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Sudden and extreme hyperthermals, low-oxygen, and sediment influx drove community phase shifts following the end-Permian mass extinction

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ABSTRACT

We present a correlated record of carbon isotope geochemistry and sedimentological analysis for the Lower Triassic Werfen Formation from the Italian Dolomites. Macro- and mid-sized fossil diversity, ecology, and climate sensitivity are included to provide an integrated account of the benthic response to paleoenvironmental change. Novel communities developed in the wake of the mass extinction during pervasive fluctuations in environmental conditions. In the sedimentary sequences of the Werfen Formation of the Italian Dolomites, microbialites, microconchids, foraminifera, and ubiquitous flat-clams, formed a complex community within the first 500,000 years. Later, increased sea-surface temperatures and inundation of the seafloor with siliciclastic sediments favored infaunal bivalves and microgastropods. Persistent trends in the environment can produce directional, often irreversible, community shifts defined here as phase shifts. Phase shifts in ecosystem structure can be driven by environmental shifts across threshold boundaries to produce an "abrupt and dramatic" novel community composition, a phenomenon readily observed during the Early Triassic. Previously described "disaster forms" including flat clams, microconchids, foraminifera, and microbialites are re-envisioned as a phase shift community. We hypothesize that the unique, persistent, and reoccurring microbialite and mid-sized fauna assemblages observed during the initial recovery from the end-Permian mass extinction and re-appearing throughout the Early Triassic typify a phase shift community. In the Smithian, infaunal bivalves and microgastropods represent a second phase shift community developed in response to a persistent, directional rise in sea-surface temperatures and enhanced sediment influx. We compare and contrast phase shifts with other models for ecosystem recovery including trophic, competition, and Earth System Succession.

1. Introduction

Approximately 252 million years ago, an ancient hyperthermal event caused by the volcanic eruption of the Siberian Traps drove the extinction of the vast majority of life on the planet. The basalt burned through deposits of coal, carbonate, and evaporite which compounded the volume of carbon input while adding toxic gasses to the atmosphere (Svensen et al., 2009; Burgess and Bowring, 2015). Terrestrial and marine life both experienced severe decreases in taxonomic diversity due to sudden global warming, toxic gas release, acid rain, the development of extensive oxygen minimum zones through reduced gradient-driven circulation, and possible ocean acidification (Algeo et al., 2011; Chen and Benton, 2012). For approximately 5 million years, throughout the Early Triassic, additional volcanic eruptions continued to perturb the ecological system as indicated by volatile excursions in the carbon isotope record (Payne and Kump, 2007). Oxygen isotope fluctuations suggest that an additional hyperthermal event, where sea-surface temperatures may have reached up to 40 °C, occurred in the late Smithian approximately 1.4 million years after the initial extinction event (Sun et al., 2012; Romano et al., 2012; Goudemand, 2014). A humid climate and record-breaking Earth surface temperatures combined to produce an interval of enhanced terrestrial weathering and siliciclastic deposition which decimated newly re-built level-bottom communities (Korte et al., 2003; Galfetti et al., 2007b).

The pattern of the Early Triassic restructuring from the end-Permian mass extinction was varied through time and location (Pietsch and Bottjer, 2014 and references therein). The relatively low age resolution of stages makes it challenging to make precise comparisons between localities across the globe. Paleoecological records correlated to chemostratigraphic, lithostratigraphic, and biostratigraphic records of climate change are necessary to achieve the most informative synthesis of the benthic recovery from the end-Permian mass extinction. To this end, we collected data on lithology, geochemistry, and paleoecology from the Early Triassic aged Werfen Formation of the Italian Dolomites to interpret benthic paleocommunity changes in response to re-

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constructed volatile environmental conditions and to draw comparison with the benthic communities studied in the southwestern United States (Fig. 1).

The Italian Werfen Formation was deposited in Paleo-Tethys and contains a record that extends from the Permian–Triassic boundary throughout the entire Early Triassic interval. Carbon isotope analyses in South China, Iran, and Italy have been interpreted to indicate that the Tethys Ocean was a high-productivity region leading to basin-wide stratification and overturn events throughout the Early Triassic (Horacek et al., 2007; Winguth and Winguth, 2012). Sensitivity studies indicate that eutrophication and an enhanced biological pump are required to drive stagnation events while the addition of a tectonic sill at the boundary of the enclosed Tethys basin with the vast Panthalassic Ocean could have further driven stagnation and low-oxygen concentrations (Winguth and Winguth, 2012). Eutrophication and stagnation would lead to anoxic conditions throughout much of the Tethys Ocean potentially punctuated by basin overturn events.

Initial work on the Werfen Formation constrained it in time through lithostratigraphic and biostratigraphic comparison both throughout the Dolomites and to neighboring sections in Hungary (Neri and Posenato, 1985; Broglio Loriga et al., 1990; Perri and Farabegoli, 2003; and Posenato, 2008b). More recently, Brandner et al. (2009) redefined some of the lithostratigraphic boundaries of the Lower Triassic Werfen Formation. Posenato (2008a) analyzed bivalve diversification and body size changes. Twitchett (1999) applied an early version of his paleoecological recovery rubric to the benthic communities of the Werfen Formation. Hofmann et al. (2011) described a diverse and complex trace fossil community from the early Siusi Member of the late Griesbachian and early Dienerian and Hofmann et al. (2015) provided a synthesis of the ecological communities of the Werfen Formation.

Our sampling scheme highlights the transitions between depositional environments and climate from different members of the Werfen Formation. This dataset investigates macrofossils (molluscs, brachiopods, echinoderms) collected in the field, microbialites, and mid-sized fauna (foraminifera, ostracods, microconchids, echinoderm fragments), that can only be discerned through thin section analysis. We use these data in order to address how macro and mid-sized taxa contributed to Early Triassic phase shift paleocommunities and to investigate which organisms had a lasting role in the restructured benthic community. A comparison of changes in the Werfen Formation with previous work on the benthic paleoecological recovery from Eastern Panthalassa (southwestern United States) was used to synthesize how changes in global climate and environmental perturbations may have impacted the benthic fauna in both the Tethys and Panthalassic Oceans. Finally, we compare phase shift communities with previously proposed theories of ecosystem restructuring following the end-Permian mass extinction including a trophic model, competition model, and the Earth-System Succession model (Chen and Benton, 2012; Hautmann et al., 2015; Hull, 2015).

2. Geology

The Werfen Formation in the Italian Dolomites of Italy has been well studied in the Val Gardena and Val Badia (Broglio Loriga et al., 1990) including detailed analysis of the stratigraphy and the benthic fauna (Neri and Posenato, 1985; Broglio Loriga et al., 1990; Wignall and Twitchett, 1996; Twitchett, 1999; Perri and Farabegoli, 2003; Farabegoli et al., 2007; Posenato, 2008a,b; Brandner et al., 2009; Hofmann et al., 2011). These studies provide a broad baseline to perform a comprehensive paleoecological community analysis of the benthic marine macrofauna.

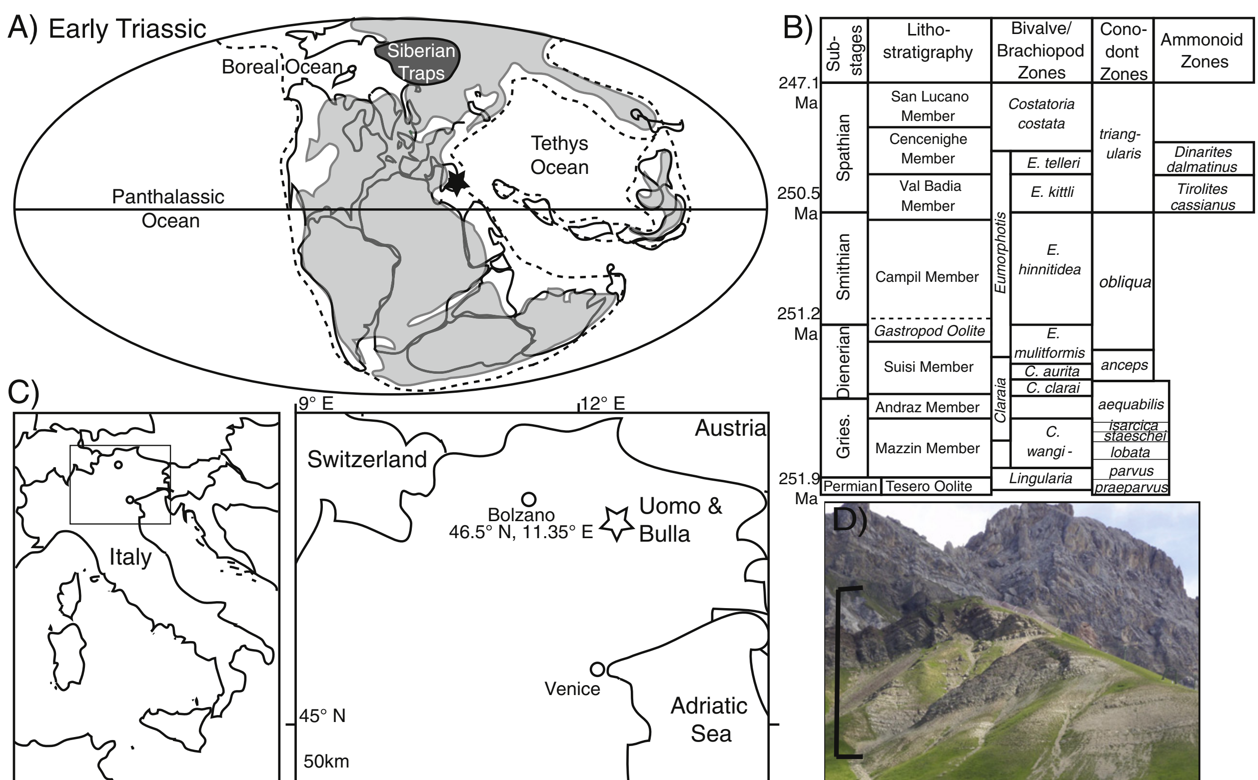

Fig. 1. Paleogeographic and temporal context for the Italian Werfen Formation. A. The Early Triassic globe showing the continents in Pangea. A star marks the location of modern day Italy (modified from Scotese, 2010). The extent of Siberian Trap volcanism is also indicated (Reichow et al., 2009; Saunders and Reichow, 2009). B. Early Triassic time scale depicts the four sub-stages and nine members of the Werfen Formation representing 5 million years. Biostratigraphy and radiometric date references are in supplement. Citations for dates, litho- and biostratigraphy in Supplemental text. C. Modern day Italy with a box representing the expanded area showing the location of the Uomo and Bulla sections in the Italian Dolomites (modified from Posenato, 2008b). D. A photo showing the entire section of Uomo from the Mazzin in the hillside to the Campil sampled at the top of the bracket. Dark green chair lift supports provide a scale. The mountains in the background are Middle Triassic in age.