Earth-Science Reviews 181 (2018) 98–121

Contents lists available at ScienceDirect

Earth-Science Reviews

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

Marine oxygenation, lithistid sponges, and the early history of Paleozoic skeletal reefs

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ARTICLE INFO

Keywords:
Cambrian
Reef gap
Dysoxia
Hypoxia
Lithistid sponge-microbial reef

ABSTRACT

Microbial carbonates were major components of early Paleozoic reefs until coral-stromatoporoid-bryozoan reefs appeared in the mid-Ordovician. Microbial reefs were augmented by archaeocyath sponges for ~15 Myr in the early Cambrian, by lithistid sponges for the remaining ~25 Myr of the Cambrian, and then by lithistid, calathiid and pulchrilaminid sponges for the first ~25 Myr of the Ordovician. The factors responsible for mid–late Cambrian microbial-lithistid sponge reef dominance remain unclear. Although oxygen increase appears to have significantly contributed to the early Cambrian 'Explosion' of marine animal life, it was followed by a prolonged period dominated by 'greenhouse' conditions, as sea-level rose and CO_2 increased. The mid–late Cambrian was unusually warm, and these elevated temperatures can be expected to have lowered oxygen solubility, and to have promoted widespread thermal stratification resulting in marine dysoxia and hypoxia. Greenhouse conditions would also have stimulated carbonate platform development, locally further limiting shallow-water circulation. Low marine oxygenation has been linked to episodic extinctions of phytoplankton, trilobites and other metazoans during the mid–late Cambrian. We propose that this tendency to dysoxia-hypoxia in shallow marine environments also limited many metazoan reef-builders. In contrast, during the mid–late Cambrian, the ability of lithistid sponges to withstand low oxygen levels allowed them to create a benthic association with microbial carbonates that dominated global reefs. These conditions ameliorated during the Ordovician, as temperature decline promoted ocean ventilation. The prolonged time gap occupied by low diversity reefs between the 'Cambrian Explosion' and the 'Great Ordovician Biodiversification Event' reflects elevated temperatures and reduced marine oxygenation that limited metazoan diversification in shallow marine environments.

1. Introduction

The early Paleozoic radiation of marine animals, commonly referred to as the 'Cambrian Explosion' (Cloud, 1948; Bowring et al., 1993; Conway Morris, 2006), stalled in the mid-Cambrian and did not regain impetus until the mid-Ordovician (Sepkoski Jr., 1981; Webby, 2002; Bambach et al., 2004) during the 'Great Ordovician Biodiversitification Event' (Webby et al., 2004). Reef development shows a similar pattern, leading to the observation that mid–late Cambrian reef communities were dominantly microbial (Fagerstrom, 1987; Zhuravlev, 1996; Rowland and Shapiro, 2002). As a result, the prolonged interval between late early Cambrian extinction of archaeocyath sponges and the Early Ordovician rise of lithistid sponge-microbial-calathiid reef communities came to be regarded as a "reef gap" (Sheehan, 1985; Zhuravlev, 1996; Rowland and Shapiro, 2002; Kiessling, 2009). Challenges to this view first emerged in the report of early Furongian (late Cambrian) lithistid sponge-microbial (LSM) reefs in Iran (Hamdi et al., 1995). Additional examples of mid–late Cambrian LSM reefs have since been recognized throughout Laurentia and Gondwana (Mrozek et al., 2003; Shapiro and Rigby, 2004; Johns et al., 2007; Kruse and Zhuravlev, 2008; Hong et al., 2012, 2016; Kruse and Reitner, 2014; Adachi et al., 2015; Lee et al., 2016a). It is now clear that LSM reef communities were globally distributed for ~25 Myr during the mid–late Cambrian. This community was augmented in the Early Ordovician by a variety of skeletal organisms, such as *Calathium*, *Pulchrilamina*, *Amsassia*, bryozoans, stromatoporoids, and *Lichenaria*, but reef diversification remained relatively slow until bryozoans, corals and stromatoporoids became common in the mid-Ordovician, ~460 Ma (Fagerstrom, 1987; Webby, 2002; Servais et al., 2009). Numerical ages used here accord with those of the International Chronostratigraphic Chart (Cohen et al., 2013). Recognition of mid–late Cambrian LSM reefs closes the "reef gap" (Lee et al., 2016a and references therein) but also raises questions. What factors contributed to lithistid success following archaeocyath decline, why did LSM reefs dominate the remainder of the

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https://doi.org/10.1016/j.earscirev.2018.04.003
Received 13 January 2018; Received in revised form 6 April 2018; Accepted 6 April 2018
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Cambrian, and why did it take so long for the bryozoan-coral-stromatoporoid community to emerge in the Ordovician? Explanations for these aspects of reef developments could shed light on broader patterns of change that continue to be debated, particularly the seemingly slow overall pace of mid–late Cambrian animal diversification (Sepkoski Jr., 1981; Pruss et al., 2010; Knoll and Fischer, 2011; McKenzie et al., 2014; Saltzman et al., 2015).

Here we explore the possibility that prolonged low levels of marine oxygenation significantly influenced the relative success and development of reef communities during the mid–late Cambrian and Early Ordovician (Webby, 2002; Saltzman et al., 2015; Lee and Riding, 2016). High mid–late Cambrian sea-level and elevated atmospheric CO_2 promoted 'greenhouse' conditions with elevated temperatures (Berner, 1990, 2009; McKenzie et al., 2014). Higher temperatures decrease oxygen solubility in seawater, increase thermal stratification of the ocean, and favor marine productivity, while simultaneously stimulating carbonate platform development that restricts shallow-water circulation. Collectively, these factors tend to induce episodic marine dysoxia-hypoxia (Saltzman, 2005; Gill et al., 2011) that has been linked to repeated extinctions of phytoplankton, trilobites and other metazoans during the mid–late Cambrian (e.g., Bambach et al., 2004).

We propose that lithistid sponges, along with microbes, were predisposed to tolerate low oxygen levels, and that this was a central factor in their development and persistence during the mid–late Cambrian. These conditions began to change in the Early Ordovician as temperature decline (Trotter et al., 2008) promoted ocean ventilation (Thompson et al., 2012; Kah et al., 2016; Young et al., 2016). In the mid-Ordovician the bryozoan-coral-stromatoporoid community established itself as the next major phase of Paleozoic reef development (Pitcher, 1964; Fagerstrom, 1987). From this perspective, the relationship between reef community evolution and dysoxia-hypoxia is a key to understanding not only the Cambrian "reef gap", but also the relatively slow progress of animal radiation in mid-Cambrian to mid-Ordovician shallow marine environments.

2. Cambrian–Ordovician marine diversity

Marine animal generic diversity shows a plateau in the late Cambrian (Furongian Epoch; Paibian and Jiangshanian ages) (~510–485 Ma) (Sepkoski Jr., 1979, 1981), before recovering near the Cambrian–Ordovician transition (Na and Kiessling, 2015). This interval of depressed diversity largely reflects archaeocyath extinctions, followed by trilobite extinctions and low levels of origination (Bambach et al., 2004). Mid–late Cambrian and Early Ordovician trilobite extinctions define "biomere" boundaries (Palmer, 1984; Taylor, 2006) that, as in the case of the late Cambrian Age 3 Sinsk Event (Zhuravlev and Wood, 1996), have been linked to influxes of anoxic and/or cold basinal waters onto shallow shelves (Stitt, 1975; Palmer, 1984; Westrop and Ludvigsen, 1987). This is consistent with survival of trilobites adapted to reduced oxygen availability at biomere boundaries (Palmer, 1984; Taylor, 2006; McKenzie et al., 2014; Saltzman et al., 2015). In addition, dysoxia-tolerant arthropod groups such as olenids (Fortey, 2000) and phosphatocopids (Williams et al., 2011) increased in diversity in the late Cambrian (Fig. 1).

Biomere and other Cambrian biotic turnovers/extinctions have in turn been linked to carbon isotope excursions (Taylor, 2006; Zhu et al., 2006; Peng et al., 2012; Saltzman et al., 2015). In addition to the ~510 Ma Sinsk Event, these include the early Paibian Marjumiid–Pterocephaliid biomere boundary and the early Jiangshanian Pterocephaliid–Ptychaspid biomere boundary, which approximately correspond with the lower and upper boundaries respectively of the Steptoean positive carbon isotope excursion (SPICE) event (Saltzman et al., 1995, 2000; Perfetta et al., 1999; Saltzman, 1999; Montañez et al., 2000; Lee et al., 2015a; Gerhardt and Gill, 2016) (for correlations see Taylor et al., 2012, fig. 1) (Fig. 1). We infer, along with others, that mid–late Cambrian extinctions occurred as poorly oxygenated basinal water encroached onto carbonate platforms, stressing shallow-water communities (Palmer, 1984; Berry et al., 1989; Taylor, 2006; Gill et al., 2011; Landing, 2012a, 2012b; Saltzman et al., 2015). Similar effects have been invoked to account for extinction of carbonate platform communities in Jurassic–Cretaceous Oceanic Anoxic Events (Schlanger and Jenkyns, 1976; Jenkyns, 1991, 2010; Parente et al., 2008).

Marine diversity greatly increased during the Ordovician (Sepkoski Jr., 1981). The Great Ordovician Biodiversification Event (GOBE) (Webby et al., 2004) was a diachronous and extended event, initiated in the Furongian and accelerating in the Darriwilian, that continued until almost the end of the Ordovician (Sepkoski Jr., 1981; Webby et al., 2004; Harper, 2006; Servais et al., 2010, 2016). Significant increases in animal biodiversity at family, genus and species level resulted in the rise of the 'Paleozoic Evolutionary Fauna', dominated by suspension-feeding organisms such as brachiopods, rugose and tabulate corals, crinoids, bryozoans, and stromatoporoids (Sepkoski Jr., 1979; Bambach et al., 2002). This community developed throughout the Early Ordovician, and by the late Darriwilian had a radical affect on reef building (Pitcher, 1964; Fagerstrom, 1987; Webby, 2002; Webby et al., 2004). In addition, global increase in phytoplankton (acritarch) diversity, broadly paralleling that of animals, occurred in the Furongian and Early Ordovician (Servais et al., 2008, 2016; Nowak et al., 2015). These Ordovician upturns in diversity have been broadly related to increase in atmospheric O_2 (Servais et al., 2008, 2010, 2016; Saltzman et al., 2011; Edwards et al., 2017) and decline in global temperature (Trotter et al., 2008).

3. Late Ediacaran–mid-Ordovician eukaryote reef development

Microbial carbonates (stromatolites, thrombolites and associated calcimicrobes) generally dominated reefs from the Ediacaran to the Early Ordovician. The earliest skeletal reefs involved Ediacaran calcified sessile benthic eukaryotes (*Cloudina*, *Namacalathus*, *Namapoikia*) and early Cambrian "*Ladatheca*". Archaeocyaths, and locally radiocyaths and coralomorphs, are conspicuous in early Cambrian reefs. Archaeocyaths and coralomorphs continued – although much reduced – during the mid–late Cambrian, when lithistid sponges were the most prominent components of skeletal reefs. Large lithistids (*Archaeoscyphia*) appeared in the Early Ordovician, augmented by calathiids, pulchrilaminids, and the first undisputed tabulate corals, bryozoans and stromatoporoids. These latter appearances set the scene for the mid-Ordovician diversification of stromatoporoids, tabulates and bryozoans, that created reefs dominated by encrusting and massive skeletons at the end of the Darriwilian.

The affinities of many Ediacaran–Ordovician skeletons remain problematic. *Namapoikia* may be a chaetetid sponge or simple colonial cnidarian (Wood et al., 2002; Wood, 2017). Archaeocyaths and lithistids are sponges. Radiocyath skeletal structure resembles that of *Calathium*, which is sponge-like (Church, 1991; Rowland, 2001), and also that of cyclocrinitids (Beadle, 1988); but these groups have also been compared with green algae (e.g., Nitecki and Debrenne, 1979). Coralomorphs comprise a heterogeneous semi-formal group encompassing massive as well as cuplike skeletons; some of them are considered real corals (e.g., Scrutton, 1997; Hicks, 2006). Pulchrilaminids are stromatoporoid-like, but regarded as a separate group of hypercalcified sponges (Webby, 2015).

Based on their eukaryote skeletal components, we distinguish six reef intervals during this ~100 Myr period (~550–444 Ma), when reefs evolved from mainly microbial into mainly skeletal structures. Time scales are based on Peng et al. (2012), Cohen et al. (2013), and Ogg et al. (2016). These main reef intervals are: I, late Ediacaran (~550–541 Ma): microbial-*Cloudina*; II, Fortunian–mid-Age 2 (541–525 Ma): microbial-"*Ladatheca*"; III, mid-Age 2/late Age 4 (525–510 Ma): microbial-archaeocyath; IV, late Age 4/end Age 10 (510–485 Ma): microbial-lithistid; V, Tremadocian–middle Darriwilian (485–460 Ma): microbial-lithistid-calathiid-pulchrilaminid; VI, late Darriwilian–end-Ordovician (460 Ma–444 Ma): stromatoporoid-bryozoan-tabulate-receptaculitid-microbial.

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