



The formation of microbial-metazoan bioherms and biostromes following the latest Permian mass extinction

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ABSTRACT

After the latest Permian mass extinction event, microbial mats filled the ecological niche previously occupied by metazoan reefs, resulting in widespread microbialites. This study focuses on the lipid biomarker (molecular fossil) and invertebrate fossil records from Neotethyan platform margin sections to understand microbial-metazoan bioherm formation. Here, we find that early Griesbachian thrombolitic and stromatolitic microbialites from Çürük Dag (Turkey) and Kuh e Surmeh (Iran) contain abundant lipid biomarkers, representing input from cyanobacteria, anoxygenic phototrophic bacteria, sulfate-reducing bacteria, and halophilic archaea. The biomarker inventory suggests that the microbialites were constructed by cyanobacteria-dominated microbial mats. Biomarkers of halophilic archaea are interpreted to reflect input from the water column, suggesting that the Neotethys experienced at least episodically hypersaline conditions. We also demonstrate that bacteria, possible keratose sponges (up to 50% of the carbonate is represented by the possible sponges), and microconchids lived synergistically to form microbial-metazoan bioherms in the immediate aftermath of the extinction along the western margin of the Neotethys. Abundant fossils of oxygen-dependent invertebrates (i.e. microconchids, bivalves, gastropods, brachiopods, and ostracods) and foraminifers were also found within these bioherms. The presence of invertebrates in conjunction with abundant molecular fossils of cyanobacteria indicates an oxygenated water column. Even though the presence of the biomarker isorenieratane in microbialites may be considered as evidence for euxinic conditions in the water column, its absence in the background sediments rather points to a source organism belonging to the mat community. The new finding of bioherms built in part by metazoans suggests that reef ecosystems underwent a major turnover across the extinction event, and shortens the 'metazoan reef gap' to just the uppermost Changhsingian. During the Early Triassic, therefore, reefal ecosystems were able to recover in oxygenated settings since the earliest Griesbachian, albeit in an impoverished state.

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1. Introduction

Lower Triassic rocks archive the aftermath of the latest Permian mass extinction, the most severe extinction of the Phanerozoic (e.g. McGhee et al., 2004; Stanley, 2016), and record the replacement of metazoan reefs with the widespread deposition of microbialites during

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the Early Triassic (e.g. Fagerstrom, 1987; Baud et al., 1997; Martindale et al., 2017). Several phases of microbialite formation occurred during the Early Triassic (Lehrmann, 1999; Pruss et al., 2006; Baud et al., 2007; Brayard et al., 2011; Kershaw et al., 2012), but the most widespread and abundant microbialites emerged in the immediate aftermath of the extinction, i.e. the Griesbachian (the first substage of the Triassic).

Based on petrographic studies, the microbialite-forming prokaryotes are thought to include cyanobacteria (Yang et al., 2011; Wu et al., 2014). Due to poor preservation and lack of morphologically distinct features, however, these taxonomic identifications are equivocal. To identify the benthic microbial community involved in the formation of microbialites, lipid biomarkers, i.e. molecular fossils, offer a more robust approach (Peckmann et al., 2004; Reitner et al., 2005; Orphan et al., 2008; Bühring et al., 2009; Heindel et al., 2015). Molecular fossils are a useful tool to reconstruct paleoecosystems, shedding light on the mode of primary production and food webs (e.g. Summons and Walter, 1990; Brocks et al., 2005; Peters et al., 2005). They have previously been used to characterize the environmental conditions associated with the latest Permian mass extinction in the Tethys, Panthalassa, and Boreal oceans (e.g. Grice et al., 2005; Hays et al., 2007; Cao et al., 2009; Nabbefeld et al., 2010; Chen et al., 2011), as well as the formation of post-extinction microbialites (e.g. Xie et al., 2005; Chen et al., 2011; Luo et al., 2013; Heindel et al., 2015). Studies of lipid biomarkers of Griesbachian microbialites are, however, restricted to sites from the Paleotethys in South China (e.g. Xie et al., 2005; Chen et al., 2011; Luo et al., 2013).

The formation mechanisms of Early Triassic microbialites are still under debate. These microbialites have been described as ‘disaster forms’ that either thrived following the partial relaxation of the ecological constraints that typically restricted them from unstressed, normal marine conditions (Schubert and Bottjer, 1992), or in harsh environments that were inhospitable to metazoans (Pruss et al., 2004). In these instances, microbialite formation was hypothesized to have been favored by the upwelling of carbonate-saturated, low-oxygen, and/or alkaline deep water that, moreover, may have suppressed grazing and bioturbation in the aftermath of the extinction (Pruss et al., 2004; Mata and Bottjer, 2011). Alternatively, sea-level changes, light penetration, and clastic input could have had a major controlling effect (Kershaw et al., 2012; Mata and Bottjer, 2012; Bagherpour et al., 2017). However, other studies have noted that the microbialite-forming microbial mats housed small (mostly just a few mm in size) metazoans, including ostracods, microconchids, bivalves, brachiopods, echinoids, crinoids, and gastropods that would have required well-oxygenated conditions (e.g. Payne et al., 2006; Yang et al., 2011, 2015; Forel et al., 2013a, 2013b; Tang et al., 2017; Foster et al., 2018). These observations led some authors to conclude that microbialite formation occurred in at least fluctuating oxic-anoxic conditions (Forel et al., 2013b; Tian et al., 2014). The metazoans are, however, rare (Yang et al., 2011), and Early Triassic microbialites have a low functional diversity (Foster and Twitchett, 2014; Foster et al., 2018). Even though metazoans have been recorded from microbialites, hitherto metazoans have not been attributed to reef building until the Olenekian (Pruss et al., 2007; Brayard et al., 2011; Marenco et al., 2012).

Our understanding of the formation mechanisms of post-extinction microbial-metazoan buildups is, therefore, incomplete. The main aim of this study is to analyze the lipid biomarker (molecular fossil) and invertebrate fossil records from Neotethyan platform margin sections in Turkey (Çürük Dag) and Iran (Kuh e Surmeh) that have hitherto not been studied. We aim to 1) identify the benthic microbial communities and to unravel the mechanisms of microbialite formation in the aftermath of the latest Permian mass extinction, 2) determine how prokaryotes and metazoans interacted in earliest reef-like ecosystems after a mass extinction, and 3) determine whether the occurrence of microbialites reflects a change in seawater chemistry (e.g. Riding and Liang, 2005), the extinction of grazing organisms and declining competition in stressed ecosystems favoring prokaryotes, or a combination of

these. To achieve these goals, lipid biomarker data were combined with petrographic and paleontological records.

2. Geological setting

The sedimentary successions recorded in Kuh e Surmeh and Çürük Dag developed on wide carbonate platforms, along the southwestern margin of the Neotethys (Fig. 1). Today, Kuh e Surmeh is in the Zagros Mountains, Iran (28°32′16.6″N; 052°29′47.6″E), whereas during the Permian-Triassic interval it was located at approximately 20°S on the Arabian Carbonate Platform margin (Fig. 1). Çürük Dag is located in the Taurus Mountains (36°41′32.4″N, 030°27′40.1″E), southwestern Turkey, and was close to the equator in the shallow interior part of Taurus Carbonate Platform (Fig. 1).

2.1. Stratigraphy of Kuh e Surmeh (Zagros, Iran)

In Kuh e Surmeh, the Upper Permian is recorded in the Dalan Formation and consists of interbedded oolitic packstones and grainstones, which grade into bioturbated mudstones or crinoidal wackestones, reflecting a transgression from a shallow to a deeper water setting (Insalaco et al., 2006). The base of the overlying Kangan Formation, which records the Permian-Triassic transition, is marked by two 0.3 m thick oolitic grainstone beds that have been inferred as Upper Changhsingian in age. These oolites are overlain by 0.7 m of platy mudstones marking the extinction by a cessation in bioturbation and strong decline in faunal diversity. The platy mudstones are overlain by 0.3 m of oolitic packstones to grainstones, which record the first appearance of *Hindeodus parvus*, marking the base of the Triassic. The thrombolitic microbialites studied here overlie the grainstones, situated 1.3 m to 4.0 m above the extinction level (Figs. 2–3). The thrombolites formed mounds up to 2.7 m in height, representing bioherms with a topographic relief above the seafloor (Fig. 3A) as revealed by onlap of detrital carbonate beds without microbial fabrics (Fig. 3C). Stromatolites were not recognized. The complete microbialite sequence is composed of five microbialite mound levels intercalated with five grainstone beds. The succession is, however, laterally variable. Around 20 m laterally

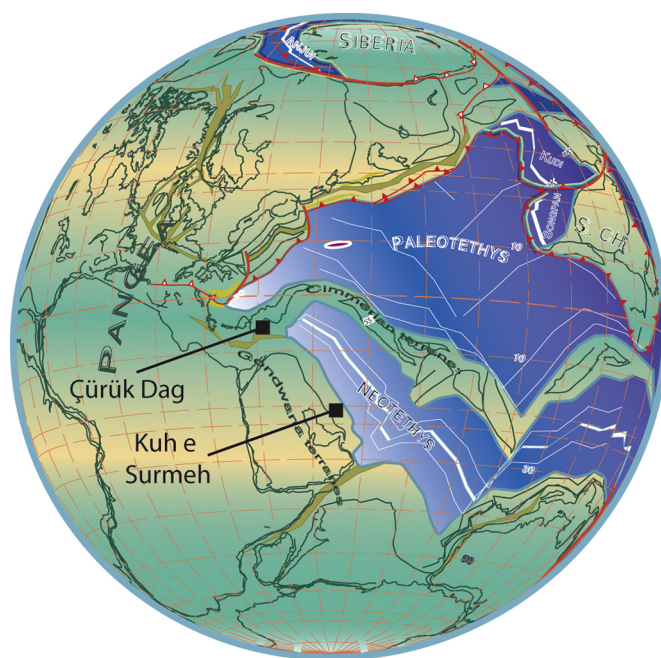


Fig. 1. Paleogeographic map of the Tethys realm during the Early Triassic showing the approximate positions of Çürük Dag (Taurus Mountains, Turkey) and Kuh e Surmeh (Zagros Mountains, Iran). Base map after Stampfli and Borel (2001).

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