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The role of abiotic factors in the Cambrian Substrate Revolution: A review from the benthic community replacements of West Gondwana

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A B S T R A C T

The Cambrian Substrate Revolution refers to a substantial and "rapid" change to the nature of marine sedimentary substrates in the early Cambrian and is widely interpreted as a biologically-driven event, a direct response to evolutionary innovations in metazoan burrowing and the development of new shelly faunas. However, abiotic factors such as tectonic and climatic evolution also had the potential to restructure Cambrian substrates, and are here shown to be more plausible drivers of change in the benthic faunas of western Gondwana. The western Mediterranean region underwent a southward drift during Cambrian times, which drove a switch from subtropical carbonates to temperate siliciclastic substrates with short-term episodes of temperate carbonate productivity. As a result, microbial and shelly carbonates disappeared diachronously in a stepwise manner across the lower–middle Cambrian boundary interval. Archaeocyathan-microbial reefs were replaced by chancelloriid-eocrinoid-(spiculate) sponge meadows, in which the stepwise immigration of new echinoderm taxa was primarily controlled by extensional tectonic events, first recorded in rifting settings and later in passive-margin platforms.

Availability of new kinds of substrate was thus the primary factor that controlled where and when evolutionary innovations in benthic strategies arose. Examples of this include the early Cambrian colonization of phosphatic hardgrounds and thrombolite crusts by chancelloriids, archaeocyathan and spiculate sponges, and the exploitation by benthos to the increasingly widespread availability of shelly grounds and carbonate firmgrounds by early-diagenetic cementation. A microbial mat/epifaunal antagonistic relationship is demonstrated for echinoderm pelmatozoans based on the non-overlapping palaeogeographic distributions of microbial reefs and mats versus mud-sticker pelmatozoans. Cambrian benthic communities thus evolved in parallel with substrates in response to abiotic factors rather than being the primary drivers of substrate change.

1. Introduction

The "Agronomic Revolution" (Seilacher and Pfluger, 1994) and "Cambrian Substrate Revolution" (Bottjer et al., 2000) are two linked events that refer to (i) the early Cambrian diversification of burrowing metazoans and (ii) a switch from microbial mat-dominated sediments to unconsolidated substrates. These two events are usually causally linked, with evolution of bioturbation seen as driving the nature of the Cambrian seafloor. Before them, microbial mats developed a barrier at the water/sediment interface, as a result of which the underlying sediment was almost completely anoxic and was inhabited by sulfate-reducing bacteria, whose emissions of H_2S made the substrate toxic to most other organisms (Bailey et al., 2006; Canfield and Farquhar, 2009). Then, bottom-dwelling metazoans fell into four palaeoecological categories: (i) mat encrusters that were permanently attached to microbial mats; (ii) mat scratchers that grazed the surface of the mats without destroying it; (iii) mat stickers or suspension feeders that were partially embedded in the mat; and (iv) undermat miners that burrowed underneath the mat and fed on decomposing mat material (Bottjer et al., 2000). Close to the Ediacaran–Cambrian boundary interval, new burrowing metazoans supposedly broke down the microbial mats and made the substrate habitable for a much wider range of organisms. The upper level of the seafloor became wetter and softer as it was constantly churned up by burrowers, allowing water and oxygen to penetrate a considerable distance below the surface and killing the oxygen intolerant micro-organisms in the lower layers. As a result, microbial mats became increasingly restricted to a limited range of environments and confined to settings where burrowing was non-existent or negligible (Hagardon and Bottjer, 1999).

Despite the well-documented worldwide decline in stromatolites, other microbial communities (in the form of thrombolites and biofilms)

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continued to play an important role in Cambrian marine environments, such as sponge–thromboid reef complexes in subtropical settings (Pratt, 1995) and the ubiquitous presence of biofilms responsible of microbially induced sedimentary structures (MISS; Hagardon and Bottjer, 1997; Dornbos et al., 2004). The occurrence and subsequent development of intense vertical bioturbation during the Cambrian created a critical transition in soft substrates, from Proterozoic-style firm unlithified substrates (with low water content, sharp sediment–water interface, and well-developed microbial mats) to Phanerozoic-style soft substrates (with a well-developed mixed layer, higher water content, and an easily resuspended, diffuse sediment–water interface; Droser et al., 1999; Hagardon and Bottjer, 1999; Seilacher, 1999; Droser et al., 2002; Seilacher et al., 2005; Henderson and Dann, 2010).

Previous work on the ecological impact of this substrate transition on benthic metazoans has focused primarily on sessile suspension-feeding echinoderms. Case studies from Laurentia and comparisons with Gondwana have revealed a strong evolutionary trend through the Cambrian toward attachment to firm and hard substrates and complex stem development (Guensburg and Sprinkle, 1992; Bottjer et al., 2000; Dornbos and Bottjer, 2000, 2001; Parsley and Prokop, 2004; Dornbos, 2006). However, palaeoenvironmental and climatic change also leads to modifications of the substrate and needs to be considered.

An excellent place to test the relative importance of biotic and abiotic factors in driving substrate and faunal change is the western Mediterranean region. There, the southward drift of West Gondwana in the Cambrian caused a diachronous switch from carbonate to siliciclastic substrates, as a result of which microbial carbonates disappeared in a stepwise manner across the lower–middle Cambrian transition, whereas clayey substrates were still commonly stabilized by biofilms that did not develop distinct carbonate stromatolites.

The aims of this work are: (i) to describe the sequence and timing of the main geodynamic and climatic events recorded in the passive-margin basins (Iberian Chains, Cantabrian Zone and Montagne Noire) and intracratonic rifts (Ossa-Morena and Morocco) of West Gondwana; (ii) to establish the sequence and timing of the main benthic communities in those same regions; and (iii) to identify correlations between geodynamic and climatic events and faunal change, especially where the environmental factors that controlled the distribution of microbial-dominated substrates (including the classical archaeoyathan-microbial reef complexes) and nonreefal meadows dominated by suspension-feeding metazoans (such as chancelloriids, echinoderms, and spiculate sponges) changed diachronously across the region. As palaeoecological relationships within early Cambrian archaeocyathan-microbial reefs and reef complexes of the western Mediterranean region has been widely described in previous contributions (see recent syntheses in Álvaro and Debrenne, 2010; Gandin and Debrenne, 2010), this paper concentrates on nonreefal benthic communities and their replacements.

2. Geodynamic evolution and basin development in West Gondwana

2.1. Palaeogeographic overview

In the Iberian Peninsula, the Variscan West Asturian–Leonese and Cantabrian Zones, and their southeastern prolongation into the Iberian Chains (Fig. 1A), have been traditionally interpreted as relics of a single early-Palaeozoic basin: the Cantabro–Iberian Basin. It was limited to the NE by the Cantabro–Ebroan Land Area, at present covered by the Cenozoic Ebro Valley. The mosaic of inner platforms that form the basin passed to the present-day SW to isolated platforms and uplifts surrounded by basinal substrates rich in kerogenous shales and phosphorites (Central-Iberian Zone). Following the Variscan Ibero-Armorican Arc, the northeastern extension of the Cantabro–Iberian Basin corresponds to the southern Montagne Noire, whereas the northern Montagne Noire represents its basinal counterpart (Álvaro et al., 2010).

Two distinct rifts are recognized to the SW of the aforementioned passive-margin style basins: Ossa-Morena and Moroccan Atlas (Fig. 2). Rifting propagated diachronously across the Ossa-Morena Zone from the Terreneuvian to the Late Ordovician, post-dating an episode of Neoproterozoic–Terreneuvian accretion of a continental arc (Cadomian Orogeny; Sánchez-García et al., 2003; Etxebarria et al., 2006). The Cambrian setting of Ossa-Morena attached to the Gondwanan margin (see an updated synthesis in Nance et al., 2008) shows some distinct peculiarities, such as: (i) its close early-Cambrian trilobite similarities with eastern Avalonia and Morocco that disappeared in the middle Cambrian; and (ii) a coeval occurrence of archaeocyathan-microbial reefs in Morocco, Ossa-Morena, and the Armorican Massif preceding their subsequent spread into the rest of the western Mediterranean region (Álvaro et al., 2003a).

The Moroccan Atlas represents another intracontinental rift, Ediacaran to Furongian in age, which started and ended diachronously, propagating from the southern Anti-Atlas to the northern Coastal Meseta (Gasquet et al., 2005). At present, the South Atlas fault (SAF in Fig. 1B) marks the boundary between the Ediacaran–early Palaeozoic platform (also named Souss Basin) and its basinal counterpart (Destombes et al., 1985; Álvaro et al., 2008). To the North of the SAF, the Moroccan rift was filled by a broad turbidite-dominated blanket deposited in SSW–NNE-trending basinal troughs (Bernardin et al., 1988).

2.2. Rifting settings: Atlas Mountains and Ossa-Morena (Fig. 3A)

In West Gondwana, carbonate sedimentation across the Neoproterozoic–Cambrian transition was constrained by the diachronic character of the Pan-African and Cadomian orogenies. The end of the Pan-African orogeny (ca. 690–605 Ma; Gasquet et al., 2005) was rapidly succeeded by the development of a carbonate belt that is exposed in the upper Ediacaran–lower Cambrian strata of the Atlas Mountains, Morocco. By contrast, carbonate productivity only spread throughout southwestern Europe after the end of the Cadomian orogeny (ca. 645–540 Ma; Samson and D'Lemos, 1999). The Botoman interval (sensu Spizharski et al., 1986) marks the peak for early Cambrian archaeocyathan-microbial reef development in this Gondwanan margin (Debrenne and Debrenne, 1995). The dimensions achieved by the reefs and reef complexes in the Armorican Massif and Montagne Noire (France), Ossa-Morena, Toledo Mountains and Cantabrian Mountains (Spain), Sardinia, and Germany were largely exceeded by the Great Atlasian Reef Complex (GARC; Álvaro and Debrenne, 2010), which spread over more than 400 km and reached maximum thickness in the Anti-Atlas. According to the syndepositional tectonic activity associated with its intracratonic Ediacaran–Furongian rift, the GARC can be subdivided into four major archaeocyathan-microbial reef episodes: (i) an Atdabanian SW–NE-trending, 400 km long, thromboid-archaeocyathan barrier reef that mainly extended across the western Anti-Atlas and contained patch-reefs surrounded by skeletal lime-sand or homogeneous shale, stacked patches becoming aggregated into bioherms and biostromes upward, and giant reef complexes, up to 60 m thick; (ii) an early Botoman development of archaeocyathan-thromboid mound complexes fringing grabens and half-grabens recorded in the western Anti-Atlas; (iii) nucleation of late Botoman dispersed archaeocyathan-microbial patch-reefs and bioherms during an interval of tectonic quiescence in the western Anti-Atlas; and (iv) an Atdabanian–Botoman interval of microbial and archaeocyathan-microbial patch-reefs and bioherms preferentially developed on the uplifted parts of tilted blocks in the southern High Atlas (Fig. 3A) (Álvaro and Debrenne, 2010).

The end of reef development in the Souss Basin is related to the progradation of siliciclastic depositional systems (Toyonian regression), considered to have caused the collapse of reef communities throughout West Gondwana. However, a last episode of stromatolite development