred pervasively in Early and early Middle Ordovician, but its onset was diachronous across different paleoaplates.

In general, a dramatic increase in diversity of skeletonized marine invertebrates during the GOBE was regarded to have been accompanied by a substantial increase in their standing biomass (Finnegan and Droser, 2008). The bulk diversity of trilobite genera in South China had a sharp decline in Early Ordovician and reached its minimum across the Tremadocian–Floian boundary (Zhou et al., 2007), which seems to have been concomitant with the decrease of relative abundance of trilobite fragments (Fig. 1). In contrast, the increase in abundance of the brachiopods from the late Tremadocian was much earlier than the onset of the brachiopod biodiversification in mid Floian (Zhan and Harper, 2006). Thus, the changes in relative abundance of brachiopods in shellbeds might have been substantially decoupled from trends in biodiversifica-
tion of South China. Similar disconnection between diversity and abundance of brachiopods has also been documented from the Middle Ordovician of Laurentia (Li and Droser, 1999).

While dramatically increasing the complexity of community structure in the marine realm, the GOBE had impacted largely on the Ordovician earth, resulting in coevolution between organic and inorganic processes. Very recent studies conducted on the South China and North China paleoaplates show that the sedimentary systems had changed substantially due to the Ordovician radiation (Liu, 2009; Liu and Zhan, 2009). Prior to the rapid biodiversification of the Paleozoic EF, transition-type sedimentary systems were developed in late Tremadocian to the earliest Floian, exhibiting a decrease in subtidal microbialite and flat-pebble conglomerate, and an increase in the extent of bioturbation as compared with pre-GOBE sedimentary systems. The present study clearly shows that the replacement of the Cambrian-type shellbeds by Paleozoic-type shellbeds occurred while the transition-type sedimentary systems were developed, all prior to the rapid diversification of the Paleozoic EF. The increase in abundance of brachiopod shells could have modified the substrate and other palaeoecological factors, and made a marked increase in the number of megaguilds; while the development of the transition sedimentary systems must have been related to the increase of infaunal tiering, the expansion of infaunal ecospace, and the appearance of new burrowers in relation to the increasing abundance of the Paleozoic EF (Liu and Zhan, 2009). Therefore, the advanced increasing abundance of the Paleozoic EF in Tremadocian should have been an important geobiological control on the regional and even global taxonomic diversity in Early Ordovician.

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