Permian-Triassic evolution of the BIVALVIA: Extinction-recovery patterns linked to ECOLOGIC and taxonomic SELECTIVITY

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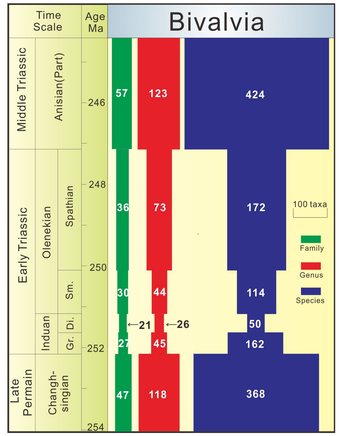
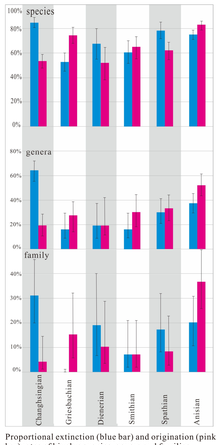
ABSTRACT

The Bivalvia is an important benthic clade that was relatively less affected than other benthos during the Permian-Triassic biotic crisis, reporting losses of 85%, 64% and 32% at the species, genus and family levels, respectively. Global bivalve occurrence data demonstrate that the initial recovery started in the Griesbachian 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.

THE PATTERNS OF EXTINCTION-RECOVERY



Taxonomic richness of bivalve species, genera and families through the P-Tr transition.



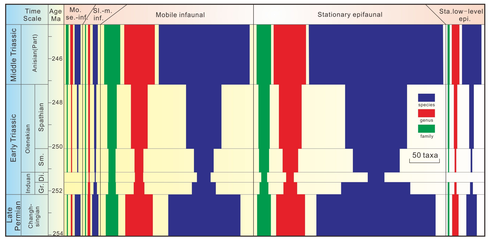
Proportional extinction (blue bar) and origination (pink bar) rates of bivalve species, genera and families.

Intervals	Numbers of extin./New taxa			Proportional extinction rates (%)			Proportional origination rates (%)		
	Species	Genera	Family	Species	Genera	Family	Species	Genera	Family
Changhs.	314/197	76/23	15/2	85	64	32	54	19	4
Griesba.	85/121	7/11	0/4	53	16	0	75	27	15
Diene.	34/26	5/6	4/2	68	19	19	52	19	10
Smithian	70/74	7/13	2/2	61	16	7	65	30	7
Spathian	136/107	22/24	6/3	79	30	17	62	33	8
Anisian	318/351	45/64	11/21	75	37	20	83	52	37

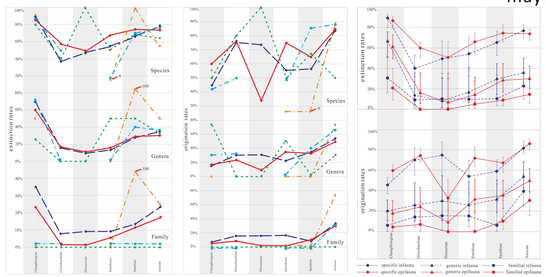
Quantitative data on proportional extinction/origination rates of bivalve species, genera and families from the Changhsingian to Anisian.

The newly updated global dataset suggests that bivalves suffered a lesser, typically moderate extinction during the PTME. The general picture of global biodiversity shows that bivalves underwent a stepwise depletion in biodiversity through the Changhsinian-Denerian interval. The lowest biodiversity occurred in the Denerian, implying that extinction might continuously occur through part or all of the Griesbachian, except of PTME. However, bivalves experienced relatively low extinction rates in the Griesbachian, which rejects the possibility of a biotic extinction between the Griesbachian and Dienerian. The lowest biodiversity in the Denerian is probably biased by Lazarus effect. The combination of a relatively high biodiversity, high origination rate, and low extinction rate indicates that an initial recovery of bivalves occurred in the Griesbachian. Then, this clade experienced a stepwise recovery from the Dienerian to Spathian. The radiation of bivalves occurred in the Anisian, evidenced by highedt biodiversity and high origination rates, coupled with rapid speciation rates. In addtion, the faunal commositions greatly changed from the Spathian to Anisian.

ECOLOGIC SELECTIVITY



Taxonomic richness at the species, genus and family levels among different bivalve life modes from the Changhsingian to Anisian.



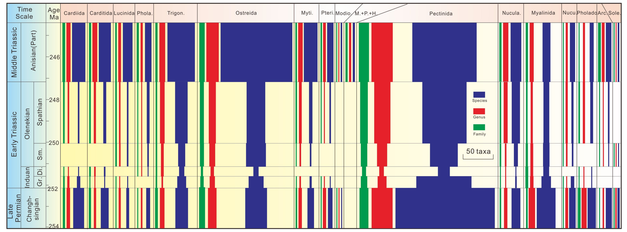
Proportional extinction and origination rates among various bivalve life modes.

Proportional extinction and origination rates between the infaunal and epifaunal bivalves.

The variations of taxonomic richness suggest that any changes in the ecological preferences of the bivalves were not obvious before and after PTME. In terms of proportional extinction/origination rates, there is noteworthy that some life modes usually consist a very small number of species, which may bias the selectivity pattern. Accordingly, all bivalves have beeb recategorized into two simple lifestyles: the infauna and epifauna. Surprisingly, no significant difference (P>0.05) is observed between these two groups at the genus and family levels within any time bin from the Changhsingian to Anisian.

TAXONOMIC SELECTIVITY

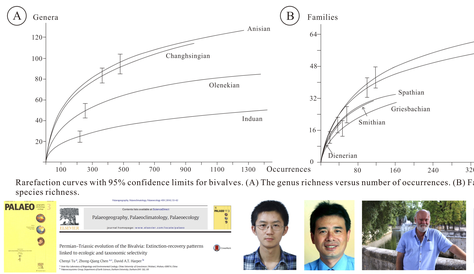
The Ostreida, Trigoniida,and Mytilida responded well during the PTME and its aftermath; the richness of them rebounded in the Anisian. In contrast, the Pectinida, Myalinida, and Pholadomyida suffered from the biotic crisis. Bivalves also underwent a switch of dominance in communities from the Pectinida to the Ostreida between the Spathian to Anisian.



Number of species, genera and families of the major bivalve orders from the Changhsingian to Anisian showing taxonomic selectivity during extinction- recovery patterns.

Our study suggests that the infaunalization did not occur, at least before the Ladinian. Thus, the start of the MMR was probably not driven by biotic processes ('Red Queen' model). Instead, environmental changes ('Court Jester'model) may be responsible for the origination and initial evolution of the MMR.

MATERIALS AND METHODS



Rarefaction curves with 95% confidence limits for bivalves. (A) The genus richness versus number of occurrences. (B) Family richness versus species richness.

All bivalve occurrences from the Changhsingian, Lower Triassic substages to the Anisian analyzed in this study are scoured from Paleobiology Database. Sample intensities are clearly variable across different geological periods, thus, rarefaction analysis was implemented to test taxonomic bias. To unravel the true extinction-recovery patterns and shed light on the ecologic selectivity within bivalvia over the P-Tr transition, both taxonomic richness and proportional extinction/origination rates were employed herein.

DRIVING FORCE OF THE MMR