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The effects of mid-Phanerozoic environmental stress on bryozoan diversity, paleoecology, and paleogeography

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ABSTRACT

Evidence of sustained environmental degradation associated with the end-Guadalupian, end-Permian, and end-Triassic extinctions has been inferred from numerous geochemical and sedimentological studies, but the long-term impacts of this extinction-associated stress on the evolutionary trajectories of marine invertebrates have not been explored. An examination of the diversity, extinction, paleoenvironmental range, and geographical distribution of marine stenolaemate bryozoans during the Permian to Jurassic interval provides striking new evidence of the taxonomic and ecological influence of these mid-Phanerozoic extinctions on one of the most abundant components of the Paleozoic Fauna. Elevated bryozoan extinction rates during the Late Permian and Late Triassic were coupled with major changes in their habitats. Bryozoans gradually disappeared from deep-water offshore settings during the Late Permian and from nearshore and offshore settings during the Late Triassic. Re-colonization of these environments in the wake of each crisis was delayed but coupled with increases in global generic diversity. The taxonomic effects of the end-Guadalupian extinction were milder than previously described, even though ecologically bryozoans were becoming restricted to nearshore settings. The end-Permian mass extinction remained the largest for bryozoans, drastically reducing global and assemblage generic diversity and triggering a permanent change in their paleoenvironmental preferences from nearshore to mid-shelf settings. The 285 Myr dominance of stenolaemate bryozoans ended during the Late Triassic when all but one order (Cyclostomata) became extinct, initiating a taxonomic switch between stenolaemate and gymnolaemate bryozoans. Moreover, spatio-temporal variations in the paleoenvironmental history of bryozoans imply that Late Permian and Late Triassic marine environmental instability resulted largely from some stressful deep-water phenomenon. High extinction rates in nearshore environments in the Late Permian provide a link between marine and terrestrial/atmosphere extinction-related perturbations.

1. Introduction

The transition between Paleozoic and Mesozoic communities is characterized by three devastating crises (Raup and Sepkoski, 1982). The end-Guadalupian (Middle Permian) and end-Permian extinctions are two independent events that took place within 8 million years (Myr) of each other in the Late Permian (e.g., Stanley and Yang, 1994; Gradstein et al., 2004; Mundil et al., 2004). Together, they contributed to the most severe drop in biodiversity of the Phanerozoic and a major shift in the taxonomic and ecological structure of marine communities (Gould and Calloway, 1980; Fraiser and Bottjer, 2005; Erwin, 2006; Clapham and Bottjer, 2007a; Fraiser and Bottjer, 2007b). Fifty-two million years later at the end of the Triassic, many of the Paleozoic survivors who had struggled to re-diversify in the wake of the Late Permian events became extinct. These three extinctions, spanning about 61 Myr, were accompanied by at least two periods of sustained environmental instability. Late Permian environmental degradation likely started at the end of the Middle Permian and persisted through the Early Triassic (e.g., Isozaki, 1997; Grice et al., 2005; Huey and Ward, 2005; Algeo et al., 2007). Late Triassic environmental stress inferred from ocean-atmosphere modeling based on elevated pCO_2 (McElwain et al., 1999; Huynh and Poulsen, 2005) was likely initiated during the Rhaetian (Ciarapica, 2007).

The end-Guadalupian and end-Permian extinctions preferentially terminated sessile members of the Paleozoic Fauna (i.e., bryozoans, brachiopods, and crinoids) (Knoll et al., 1996, 2007). While all groups suffered considerable losses at the end of the Permian, members of the Modern Fauna (i.e., bivalves, gastropods) fared better in the immediate aftermath. Knoll et al. (2007) reviewed the effects of environmental perturbations on both faunas and concluded that extinction selectivity in the Late Permian was linked to environmental stress, specifically hypercapnia. Hypercapnia, or CO_2-poisoning, is one of several proposed mechanisms for the end-Permian extinction; others include various oceanographic, climatic, and extraterrestrial processes (Erwin, 2006). Regardless of the trigger, Late Permian–Early Triassic environmental

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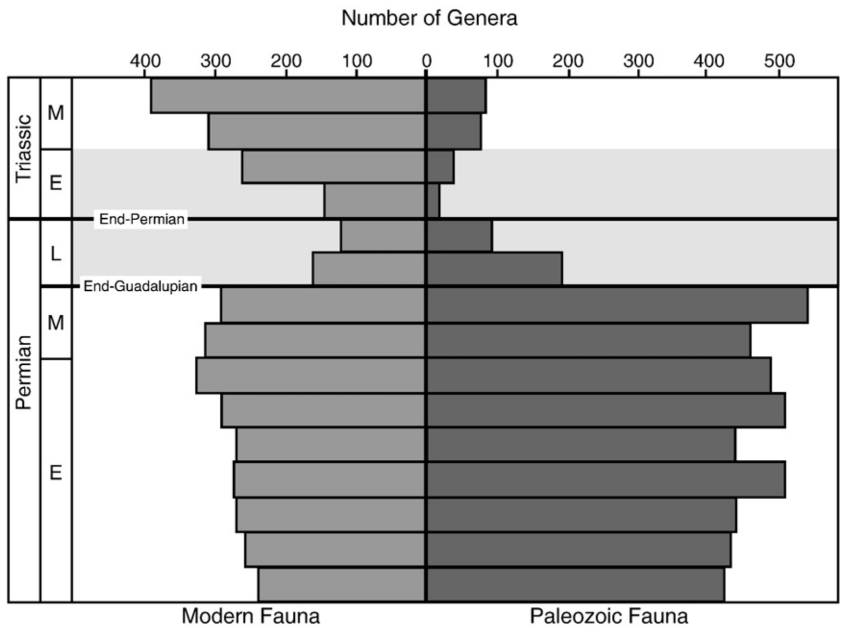

Fig. 1. Changes in the generic diversity of members of the Paleozoic and Modern Faunas across the end-Guadalupian and end-Permian extinctions. Modified from Knoll et al. (1996). Gray area represents the duration of extinction-related environmental stress based on sedimentological and geochemical evidence (Isozaki, 1997; Woods et al., 1999; Payne et al., 2004; Pruss et al., 2004).

stress had a more lasting effect on members of the Paleozoic Fauna. Secular changes in biodiversity during the Permian–Triassic (P/T) interval indicate that the re-diversification of sessile organisms during the Early Triassic was slow and that pre-extinction (Middle Permian) diversity levels were not yet re-established as of the Late Triassic (Fig. 1).

In this study, we examined the transition of bryozoans through the Permian to Jurassic interval in an attempt to constrain the effects of mass extinction-related environmental stress on their evolutionary history. Stenolaemate bryozoans, diverse and abundant members of the Paleozoic Fauna, nearly became extinct at the end of the Triassic (one group, Cyclostomata, survived) and were replaced as the dominant post-Jurassic group by the Modern Fauna gymnolaemate bryozoans (Fig. 2) (Sepkoski, 1981; Taylor and Larwood, 1990). Analyses of bryozoan diversity changes, paleoenvironmental transitions, and paleogeographic distribution have the potential to reveal why these mid-Phanerozoic extinctions had a much more significant impact on some groups (i.e., the Paleozoic Fauna) than others.

2. Mid-Phanerozoic extinctions: sources of environmental stress

2.1. End-Guadalupian extinction

The end-Guadalupian extinction is an independent Late Permian event with species extinction rates comparable to those of the end-Permian (Stanley and Yang, 1994). Although still a matter of contention, volcanism (Emeishan igneous province), global sea level fall, and a late Middle Permian high bio-productivity period (the "Kamura" event) are all potential kill mechanisms (Hallam and Wignall, 1999; Zhou et al., 2002; Isozaki et al., 2007). However, negative carbon isotopic excursions across the extinction boundary and a gradual trend towards decreasing values during the early Late Permian suggest that the causal mechanism was gradual, which precludes catastrophic processes (i.e., extraterrestrial impact, gas hydrate release) and implies that extinction-related environmental instability was likely protracted through the Middle–Late Permian boundary (see Isozaki et al., 2007, Fig. 4). In fact, lithological studies have shown that the development of deep-water anoxia associated with the P/T superanoxia event was initiated at the end of the Middle Permian (Isozaki, 1997) and is the likely source of the sustained Late Permian environmental degradation.

2.2. End-Permian extinction

The end-Permian mass extinction is arguably the largest such event, marked by the disappearance of about 80% of marine species and 49% and 63% of marine and terrestrial families, respectively (Raup and Sepkoski, 1982; Stanley and Yang, 1994; Benton, 1995). Hypothetical causal mechanisms for the end-Permian extinction include a range of gradual and catastrophic processes: widespread oceanic and

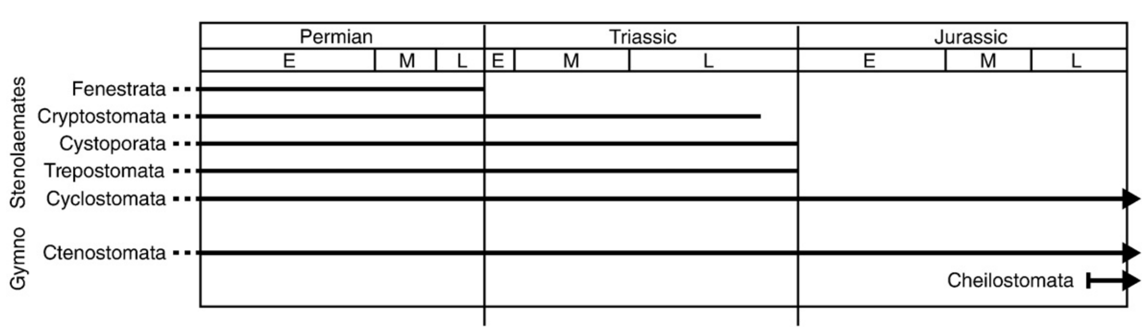

Fig. 2. Schematic illustrating the range of stenolaemate and gymnolaemate (Gymno) bryozoans through the Permian to Jurassic interval. Data from Powers and Pachut (2008).