



Andean sponges reveal long-term benthic ecosystem shifts following the end-Triassic mass extinction



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ABSTRACT

Thick cherts and cherty dolomites in the basal Jurassic Aramachay Formation of Peru preserve a thriving continental shelf community dominated by siliceous sponges that followed the end-Triassic collapse of metazoan-rich carbonate accumulation. Similar Hettangian and Sineumurian deposits from Nevada, U.S.A., Austria, and Morocco suggest that an Early Jurassic siliceous sponge takeover was a widespread phenomenon that persisted for ~2 m.y. until metazoan-driven carbonate sedimentation recovered. The post-extinction dominance of siliceous sponges likely resulted from the confluence of metazoan carbonate reef collapse (removal of incumbents) and geochemical conditions that fostered the success of the siliceous sponge-dominated ecosystem. Simple mass balance calculations suggest the siliceous sponge takeover was likely permitted by an increased silica flux as a consequence of weathering Central Atlantic Magmatic Province (CAMP) basalts. The CAMP basalts alone could supply all the silica needed to sustain the sponge takeover, although contributions were also likely from increased hot-climate weathering of other silicates and possible reductions in dissolved silica demand by radiolarians. Detailed sedimentological, fossil, and microfacies analyses were conducted at six field sites across a shallow shelf system recorded in the central Peruvian Andes (Yauli Dome), focusing on the metazoan contribution to sedimentation. Sedimentary structures at all six sites demonstrated on-shelf deposition, similar to the underlying upper Triassic Chambará Formation (in contrast to the black shale-rich facies of the Aramachay Formation in other areas of Peru). Examination of up to 147 m of cherty dolomite from the Aramachay Formation revealed a siliceous sponge-dominated ecosystem, including sponge body fossils, compressed in situ sponge materials, and abundant transported spiculite sediments. Siliceous sponges, mostly demosponges and rare hexactinellids, account for the chert lithology and apparently dominated the local ecology for approximately two million years. The role of metazoan biocalifiers in sediment production and ecological structure was profoundly reduced compared to the under- and overlying formations, representing a clear ecological state shift from pre-extinction carbonate to post-extinction siliceous dominated ecosystems before the carbonate system recovered ~2 m.y. after the extinction.

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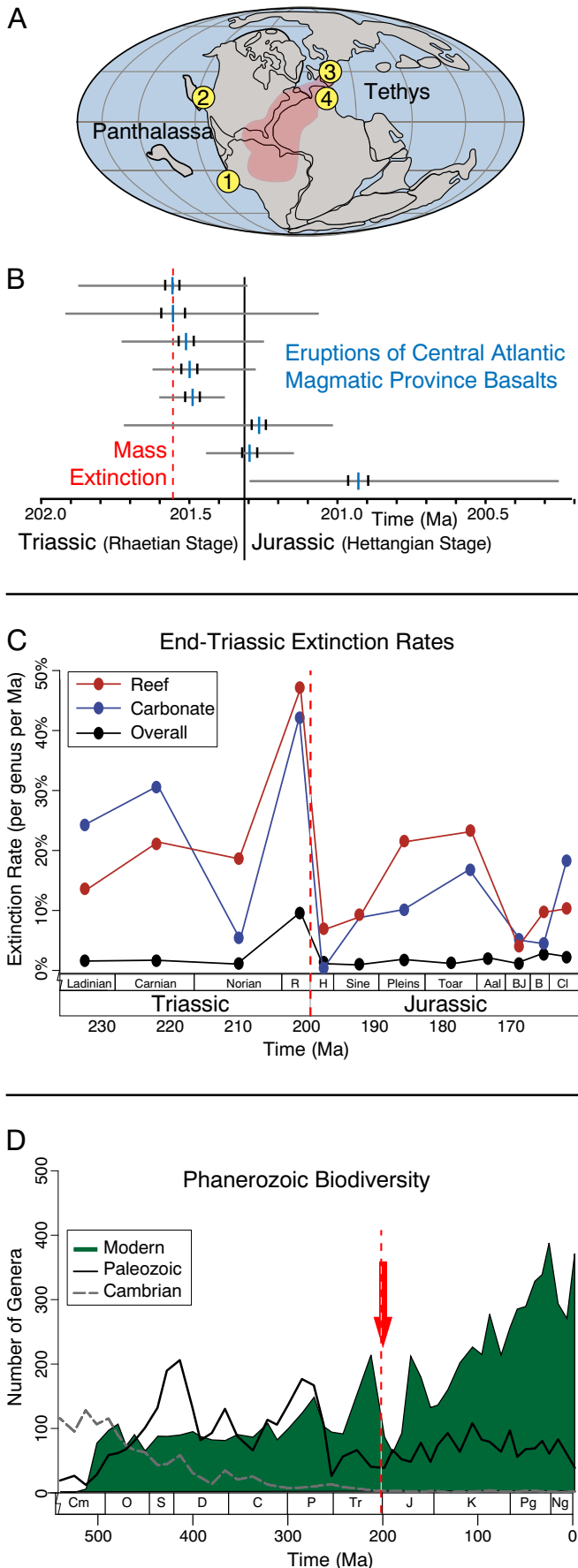
1. Introduction

Once considered among the smallest of the so-called big five mass extinctions (Rau and Sepkoski, 1982), recent analyses reveal that the end Triassic mass extinction may have resulted in the largest biodiversity drop of modern marine invertebrate faunas in Earth's history (Alroy, 2010; Alroy et al., 2008) and coincided with global environmental upheaval (Fig. 1). The Central Atlantic Magmatic Province (CAMP) has been considered a likely influence on the extinction since its recognition as the most widespread flood basalt of the Phanerozoic with an

approximate area of 1×10^6 km² (e.g., Wignall, 2001; Pálffy et al., 2002; McHone, 2003; Marzoli et al., 2004; Berner and Beerling, 2007; Nomade et al., 2007; Whiteside et al., 2010; Greene et al., 2012b; Pálffy and Zajzon, 2012; Jaraula et al., 2013; Dal Corso et al., 2014). Recent work shows that the major eruptions of basalts and volatiles were concentrated into three ~30 kyr intervals during a 600 kyr span across the Triassic–Jurassic transition (Schaller et al., 2011; Blackburn et al., 2013; Dal Corso et al., 2014). Atmospheric carbon dioxide levels, temperature, precipitation, and terrestrial weathering all increased (McElwain et al., 1999; Michalik et al., 2010; Schaller et al., 2011; Kuroda et al., 2010; Bonis and Kürschner, 2012). Marine carbonate sedimentation terminated at most sites recorded worldwide (Greene et al., 2012b, fig. 5), and the robust Late Triassic reef system collapsed (Kiessling et al., 2009). Initiation of the carbonate gap has been attributed to ocean acidification, though longer-term shifts in carbonate

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construction by metazoans and diagenetic processes better explain the magnitude of the lithologic change (see Greene et al., 2012b, for a review).

The end-Triassic mass extinction was ecologically severe. Marine invertebrate extinction rate was second only to the end-Permian event (Alroy, 2010), but was much more selective. Modern fauna invertebrates (e.g., Sepkoski, 1981), chiefly mollusks, and additionally scleractinian corals, show a much more severe diversity drop than other faunas (Kiessling et al., 2007; Alroy, 2010). Corals, calcareous sponges, and other benthic taxa associated with reef settings had significantly higher extinction rates than those in level bottom habitats (Kiessling et al., 2007) and reefs disappeared worldwide for nearly a million years (Kiessling et al., 2009). Benthic taxa associated with carbonate settings experienced more severe extinction rates than those in siliciclastic settings (Kiessling et al., 2007).

Two main seaways dominated the Triassic–Jurassic world, the large, equatorial, and somewhat enclosed Tethys Ocean and the massive Panthalassic Ocean (the proto-Pacific). Arguably, the best-studied sites are in the Tethyan realm in Europe, so fossil records from Panthalassa are necessary to understand truly global vs. local trends (see Greene et al., 2012b: fig. 5). Furthermore, the stratigraphic expression of the Triassic–Jurassic interval tends to be condensed in certain better-studied Tethyan sections, so stratigraphically expanded sections, such as the one from Peru studied here, are key to understanding the ecosystem shifts (Ritterbush et al., in press).

Resolving the marine ecological consequences of the extinction requires both 1) examination of communities established in the Earliest Jurassic, and 2) an understanding of community interactions with the post-extinction environmental state. Particularly, because the ecological crisis occurred primarily within metazoan-mediated depositional systems (reefs and carbonate ramps; Kiessling et al., 2007) the role of metazoans in post-extinction sediment production deserves critical study (Ritterbush et al., in press). For example, typical Phanerozoic paleoenvironmental analysis includes biofacies to understand the ancient environmental setting (e.g., Taylor, 1982; Taylor et al., 1983). However, in the aftermath of a mass extinction, it can be difficult to untangle the effects of extinction vs. local environmental control on the distribution of benthic organisms, and for some time the traditional application of biofacies breaks down (Brett et al., 2012). As in the Precambrian, before the advent of a metazoan contribution to sediments, the paleoenvironment is first determined using physical sedimentological clues. Then, the biota is placed into the paleoenvironmental framework to understand the paleoecological structure in the aftermath of the extinction. A clear example of biofacies bias involves siliceous sponges: traditionally considered deeper water forms, their mere presence would typically conjure a deeper water paleoenvironment in a traditional facies analyses (Bodzioch, 1994: p. 96). Post-extinction paleoecology can be unusual, and typical biofacies analyses can break down. In the present study, the paleoenvironment is investigated first, and the biofacies placed into that framework.

Fig. 1. Context for the end-Triassic mass extinction. The map shows supercontinent Pangea between the Tethys sea and global ocean Panthalassa, and extent of the Central Atlantic Magmatic Province (CAMP) basalts (shaded; after Schoene et al., 2010 and Whiteside et al., 2010). Numbers indicate paleogeographic locations of sites discussed in the text: 1. Central Andes, Peru; 2. Gabbs Valley Range, Nevada, USA; 3. Northern Calcareous Alps, Austria; 4. High Atlas Mountains, Morocco. Ages of CAMP zircons from 8 samples across North America and Morocco are summarized from Blackburn et al. (2013) as ranges, with vertical bars marking mean and 2 standard deviations for each sample. CAMP volcanism ensued prior to or concomitant with global mass extinction (red line), which is estimated as 250–300 kyr before the appearance of Jurassic-boundary-indicative ammonoids (Schoene et al., 2010). End-Triassic mass extinction rates (center graph) were more severe for benthic invertebrates associated with reef settings and with carbonate settings, compared to benthic invertebrates altogether (data from Kiessling and Aberhan, 2007: fig. 10 after Greene et al., 2012b). The end-Triassic mass extinction was the Phanerozoic's largest decrease in Modern Fauna biodiversity (bottom graph; after Alroy, 2010). Note the contrast to the Devonian and end-Permian diversity drops, from extinctions which affected primarily the Paleozoic Fauna.

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