



# Permian–Triassic evolution of the Bivalvia: Extinction–recovery patterns linked to ecologic and taxonomic selectivity



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## ABSTRACT

The Bivalvia is an important benthic clade that was relatively less affected than other benthos during the Permian–Triassic (P–Tr) biotic crisis, reporting losses of 85%, 64%, and 32% at the species, genus and family levels, respectively. This clade proliferated immediately after the P–Tr mass extinction (PTME) to become one of the key elements of the ‘Modern Evolutionary Fauna’ following the P–Tr ‘Great Dying’. Global bivalve occurrence data demonstrate that the initial recovery started in the Griesbachian, a substage immediately after the PTME, and are characterized by relatively high origination and low extinction rates. Thus, unlike other fossil groups, bivalves did not significantly engage in the survival interval. The initial Griesbachian recovery is followed by a stepwise recovery during the Dienerian to Spathian. Then, a remarkably rapid radiation occurred in the Anisian, indicated by extremely high proportional origination and extinction rates. Infaunalization has long been considered the most significant adaptation during the Mesozoic Marine Revolution (MMR), which was thought to have commenced in the Early–Middle Triassic. However, the proportion of infauna in communities remained virtually unchanged before and after the P–Tr biotic crisis; additionally there was no significant difference in proportional extinction/origination rates between infaunal and epifaunal taxa at the genus and family levels through the entire P–Tr transition, implying the absence of ecological selectivity, a conclusion that differs from some previous studies. Therefore, if escalating predatory pressure indeed played a crucial role in driving the initial phases of the MMR, infaunalization was not marked prior to the Ladinian. Alternatively, infaunalization may have played a minor role in facilitating the MMR during the entire era. If so, changes in the physical and chemical environment (‘Court Jester’ model) (i.e. amelioration of marine environments in late Early Triassic), rather than biotic processes (‘Red Queen’ model), may be crucial for the origination and initial phases of the MMR during the early Mesozoic.

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## 1. Introduction

Of the ‘Big Five’ mass extinctions, the Permian–Triassic (P–Tr) biotic crisis resulted in the largest drop in biodiversity and the most devastating ecosystem collapse during the Phanerozoic (Sepkoski, 1981, 1984). Global biodiversity data show that various fossil groups behaved differently during and after the PTME. Some clades like brachiopods and corals that suffered substantially during the biotic crisis recovered much later than some other groups (Hallam and Wignall, 1997; Erwin, 1998; Chen et al., 2005a, b); others such as ammonoids (Brayard et al., 2009), foraminiferans (Song et al., 2011), and ophiuroid echinoderms (Chen and McNamara, 2006) rebounded earlier after the

P–Tr crisis. The distinctive responses to the PTME and its aftermath may be due to the different roles that various clades played within the trophic structure of the marine ecosystem (Chen and Benton, 2012). The biotic groups within the low-level trophic structure may have garnered relatively less attention from the PTME, and thus rebounded earlier than the meso-consumers or predators (Chen and Benton, 2012). Alternatively, physiologic adaptation in some key groups may have developed resistance to environmental devastation such as widespread anoxia, ocean acidification, and extreme hot seawater temperatures (Knoll et al., 2007; Payne and Clapham, 2012); such resistance may be accountable for the biodiversity variations within the various groups over the P–Tr transition. Thus, both the physiology and ecological function of organisms provide some clues for unraveling the causes of the PTME and its protracted recovery (Knoll et al., 2007). Nevertheless, to date, debate still continues on whether the physical and chemical environment (‘Court Jester’

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model) or biotic processes ('Red Queen' model) have driven biotic macroevolution over this critical interval (Benton, 2009; Chen and Benton, 2012).

Like many other clades, the Bivalvia underwent its greatest macroevolutionary turnover during the P–Tr transition (Erwin, 1994, 2006; Hallam and Wignall, 1997). They were subordinate in Permian communities, but became the most numerically abundant shelly fossils in the Griesbachian, the first substage following the PTME. Bivalves, together with other molluscs (i.e. ammonoids and gastropods), successfully usurped brachiopod dominance in marine shelly communities through the P–Tr transition (Thayer, 1985; Fraiser and Bottjer, 2007; Chen et al., 2010). This is possibly because they are less sensitive to anoxia (Taylor and Brand, 1975; Bayne and Livingstone, 1977; Wang and Widdows, 1993a, b; Diaz and Rosenberg, 1995; Sobral and Widdows, 1997; MacDonald et al., 1998; Ballanti et al., 2012).

Another feature of the PTME is the switch from brachiopod-dominated Paleozoic Evolutionary Fauna (EF) to mollusc-dominated Modern EF in marine ecosystems (Gould and Calloway, 1980; Sepkoski, 1981, 1984; Bambach et al., 2002; Fraiser and Bottjer, 2007; Alroy, 2010; Chen et al., 2010). The marine ecosystem has undergone an unprecedented, far-reaching transformation in the aftermath of the PTME that is mainly responsible for the marine ecosystem we have today. The term "restructuring" is more appropriate than "rebound" or "recovery" to describe the turnover in the biosphere (Dineen et al., 2014).

Previous studies show that the Bivalvia only suffered moderate disruption during the PTME based on variation in taxonomic richness and extinction rates (Nakazawa and Runnegar, 1973; Yin, 1985, 1987; Li, 1995; Fang, 2004; Huang et al., 2014). They underwent a gradual and stepwise recovery after the PTME (McRoberts, 2001). However, these observations were based mainly on changes in taxonomic richness without consideration of other important proxies, like proportional extinction and origination rates, as well as ecological selectivity through this critical interval. The updated, global database for the bivalves mitigates sampling bias and Lazarus effects that would largely obscure the real changing pattern of biodiversity. In addition, bivalve lifestyles are categorized into five types: infaunal motile, infaunal slow-moving, semi-infaunal motile, epifaunal stationary and low-level epifaunal stationary modes (Li, 1995; Komatsu et al., 2008; Huang et al., 2014). They represent various physiologic types associated with different habitats and climatic regimes. The proportional extinction and origination rates of the various physiologic groups may provide some insight into the environmental and climatic extremes associated with the PTME and subsequent events.

Infaunalization was supposedly prevalent among Early Mesozoic bivalves (McRoberts, 2001) by the fact that the proportion of the infauna was higher, possibly much higher than that of the epifauna (Vermeij, 1977; Thayer, 1979). Although the origination rates of the epifauna and infauna showed no significant differences, the epifauna had much higher extinction rates than that of the infauna during the same interval (McRoberts, 2001). Here, we probe the extinction and recovery patterns of the Bivalvia and their ecologic selectivity over the P–Tr transition by re-examining the global dataset derived from the Paleobiology Database with emphasis on the variations in taxonomic richness, and proportional extinction and origination rates at the species, genus and family levels, respectively. Infaunalization through the entire Early Triassic is also assessed on the basis of proportions of infauna/epifauna in the aftermath of the PTME, testing the possible driving force of the MMR in the early Mesozoic.

## 2. Materials and methods

All bivalve occurrences from the Changhsingian (highest Permian), Lower Triassic substages to the Anisian (Middle Triassic) analyzed in this study are sourced from Paleobiology Database [<http://fossilworks.org/bridge.pl?a=displayBasicDownloadForm>] and were downloaded in

May 2014. To enhance the resolution of the geological timescale, the Induan and Olenekian were subdivided into the Griesbachian and Dienerian, the Smithian and Spathian substages, respectively. Thus, a total of six time bins (Changhsingian, Griesbachian, Dienerian, Smithian, Spathian, and Anisian) are employed to calculate biodiversity (taxonomic richness) and proportional extinction and origination rates. Species, genus, and family richness of each time bin were taken into account in examining biodiversity variations from the Changhsingian to Anisian. All genera have formal taxonomic names. And species of uncertain taxonomic status (i.e., Genus sp.) were included, in agreement with some previous studies (Chen et al., 2011; Huang et al., 2014), but they were counted only once within each named genus in order to minimize taxonomic bias. The species qualified with terms like "cf." or "aff." are also included in this study. However, sample intensities are clearly variable across different geological periods, thus, rarefaction analysis (Raup, 1975) computed by the palaeontological software package PAST (Hammer et al., 2001) was implemented to test taxonomic bias (e.g., Chen et al., 2010, Chen et al., 2011). It is common to plot specimen counts against the numbers of a defined taxonomic rank (i.e. numbers of species or genera) in rarefaction analysis. Nevertheless, information on specimen counts is not available in the Paleobiology Database. Therefore, the rarefaction of occurrences against genera (Fig. 1A) and two adjacent taxonomic ranks plotted against each other (Fig. 1B) were both used herein. Concerning the latter, it is noteworthy that rarefaction analysis between two adjacent ranks (i.e. species/genus or genus/family) is likely to decrease or obscure the difference between diversity curves with relatively high confidence limits (i.e. 95% confidence limit) (Shen et al., 2000). Therefore, the rarefaction analysis of species richness against family richness is employed to determine sampling quality (Fig. 1B). Moreover, a confidence limit (95%) was used to examine the robustness of rarefaction curves. To better understand the taxonomic selectivity of bivalves through the P–Tr transition, all orders of this clade were investigated using biodiversity at different taxonomic levels.

To unravel the true extinction and recovery patterns of the Bivalvia over the P–Tr transition, we also calculated the proportional extinction and origination rates (Harper and Gallagher, 2001; Bambach et al., 2004) in each time bin, from the Changhsingian to Anisian at the species, genus, and family levels, respectively, according to the equations below:

$$\text{Proportional Extinction rate} = N_{\text{extin}}/N_0 \times 100\%,$$

Proportional Origination rate =  $N_{\text{orig}}/N_0 \times 100\%$ , where  $N_0$  represents the number of all taxa during certain stage (substage),  $N_{\text{extin}}/N_{\text{orig}}$  represents the number of extinction/origination taxa over the same interval, respectively. The 95% confidence interval of sample sizes was shown using the "Wilson Score Interval" method programmed in R software. Moreover, a z-test was performed to examine the significance of the differences in extinction/origination rate between the next two time bins, which may provide some insights into the actual evolutionary patterns of the Bivalvia.

To shed light on the ecologic selectivity over the P–Tr transition, both taxonomic richness and proportional extinction/origination rates were employed to analyze the different physiological groups of bivalves at the species, genus, and family levels, respectively. However, several physiological groups have a very small number of taxa in some time bins, which can bias understanding of true ecologic selectivity. Thus, we subdivided, collectively, the bivalves into two ecologic types: infaunal and epifaunal lifestyles. The former includes infaunal motile, infaunal slow-moving, and semi-infaunal motile, while the latter comprises epifaunal stationary and low-level epifaunal stationary. Their proportional extinction/origination rates were re-calculated. A z-test was applied not only to test the significance of differences in richness between two adjacent time bins but also to examine the significance

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