Gondwana Research 25 (2014) 966–974

Contents lists available at ScienceDirect

Gondwana Research

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

Sedentary habits of anthozoa-like animals in the Chengjiang Lagerstätte: Adaptive strategies for Phanerozoic-style soft substrates

Qian-Ping Lei [a,b,*], Jian Han [c], Qiang Ou [d], Xiao-Qiao Wan [d]

[a] State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, 210008, China
[b] Graduate University of Chinese Academy of Sciences, Beijing, 100049, China
[c] Early Life Institute and State Key Laboratory for Continental Dynamics, Northwest University, Xi'an, 710069, China
[d] Early Life Evolution Laboratory, School of Earth Sciences and Resource, China University of Geosciences, Beijing, 100083, China

ARTICLE INFO

Article history:
Received 30 August 2012
Received in revised form 12 January 2013
Accepted 19 January 2013
Available online 18 February 2013

Keywords:
Sedentary habit
Anthozoa-like animals
Soft substrate
Chengjiang Lagerstätte
Cambrian

ABSTRACT

Substrates have perpetually played a crucial role in shaping the morphology of animal bodies, particularly the sedentary apparatus of benthic suspension feeders. In-situ preservation of sedentary forms from Cambrian Lagerstätten, especially the Lower Cambrian Chengjiang Lagerstätte, Yunnan Province, southwestern China, provides a unique opportunity for studying ancient interactions between the benthos and their substrates. The sedentary apparatuses of anthozoa-like animals *Xianguangia sinica* Chen & Erdtmann, 1991, *Archotuba conoidalis* Hou et al., 1999 and *Archisaccophyllia kunmingensis* Hou et al., 2005 from the Chengjiang Lagerstätte are investigated in their sedimentary context. *X. sinica* bears a cylindrical, rigid column and a basal, rounded, cuticularized attachment disc that partially attached into the soft muddy substrate; *A. kunmingensis* has a prominent, flexible pedal-shaped disc that attached directly to the substrate by expanding its disc surface area; whereas *A. conoidalis* has a unique, posterior-tapering tube and probably might have secreted mucus to firmly attach to the 'sclerotized' substrates. These three sedentary taxa employed different adaptive strategies, i.e., the 'iceberg', the 'snowshoe' and one newly defined but later widespread in Phanerozoic period, the 'anchoring-nail', to cope with the soft substrates. Furthermore, the anchoring-nail mode, sclerite-sticking behavior represented by *Archotuba* is a Phanerozoic innovative strategy in response to the appearance of pelagic larvae and small shelly fossils, especially to the first widespread biomineralization event at the beginning of the Cambrian, whereas the other two modes have already developed for about 90 Ma from the Ediacaran.

1. Introduction

During the Ediacaran to Cambrian period, a tectonic backdrop for many biological, climatological, tectonic and geochemical changes leading to the Cambrian radiation was probably provided by the rifting of a possible supercontinent and the formation of a second, slightly smaller supercontinent (Meert and Lieberman, 2004, 2008). Evidences for this radiation event in the biosphere includes the well-known Ediacaran biota, the small shelly fossil assemblages and the Chengjiang Lagerstätte, etc. (Dzik, 1994; McCall, 2006; Shu, 2008). Furthermore, the study on the sessile habits can provide significant information on the origin and early evolution of the sessile metazoans, and on their primitive lifestyles.

Seilacher and Pflüger (1994) and Seilacher (1999) proposed four lifestyles in the Neoproterozoic benthic metazoans centered on seafloor-encrusting microbial mats: mat encrusters, mat scratchers, mat stickers and undermat miners. Some of the aforementioned strategies are also employed in metazoans during the Cambrian period (Dornbos et al., 2004, 2005; Carrera and Botting, 2008). As the depth and intensity of bioturbation increased through the Proterozoic–Phanerozoic transition, the substrates on which marine benthos lived started to change from typical Proterozoic-style soft substrates (poor bioturbation, prevailing seafloor microbial mat) to more typical Phanerozoic-style soft substrates (significant horizontal and vertical bioturbations, absence of well-developed seafloor microbial mats) (e.g., Droser, 1987; Droser and Bottjer, 1988; Seilacher and Pflüger, 1994; Droser et al., 1999, 2002; Seilacher, 1999). Thus, the Early Cambrian is an important period that contains both Proterozoic-style substrates with matgrounds and a sharply defined sediment–water interface to more Phanerozoic-style soft substrates with a well-developed mixed layer and a diffuse sediment–water interface (Zhu et al., 2001; Hu, 2005; Zhao et al., 2012).

The Chengjiang Lagerstätte in southwestern China, generally correlated to Stage 3, Series 2 of the Cambrian (Babcock et al., 2001; Ou et al., 2009), has been celebrated for yielding abundant fossils of soft-bodied organisms (e.g., Chen and Zhou, 1997; Shu et al., 2003; Chen, 2004; Hou et al., 2004), which offer unique insights into the evolutionary acquisition of morphological novelties in marine communities.

* Corresponding author at: State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, 210008, China. Tel.: +86 25 85282580; fax: +86 25 83357026.
E-mail addresses: cicelyapple@126.com (Q.-P. Lei), elihanj@nwu.edu.cn (J. Han).

1342-937X/$ – see front matter © 2013 International Association for Gondwana Research. Published by Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.gr.2013.01.007

Specifically, in-situ preservation of sedentary forms from the Chengjiang Lagerstätte provides a unique opportunity for studying ancient interactions between the benthos and their muddy siliciclastic substrates. This study deals mainly with the morphological characteristics, especially those of the attachment apparatus of anthozoa-like animals from the Chengjiang Lagerstätte, including *Xianguangia sinica* Chen & Erdtmann, 1991, *Archisaccophyllia kunmingensis* Hou et al., 2005 and *Archotuba conoidalis* Hou et al., 1999. We aim to provide behavioral interpretations and discuss the possible evolutionary implications of these apparatuses.

2. Materials

The specimens examined in this work were collected from mudstone of the lithofacies 3 (Zhu et al., 2001) of the Yu'anshan Formation (*Eoredlichia–Wutingaspis* Zone), which contains abundant soft-bodied fossils, of Stage 3, Series 2 (Fig. 1), and is widely exposed in eastern Yunnan (Luo et al., 1999). The mudstones are fine-grained enough to preserve the fossils with remarkable fidelity in great detail. All materials were collected from the Erjie section, Jinning County and Jianshan section, Haikou Town (Fig. 1; see also Zhang et al., 2009, fig 1). Specimens ELI-0024JS and JSWM0117 are deposited in the Early Life Institute, Northwest University, Xi'an, China (ELI), and others in the Early Life Evolution Laboratory, China University of Geosciences, Beijing, China (ELEL).

3. Substrates of the Chengjiang Lagerstätte

The Yu'anshan Formation ranges from 130 to 150 m thick (Zhu et al., 2001) in Chengjiang area and is composed of yellowish-green mudstones intercalated with siltstones, finally topped by thick sandstones. Based on lithologic and sedimentological evidences, Zhu et al. (2001) proposed four lithofacies in the Yu'anshan Formation. The soft-bodied Chengjiang fossils are mainly hosted within the argillaceous or silty mudstone of lithofacies 3 which represents a proximal offshore to lower shoreface environment formed during the early stages of the regressive phase (Zhu et al., 2001).

The nature of the muddy substrates that the Chengjiang biota lived on has already been documented recently (e.g., Zhu et al., 2001; Dornbos et al., 2005; Hu, 2005). According to Zhu et al. (2001, pl. 5, figs 2, 5, 7), lithofacies 3 exhibits very little evidence of bioturbation, which becomes increasingly common in the upper part of this section. Dornbos et al. (2005) examined the core samples of the Yu'anshan Formation in Chengjiang and also found extremely low levels of bioturbation, and thus they concluded that the substrate there was basically soft but with enough firmness to account for the presence of microbial mats and restricted bioturbation. But the substrates supporting the Chengjiang biota in Diandong basin are quite uneven with bioturbated mudstones distributed in the area from Wuding to Chengjiang County (Hu, 2005; Zhao et al., 2012, fig 13). In the central Haikou–Chengjiang area, strongly bioturbated mudstones are found in the uppermost siltstone member (lithofacies 4), and they commonly occur throughout the entire Sapushan section in the Wuding area (Zhu et al., 2001; Hu, 2005, pl. 3, figs 1, 2), which also supports some evidence for the beginning of the mixed layer development in the rocks. The strong bioturbation in this area may be consistent with the ecological abundance of burrowing priapulids which could be found in all the sections of Chengjiang deposits (Fig. 2A–B, see also Nicholson, 2004; Zhang et al., 2006; Dornbos and Chen, 2008; Vannier et al., 2010). As one of the earliest infaunal colonizers of the substrate, priapulids are playing a leading role as the important subhorizontal bioturbators in the early stages of the "Cambrian Substrate Revolution" (Vannier et al., 2010).

So far, most previous work on the Cambrian substrate revolution has mainly focused on the evolutionary response of benthic sponges, echinoderms and early grazing molluscs to these substrate changes (Bottjer et al., 2000; Dornbos and Bottjer, 2000; Dornbos et al., 2004, 2005; Carrera and Botting, 2008). In the study by Dornbos et al. (2005), 88% of the benthic suspension feeders are well adapted

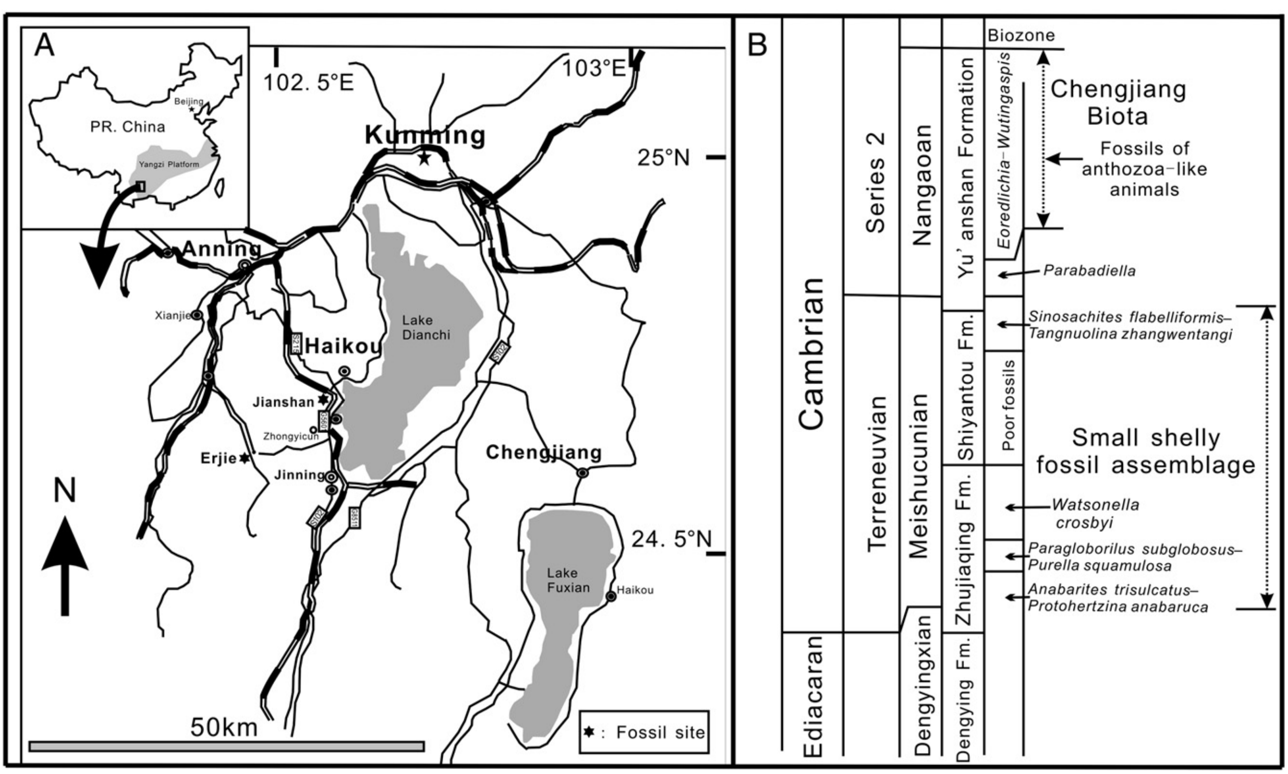

Fig. 1. (A): Map showing the localities where the anthozoa-like fossils were collected; (B): schematic stratigraphical section of the mud-rich deposits yielding the Chengjiang biota including anthozoa-like fossils in the Erjie section at Jinning, Kunming, China.
According to Zhang et al. (2001), Steiner et al. (2007), and Zhang et al. (2009).