Earth-Science Reviews 151 (2015) 266–287

Contents lists available at ScienceDirect

Earth-Science Reviews

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

Invited review

Survival on a soft seafloor: life strategies of brachiopods from the Cambrian Burgess Shale

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ARTICLE INFO

Article history:
Received 15 June 2015
Received in revised form 30 October 2015
Accepted 30 October 2015
Available online 31 October 2015

Keywords:
Palaeoecology
Tiering
Lagerstätte
Benthic
Filter feeders
Cambrian Explosion

ABSTRACT

Understanding the structure of benthic communities in the Cambrian remains a major challenge. Direct evidence for species interrelationships is rare and therefore past ecological interactions typically cannot be reconstructed with great accuracy. Here we reveal the community patterns and modes of life of brachiopods – one of the most important filter-feeding groups of Cambrian ecosystems – from the Cambrian Burgess Shale Lagerstätte. Burgess Shale brachiopods attached to a range of hard substrates, including skeletal debris, conspecific brachiopods and enigmatic tubes, with an overwhelming preference for attachment on the demosponge *Pirania muricata*. The dominance of *P. muricata* as a substrate choice – even in bedding assemblages where *P. muricata* individuals are rare – and similarities to the gregarious attachment strategies of extant brachiopod species suggests that brachiopods larvae in the Burgess Shale community selected their attachment substrates. The distribution of brachiopod taxa is also intricately linked with the presence of suitable hard substrates, with species declining in bedding assemblages where their preferred hard substrates are absent. In addition, brachiopods in the Burgess Shale community are predominantly low epifaunal tierers and do not exploit niches high in the water column, despite the presence of suitable attachment sites. Our analysis of tiering height versus host height indicates that there is no selection by brachiopod larvae in regard to the height of attachment and individuals attached at the first point of contact with the selected substrate. Through comparisons with the 'early' Cambrian Chengjiang Biota, we confirm that by the 'middle' Cambrian (Series 3, Stage 5) brachiopods had already developed a range of attachment strategies similar to some modern brachiopod populations. Our results provide significant insight into the ecological constraints and adaptability of brachiopods in the earliest animal communities of the Cambrian.

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http://dx.doi.org/10.1016/j.earscirev.2015.10.015
0012-8252/

1. Introduction

Amidst the great radiation of animal life during the Cambrian, brachiopods were one of the first animal phyla to emerge, establishing themselves as one of the most important filter-feeding groups in Cambrian ecosystems (Pelman, 1977; Holmer et al., 1996; Ushatinskaya, 2008; Topper et al., 2013a; Skovsted et al., 2015).

These bivalved lophophorates rapidly diversified and dispersed to all major palaeocontinental blocks by the third stage (ca. 520 Ma) of the Cambrian (Holmer et al., 1996; Brock et al., 2000; Ushatinskaya, 2008). As a result of their biomineralized valves, brachiopods are endowed with one of the most extensive and complete fossil records of any animal phylum (Sepkoski, 1981; Behrensmeyer et al., 2005), however, the rarity of preserved soft-tissues has impeded synecological studies and hindered key discussions regarding their early evolution. Knowledge of the group is heavily skewed towards their taxonomy and systematic relationships, based mainly on biomineralized characters, and substantial gaps exist in our knowledge of their ecology and interactions with other organisms.

Our understanding of the evolution and ecology of animals during the crucial Cambrian interval is largely driven by the examination of exquisitely preserved, soft-bodied organisms from a number of Burgess Shale-type deposits. The 'early' Cambrian Chengjiang Lagerstätte has provided much of our knowledge regarding the early ecology and adaptive morphologies of the Brachiopoda (e.g., Zhang et al., 2003; 2004; 2005; 2007a, b, c; 2008; 2009: Zhang and Holmer, 2013). Brachiopods from the 'middle' Cambrian Burgess Shale Lagerstätte have received little attention, with some exceptions (Holmer and Caron, 2006; Pettersson Stolk et al., 2010), since the original descriptions in the early 20th century (Walcott, 1912; Walcott, 1924). The exceptional preservation and minimal transportation of the Burgess Shale community (Caron and Jackson, 2006) provide a superb opportunity to investigate the ecological interactions between brachiopods and their chosen substrates. Reports of direct ecological interactions between brachiopods, sponges, and the stem-mollusk *Wiwaxia* were first noted nearly three decades ago (Whittington, 1985; Conway Morris, 1985; Rigby, 1986) and only recently have such associations been given detailed consideration (Topper et al., 2014; Topper et al., 2015).

A change of ecological strategies in Cambrian echinoderms (Dornbos 2006; Zamora and Smith, 2010) and grazing mollusks (Bottjer et al., 2000; Dornbos et al., 2005, Caron et al., 2006; Smith, 2012) has been linked to the modification of substrate during the Cambrian, as increased endobenthic activity mixed and churned the Cambrian seafloor (Droser and Bottjer, 1989; Seilacher and Pflüger, 1994; Seilacher, 1999 Bottjer et al., 2000; Dornbos et al., 2005; Dornbos, 2006; Álvaro et al., 2013; Kloss et al., 2015). The ecological response of Cambrian brachiopods to this change in substrate remains inadequately documented. Brachiopods have also been considered to contribute little to tiering complexity during the Phanerozoic (Bottjer and Ausich, 1986). Specimens attached to biological substrates suggest that brachiopods exploited and developed more variable levels of tiering in benthic communities than previously thought. It remains unclear, however, if attachment to a particular biological substrate is random or selective. Specifically, do brachiopods selectively settle on particular taxa to use as substrates or on particular body parts of these taxa (e.g., extremities)?

Here we provide the first detailed palaeoecological study of a Cambrian Lagerstätte brachiopod assemblage. Our main goal is to analyze brachiopod community patterns and modes of life to increase our understanding of the structure and ecology of the Cambrian benthos. We focus specifically on the intimate relationship shared between brachiopods and their chosen substrates, given the importance of substrate as primary control on species distribution (Taylor and Wilson, 2003; Solan et al., 2004; Bromley and Heinberg, 2006), and investigate a relatively unexplored area, the evolution of tiering in Cambrian brachiopod communities.

2. Material and methods

2.1. Material

This study is based on 1422 brachiopod individuals representing seven brachiopod species from the 'middle' Cambrian (Series 3, Stage 5) Burgess Shale in British Columbia, Canada (Figs. 1–8). The studied material is housed at the Royal Ontario Museum (ROM), the National Museum of Natural History of the Smithsonian Institution (USNM), and a small selection (all from the Phyllopod Bed) at the Geological Survey of Canada in Ottawa (GSC). Specimens predominantly come from the "thick" and "thin" expressions of the Stephen Formation (for the latter see Caron and Jackson, 2008) that crop out on Fossil Ridge and Mount Stephen in Yoho National Park (Fletcher and Collins, 1998). We focus on specimens from two stratigraphic intervals of the "thick" Stephen Formation, the Walcott Quarry Shale Member (WQ and BW prefixes, BW referring to the distance below the base of the Phyllopod Bed) and the slightly younger Raymond Quarry (RQ sample prefix) Shale Member (Fletcher and Collins, 1998). The majority of specimens were collected in situ within particular bedding assemblages or narrow stratigraphic intervals representing different burial deposits, but a number of specimens were also collected from talus picking above (RT) and below (WT) the Walcott Quarry. In addition to the previous material, which was collected by the Royal Ontario Museum (ROM), original specimens from the so-called 'Phyllopod Bed' (locality 35k) were also examined (see Whittington, 1971; Caron and Jackson, 2006, 2008) and are part of the Walcott collection at the Smithsonian Institution (SI). In contrast with the ROM collections, the SI specimens represent assemblages of unknown duration, as precise stratigraphic provenance is unknown (Caron and Jackson, 2006, 2008). Additional material collected by the ROM from the Mount Stephen Trilobite Beds (ST), Odaray Mountain (O, ODE, OR, ORU), Stanley Glacier, the so-called Tulip Beds (S7), and also from the Emerald Lake Oncolite Member were also examined (see Rigby and Collins, 2004 and O'Brien and Caron, 2012 for details on localities).