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# 二叠纪—三叠纪之交双壳类的灭绝与复苏过程

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**摘要:** 为了建立早—中三叠世双壳类的残存—复苏模式及深入探讨双壳类迟缓复苏的原因, 对全球范围内该时期双壳类属的时限分布进行了统计。总体来看, 3个亚纲(Pteriomorphia、Palaeotaxodonta和Heteroconchia亚纲)和5种生活方式(外栖活动类、外栖固着类、半内栖类、内栖浅掘穴类和内栖深掘穴类)的双壳类均展示出了一致的规律, 属级分异度直到中三叠世Anisian期才恢复到晚二叠世末生物大灭绝之前的水平。二叠纪残存类型在早—中三叠世双壳类中所占的比例逐步降低, 从占过渡层的77.3%降低到了中三叠世Anisian期的33.7%, 指示双壳类的缓慢复苏过程。而在整个早三叠世的漫长复苏期中, 双壳类仅遭受背景灭绝, 表明双壳类的迟缓复苏受限于长时期的高压环境, 随着海洋环境的逐步好转, 才逐渐出现新的类型。

**关键词:** 晚二叠世; 早三叠世; 双壳类; 生物灭绝; 生物复苏; 地层学; 环境影响。

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## The Extinction and Delayed Recovery of Bivalves during the Permian-Triassic Crisis

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**Abstract:** In order to reconstruct the survival and recovery pattern of bivalves and probe into the reasons in the aftermath of the Permian-Triassic mass extinction, all available data of the Late Permian to Middle Triassic bivalve genera all around the world have been counted and analyzed. The bivalves belonging to 3 subclasses (Pteriomorphia, Palaeotaxodonta, and Heteroconchia) and 5 lifestyles (epifaunal attached, epifaunal motile, semi-infaunal, shallow infaunal, and deep infaunal) show a similar recovery pattern. The diversity curves of bivalves display that the recovery of bivalves was delayed to Anisian, when the genus diversity increased nearly to the similar value of the Changhsingian prior to the End-Permian mass extinction. In addition, Permian survivors including long-term survivors, holdover species, and Lazarus taxa dominated the bivalves during the Early Triassic, but not in the Anisian (Middle Triassic). Bivalves only suffered background extinction rates during the Early Triassic, indicating the delayed recovery of bivalves resulted from long-term hostile environments.

**Key words:** Late Permian; Early Triassic; bivalves; mass extinction; biotic recovery; stratigraphy; environment effects.

晚二叠世末期发生了显生宙历史上规模最大的一次生物灭绝事件(Raup, 1979; Erwin, 1993; Alroy *et al.*, 2008), 同时导致以腕足类占主导的古生代型

底栖生态系转变为以软体动物双壳类、腹足类等占主导的中生代型底栖生态系(Sepkoski, 1981; Hallam and Wignall, 1997; Fraiser and Bottjer, 2007b;

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Chen and Benton, 2012; Song *et al.*, 2013). 二叠纪—三叠纪之交生物大灭绝之后的生物复苏, 历时可能超过 5 个百万年 (童金南, 1997; Lehrmann *et al.*, 2006; Bottjer *et al.*, 2008), 直到中三叠世 Anisian 晚期才真正复苏起来 (Chen and Benton, 2012), 因而成为显生宙历史上跨时最长的生物迟缓复苏。然而近些年来研究表明, 不同生物门类的生物复苏是不等时、不同步的, 游泳型菊石和牙形石的复苏较早 (McGowan, 2004, 2005; Brayard *et al.*, 2006, 2009; Orchard, 2007), 底栖有孔虫在早三叠世 Smithian 早期开始复苏 (Song *et al.*, 2011), 而底栖型的双壳类、腹足类、腕足类等则直到中三叠世 Anisian 晚期才真正复苏 (陈金华, 2004; Chen *et al.*, 2005; Nützel, 2005)。从生态系角度来说, 营养结构“金字塔”底端到顶端的逐步复苏历时较长, 直到早三叠世晚期 (Spathian 期) 才重新出现了稳定、复杂的生态系 (童金南, 1997; Tong *et al.*, 2010; Chen and Benton, 2012)。此外, 在早三叠世还发生了数次小规模灭绝事件, 如 Smithian-Spathian 期之交的灭绝事件, 主要表现在游泳型菊石和牙形石类群的分异度变化上 (Galfetti *et al.*, 2007b; Orchard, 2007; Brayard *et al.*, 2009; Stanley, 2009)。

那么, 是什么原因导致了生物的迟缓复苏呢? 这可能归因于当时持续波动的高压环境 (Payne *et al.*, 2004; Fraiser and Bottjer, 2007a; Tong *et al.*, 2007; Algeo and Twitchett, 2010; Song *et al.*, 2012, 2014; Sun *et al.*, 2012; Grasby *et al.*, 2013; 左景勋等, 2013; Pietsch *et al.*, 2014)。早三叠世的“错时相”沉积 (Lehrmann, 1999; Woods *et al.*, 1999; Lehrmann *et al.*, 2001; Pruss *et al.*, 2004, 2006; Baud *et al.*, 2007; Zhao *et al.*, 2008) (如微生物岩、皱纹构造、胶结扇等) 和“缺煤” (Retallack *et al.*, 1996)、“缺礁” (Flügel and Stanley, 1984) 等沉积记录指示, 当时的海洋环境条件与前寒武纪末期生命大爆发前的海洋状态极为相似。早三叠世的碳酸盐岩无机和有机碳同位素曲线经历了多次的强烈波动, 指示当时的碳循环极为异常 (Payne *et al.*, 2004; Tong *et al.*, 2007; Meyer *et al.*, 2013), 而硫同位素与碳同位素的耦合揭示硫循环也存在异常 (Song *et al.*, 2014)。牙形石氧同位素数据表明自晚二叠世末期开始的表层海水高温一直持续到了早三叠世 Spathian 期 (Sun *et al.*, 2012; Romano *et al.*, 2013), 而牙形石微量元素数据指示早三叠世经历了多期海洋缺氧事件 (Song *et al.*, 2012)。部分研究者

通过分析不同环境因素对海洋无脊椎动物的影响, 提出早三叠世的海水高温和海洋缺氧事件共同作用于生物的迟缓复苏 (Pietsch *et al.*, 2014; Song *et al.*, 2014)。

双壳类在古、中生代地层记录中化石数量丰富, 在二叠纪—三叠纪之交遭受了中等程度的灭绝 (殷鸿福, 1983; 李玲, 1995; 方宗杰, 2004; Huang *et al.*, 2014), 随后在三叠纪初期的底栖生态系中占据绝对优势地位 (Fraiser and Bottjer, 2007b)。地区性和全球性的双壳类属级分异度演化曲线均显示双壳类经历了长时间的生物迟缓复苏, 直到中三叠世 Anisian 期才真正复苏、辐射 (陈金华等, 2003; 陈金华, 2004; Komatsu *et al.*, 2004; Posenato, 2008; Ros and Echevarria, 2011)。但是, 双壳类迟缓复苏的机制是怎么样的呢? 是受控于内因 (生物因素) 还是外因 (环境因素)? 这些问题还没有得到很好的解决。本研究拟以该段时期内全球的双壳类为研究对象, 从生态学的角度探讨二叠纪—三叠纪之交双壳类的迟缓复苏过程。

## 1 研究数据

本研究在统计文献资料及参照国际古生物学数据库 (Paleobiology Database, <http://www.paleodb.org>) 的基础上, 总结了全球范围内自晚二叠世 Changhsingian 期至中三叠世 Anisian 期双壳类属的分布时限及生活方式 (图 1)。本研究将该段时期划分为 Changhsingian 期、过渡层、Griesbachian 期、Dienerian 期、Smithian 期、Spathian 期和 Anisian 期, 其中, 过渡层代表两幕灭绝之间的时期 (Song *et al.*, 2013), 其跨越了二叠纪—三叠纪界线。双壳类的系统分类采用 Carter *et al.* (2011) 的划分方案, 将双壳类划分为 3 个亚纲, 即 Pteriomorpha, Palaeotaxodont 和 Heteroconchia 亚纲。其中, Pteriomorpha 亚纲划分为 Arcida, Myalinida, Mytilida, Ostreida, Pectinida 等 5 目, Palaeotaxodont 亚纲划分为 Nuculanida, Nuculida, Solemyida 等 3 目, Heteroconchia 亚纲划分为 Cardiida, Carditida, Hiatalida, Lucinida, Modiomorphida, Pholadida, Pholadomyida, Trigoniida 等 8 目。双壳类的生活方式可划分为 5 种, 分别是外栖固着类、外栖活动类、半内栖类、内栖浅掘穴类和内栖深掘穴类。其中, 外栖固着类包括外栖足丝固着类、外栖壳体固着类等, 而外

亚纲	目	属	外栖固着类	外栖活类	半内栖类	浅掘穴类	深掘穴类	Changhsingian	Gries.	Dien.	Smith.	Spath.	Anisian	
Heterocoenobia	Cardiida	<i>Astartopis</i>				*								
		<i>Curionia</i>				*								
		<i>Myoconcha</i>				*								
		<i>Netschajewia</i>				*								
		<i>Permophorus</i>				*								
		<i>Pseudomyoconcha</i>				*								
		<i>Tellina</i>				*		*						
	<i>Triaphorus</i>					*								
	<i>Stuechburia</i>					*								
	Carditida	<i>Astarte</i>					*							
		<i>Astartella</i>					*							
		<i>Astartellopsis</i>					*							
		<i>Cardinia</i>					*							
		<i>Coelopsis</i>					*							
		<i>Gujocardita</i>					*							
		<i>Myophoricardium</i>					*							
		<i>Myophoriopsis</i>					*							
		<i>Oriocrassatella</i>					*							
	<i>Pseudocorbula</i>					*								
	<i>Sementiconcha</i>					*								
	Hiatellida	<i>Edmondia</i>					*							
Lucinida	<i>Alula</i>					*								
	<i>Dyasmya</i>					*								
	<i>Praeundulomya</i>					*								
	<i>Sanguinolites</i>					*								
	<i>Schafhaeutlia</i>					*								
	<i>Sedgwickia</i>					*								
	<i>Sinbadiella</i>					*								
<i>Unicardium</i>					*									
<i>Wilkingia</i>					*									
Megalodontida	<i>Physocardia</i>					*								
Modiomorphida	<i>Taimyria</i>	*				*								
Pholadida	<i>Myonia</i>					*								
	<i>Pachymyonia</i>					*								
	<i>Pleuromya</i>					*								
	<i>Vacunella</i>					*								
	<i>Arcomya</i>					*								
Pholadomyida	<i>Astartila</i>					*								
	<i>Chaenomya</i>					*								
	<i>Megadesmus</i>					*								
	<i>Ochotomya</i>					*								
	<i>Pleurikodonta</i>					*								
<i>Pyramus</i>					*									
Trigoniida	<i>Actinodontophora</i>					*								
	<i>Costatoria</i>					*								
	<i>Elegantinia</i>					*								
	<i>Eoastarte</i>					*								
	<i>Guizhoumyophoria</i>					*								
	<i>Heminajas</i>					*								
	<i>Leviconcha</i>					*								
	<i>Lyroschizodus</i>					*								
	<i>Neoschizodus</i>					*								
	<i>Paraschizodus</i>					*								
	<i>Schizodus</i>					*								
	<i>Trigonodus</i>					*								
	<i>Unionites</i>					*								
Nuculanida	<i>Dacryomya</i>					*								
	<i>Glyptoleda</i>					*								
	<i>Nuculana</i>					*								
	<i>Palaeoneilo</i>					*								
	<i>Phaenodesmia</i>					*								
	<i>Phestia</i>					*								
	<i>Prosoleptus</i>					*								
<i>Polidevcia</i>					*									
Nuculida	<i>Nuculavus</i>					*								
	<i>Nuculoma</i>					*								
	<i>Nuculopsis</i>					*								
	<i>Palaeonucula</i>					*								
<i>Trigonucula</i>					*									
Solemyida	<i>Janeia</i>					*								
<i>Solemya</i>						*								
Arcida	<i>Elegantarca</i>					*								
	<i>Eophilobryoidella</i>					*								
Myalinida	<i>Grammatodon</i>					*								
	<i>Parallelodon</i>					*								
	<i>Atomodesma</i>					*								
	<i>Evenia</i>					*								
	<i>Intomodesma</i>					*								
	<i>Leidapoconcha</i>					*								
	<i>Liebea</i>					*								
	<i>Maitaia</i>					*								
	<i>Myalina</i>					*								
	<i>Myalinella</i>					*								
	<i>Najadites</i>					*								
	<i>Orthomyalina</i>					*								
	<i>Promyalina</i>					*								
	<i>Promysidiella</i>					*								
	<i>Qingyaniola</i>					*								
<i>Ramonalina</i>					*									
<i>Septimyalina</i>					*									
<i>Trabeculatia</i>					*									
<i>Waijiaoella</i>					*									
Mytilida	<i>Botulopsis</i>		*											
	<i>Falcimytilus</i>		*											

图 1a 二叠纪—三叠纪之交双壳类属系统分类、生活方式和时限分布,灰色区域代表过渡层  
 Fig.1a Taxonomy, life styles, and temporal distribution of bivalves during the Permian-Triassic  
 Gries. 为 Griesbachian; Dien. 为 Dienerian; Smith. 为 Smithian; Spath. 为 Spathian

亚纲	目	属	外栖固着类	外栖活动类	半内栖类	浅掘穴类	深掘穴类	Changhsingian	Gries.	Dien.	Smith.	Spath.	Anisian	
Pteriomorpha	Mytilida	<i>Joannia</i>	*											
		<i>Lithodomina</i>	*											
		<i>Modiolus</i>			*									
		<i>Mysidiella</i>	*											
		<i>Mytilus</i>	*											
		<i>Promytilus</i>			*									
		<i>Protopsis</i>	*											
	<i>Septifer</i>	*												
	Ostreida	<i>Arcavicula</i>	*											
		<i>Atrina</i>	*			*								
		<i>Avicula</i>	*											
		<i>Aviculopinna</i>			*									
		<i>Bakevellia</i>			*									
		<i>Bostrea</i>	*											
		<i>Cassianella</i>	*											
		<i>Cultrioopsis</i>	*											
		<i>Daonella</i>	*											
		<i>Enantiostreon</i>	*											
		<i>Ensipteria</i>	*											
		<i>Enteropleura</i>	*											
		<i>Gervillaria</i>	*											
		<i>Hoernesia</i>	*											
		<i>Isognomon</i>	*											
		<i>Langsonella</i>	*											
		<i>Leptodesma</i>	*											
		<i>Lopha</i>	*											
		<i>Permoperna</i>	*											
		<i>Pinna</i>	*			*								
		<i>Posidonia</i>	*											
		<i>Preria</i>	*											
		<i>Pteronites</i>	*			*								
	<i>Ptychopteria</i>	*												
	<i>Tambanella</i>	*												
	<i>Towapteria</i>	*												
	Pectinida	<i>Acanthopecten</i>	*											
		<i>Annuliconcha</i>	*											
		<i>Anomia</i>	*											
		<i>Anshunpecten</i>	*											
		<i>Aviculopecten</i>	*											
		<i>Asoella</i>	*											
		<i>Avichlamys</i>	*											
		<i>Chlamys</i>	*											
		<i>Claraia</i>	*											
		<i>Clavicosta</i>	*											
		<i>Corrugospecten</i>	*											
		<i>Crenipecten</i>	*											
		<i>Crittidentia</i>	*											
		<i>Cyrtorostra</i>	*											
		<i>Dimorphoconcha</i>	*											
		<i>Entolium</i>	*		*									
<i>Entalioides</i>		*		*										
<i>Eopecten</i>		*		*										
<i>Etalia</i>		*												
<i>Etheripecten</i>		*												
<i>Euchondria</i>		*												
<i>Eumorphotis</i>		*												
<i>Fasciculiconcha</i>		*												
<i>Girtypecten</i>		*												
<i>Guichiella</i>		*												
<i>Guizhoupecten</i>		*												
<i>Hayasakapecten</i>		*												
<i>Heteropecten</i>		*												
<i>Hunanopecten</i>		*												
<i>Janopecten</i>		*			*									
<i>Leptochondria</i>		*												
<i>Lima</i>		*												
<i>Limatula</i>		*		*										
<i>Limea</i>		*		*										
<i>Limipecten</i>		*												
<i>Meleagrinnella</i>		*												
<i>Mysidioptera</i>		*												
<i>Neomorphotis</i>		*												
<i>Noetlingiconcha</i>		*												
<i>Ochotochlamys</i>		*			*									
<i>Ornithopecten</i>		*												
<i>Palaeolima</i>		*												
<i>Paradoxipecten</i>		*												
<i>Pegmavalvula</i>	*													
<i>Periclaraia</i>	*													
<i>Pernopecten</i>	*			*										
<i>Placunopsis</i>	*													
<i>Plagiostoma</i>	*													
<i>Pleuronectites</i>	*			*										
<i>Plicatula</i>	*													
<i>Praechlamys</i>	*													
<i>Protostrea</i>	*													
<i>Pseudomonotis</i>	*													
<i>Pseudoplacunopsis</i>	*													
<i>Scythenolium</i>	*													
<i>Serania</i>	*													
<i>Streblochondria</i>	*			*										
<i>Streblopteria</i>	*													
<i>Terquemia</i>	*													
<i>Xinanopecten</i>	*			*										

图 1b 二叠纪—三叠纪之交双壳类属系统分类、生活方式和时限分布,灰色区域代表过渡层  
Fig.1b Taxonomy, life styles, and temporal distribution of bivalves during the Permian-Triassic

Gries.为 Griesbachian;Dien.为 Dienerian;Smith.为 Smithian;Spath.为 Spathian

栖活动类包括假漂游类和游泳类。

## 2 二叠纪—三叠纪之交双壳类分异度的演化

晚二叠世大灭绝前的 Changhsingian 期共有双壳类 105 属,在第一幕灭绝中有 57 属灭绝,灭绝率为 54.3%;第一幕灭绝后的过渡层有 22 属,其中含 5 个新生属,过渡层末期有 3 个属灭绝,第二幕灭绝率为 13.6%;第二幕灭绝后的 Griesbachian 期有 40 属,其中含 10 个新生属,Griesbachian 期末有 3 个属灭绝,灭绝率为 7.5%;Dienerian 期有 30 属,其中含 4 个新生属,Dienerian 期末有 1 个属灭绝,灭绝率为 3.3%;Smithian 期有 43 属,其中含 7 个新生属,Smithian 期末有 6 个属灭绝,灭绝率为 14.0%;Spathian 期有 58 属,其中含 10 个新生属,Spathian 期末有 12 个属灭绝,灭绝率为 20.7%;Anisian 期有 95 属,其中含 39 个新生属。

### 2.1 各亚纲的属级分异度变化

Heteroconchia 亚纲:晚二叠世大灭绝之前有 31 属,在第一幕灭绝中有 23 属灭绝,灭绝率为 74.2%;第一幕灭绝后的过渡层有 4 属,其中有 1 个新生属,没有双壳类属灭绝;第二幕灭绝后的 Griesbachian 期有 12 属,其中含 5 个新生属,Griesbachian 期末有 1 个属灭绝,灭绝率为 8.3%;Dienerian 期有 10 属,其中含 3 个新生属,Dienerian 期末有 1 个属灭绝,灭绝率为 10.0%;Smithian 期有 15 属,其中含 6 个新生属,Smithian 期末有 1 个属灭绝,灭绝率为 6.7%;Spathian 期有 19 属,其中

含 2 个新生属,Spathian 期末有 3 个属灭绝,灭绝率为 15.8%;Anisian 期有 23 属,其中含 6 个新属(图 2)。

Palaeotaxodonta 亚纲:晚二叠世大灭绝之前有 10 属,在第一幕灭绝中有 2 属灭绝,灭绝率为 20%;第一幕灭绝后的过渡层有 3 属,过渡层末期有 1 个属灭绝,第二幕灭绝率为 33.3%;第二幕灭绝后的 Griesbachian 期有 3 属,没有新生属和灭绝属;Dienerian 期有 2 属,没有新生属和灭绝属;Smithian 期有 4 属,其中含 1 个新属,Smithian 期末有 1 属灭绝,灭绝率为 25.0%;Spathian 期有 4 属,其中含 1 个新属,没有灭绝属;Anisian 期有 9 属,其中含 2 个新属(图 2)。

Pteriomorphia 亚纲:晚二叠世大灭绝之前有 64 属,在第一幕灭绝中有 32 属灭绝,灭绝率为 50.0%;第一幕灭绝后的过渡层有 15 属,其中含 4 个新生属,过渡层末期有 2 个属灭绝,第二幕灭绝率为 13.3%;第二幕灭绝后的 Griesbachian 期有 25 属,其中含 5 个新生属,Griesbachian 期末有 2 个属灭绝,灭绝率为 8.0%;Dienerian 期有 18 属,其中含 1 个新生属,Dienerian 期末没有灭绝;Smithian 期有 24 属,没有新生分子,Smithian 期末有 4 个属灭绝,灭绝率为 16.7%;Spathian 期有 35 属,其中含 7 个新属,Spathian 期末有 9 个属灭绝,灭绝率为 25.7%;Anisian 期有 63 属,其中含 31 个新属(图 2)。

### 2.2 各生活方式的属级分异度变化

外栖固着类:晚二叠世大灭绝之前有 42 属,在第一幕灭绝中有 22 属灭绝,灭绝率是 52.4%;第一

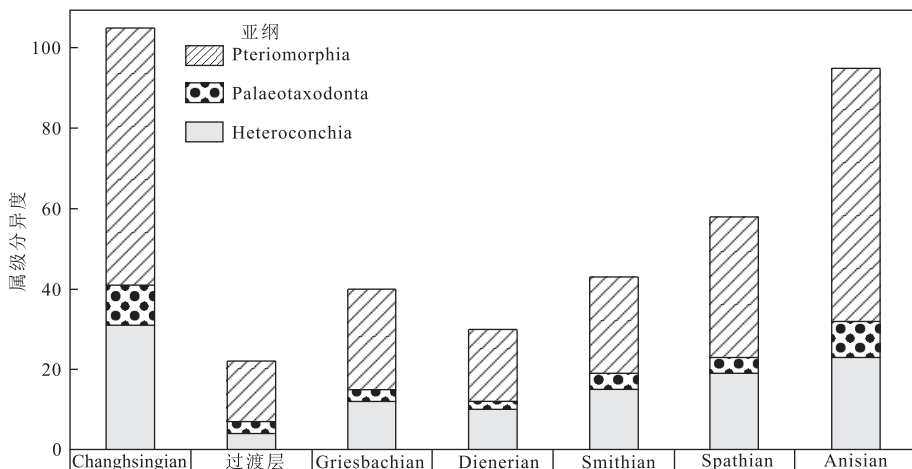


图 2 晚二叠世末期至中三叠世 Anisian 期不同亚纲双壳类属级分异度

Fig.2 Genus diversity of different subclasses among bivalves from Late Permian Changhsingian to Middle Triassic Anisian

幕灭绝后的过渡层有 12 属,其中含 4 个新生属,过渡层末期有 2 个属灭绝,第二幕灭绝率为 16.7%;第二幕灭绝后的 Griesbachian 期有 14 属,其中含 2 个新属,Griesbachian 期末有 2 个属灭绝,灭绝率是 14.3%;Dienerian 期有 9 属,无新生属,Dienerian 期末没有灭绝;Smithian 期有 12 属,Smithian 期末有 2 个属灭绝,灭绝率是 16.7%;Spathian 期有 21 属,其中含 7 个新属,Spathian 期末有 4 个属灭绝,灭绝率是 19.0%;Anisian 期有 42 属,其中含 19 个新属(图 3).

外栖活动类:晚二叠世大灭绝之前有 6 属,在第一幕灭绝中有 1 个属灭绝,灭绝率是 16.7%;第一幕灭绝后的过渡层有 1 属,没有新生和灭绝分子;第二幕灭绝后的 Griesbachian 期有 4 属,其中含 2 个新生属,没有灭绝分子;Dienerian 期有 2 属,其中含 1 个新属,无灭绝分子;Smithian 期有 5 属,Smithian 期末有 1 个属灭绝,灭绝率是 20.0%;Spathian 期有 6 属,Spathian 期末有 2 个属灭绝,灭绝率是 33.3%;Anisian 期有 9 属,其中含 4 个新属(图 3).

半内栖类:晚二叠世大灭绝之前有 5 属,在第一幕灭绝中有 2 个属灭绝,灭绝率是 40.0%;第一幕灭绝后的过渡层有 1 属,没有新生和灭绝分子;第二幕灭绝后的 Griesbachian 期、Dienerian 期、Smithian 期各有 2 属,均没有新生和灭绝分子;Spathian 期有 4 属,没有新生分子,Spathian 期末有 1 个属灭绝,灭绝率是 25.0%;Anisian 期有 5 属,其中含 2 个新属(图 3).

内栖浅掘穴类:晚二叠世大灭绝之前有 42 个属,在第一幕灭绝中有 23 个属灭绝,灭绝率是

54.8%;第一幕灭绝后的过渡层有 8 属,其中含 1 个新生属,过渡层末期有 1 个属灭绝,第二幕灭绝的灭绝率为 12.5%;第二幕灭绝后的 Griesbachian 期有 19 属,其中含 5 个新生属,Griesbachian 期末有 1 个属灭绝,灭绝率是 5.3%;Dienerian 期有 17 属,其中含 3 个新生属,Dienerian 期末有 1 个属灭绝,灭绝率是 5.9%;Smithian 期有 22 属,其中含 5 个新属,Smithian 期末有 2 个属灭绝,灭绝率是 9.1%;Spathian 期有 25 属,其中含 2 个新属,Spathian 期末有 5 个属灭绝,灭绝率是 20.0%;Anisian 期有 36 属,其中含 13 个新属(图 3).

内栖深掘穴类:晚二叠世大灭绝之前有 10 属,在第一幕灭绝中有 9 个属灭绝,灭绝率是 90.0%;第一幕灭绝后的过渡层和 Dienerian 期未见报道;Griesbachian 期仅有 1 个新属,未灭绝;Smithian 期有 2 个新属,Smithian 期末没有灭绝;Spathian 期有 2 属,其中含 1 个新属,Spathian 期末没有灭绝;Anisian 期有 3 属(图 3).

### 3 早三叠世双壳类生物面貌

多种术语被用来描述灭绝—残存—复苏期的生物,如灾难种(disaster taxa)、长期残存种(long-term survivor)、避难种(Lazarus taxa)、孑遗种(holdover species)、危机先驱分子(crisis progenitor)、新生种(new species)等(Harries *et al.*, 1996; Kauffman and Harries, 1996; 戎嘉余等, 1996),其中,描述二叠纪类型的术语有长期残存种、避难种、孑遗种等(表 1).从壳体形态上看,早三叠世占主导

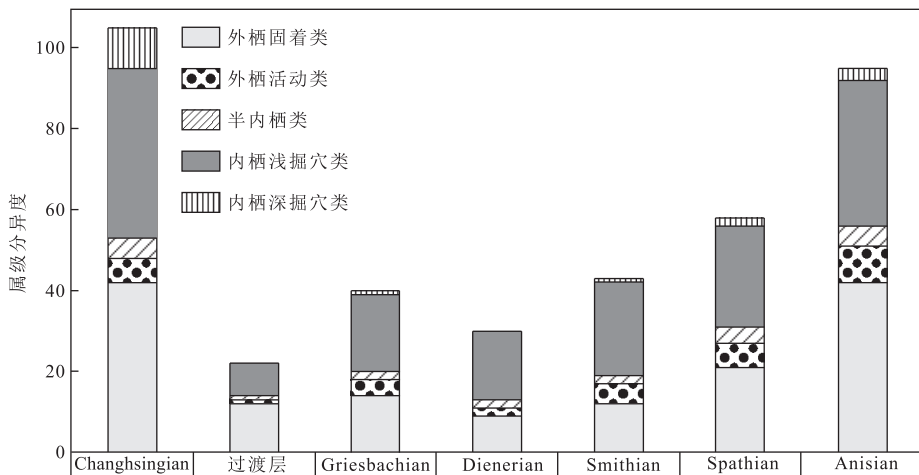


图 3 晚二叠世末期至中三叠世 Anisian 期不同生活方式双壳类的属级分异度

Fig.3 Genus diversity of bivalves with different life styles from Late Permian Changhsingian to Middle Triassic Anisian

表 1 晚二叠世末生物大灭绝后的残存双壳类属

Table 1 Survival genera among bivalves following the End-Permian mass extinction

残存的二叠纪双壳类	属分异度	属名
长期残存属	18	<i>Myoconcha</i> , <i>Permophorus</i> , <i>Costatoria</i> , <i>Neoschizodus</i> , <i>Unionites</i> , <i>Palaeoneilo</i> , <i>Palaeonucula</i> , <i>Myalina</i> , <i>Modiolus</i> , <i>Mytilus</i> , <i>Bakevellia</i> , <i>Posidonia</i> , <i>Pteria</i> , <i>Chlamys</i> , <i>Entolium</i> , <i>Leptochondria</i> , <i>Lima</i> , <i>Palaeolima</i>
孑遗属	18	<i>Stuchburia</i> , <i>Astartella</i> , <i>Megadesmus</i> , <i>Phestia</i> , <i>Nuculopsis</i> , <i>Maitaia</i> , <i>Myalinella</i> , <i>Promyalina</i> , <i>Promytilus</i> , <i>Leptodesma</i> , <i>Towapteria</i> , <i>Claraia</i> , <i>Etheripecten</i> , <i>Guichiella</i> , <i>Limipecten</i> , <i>Pegmavalvula</i> , <i>Pernopecten</i> , <i>Streblochondria</i>
避难属	19	<i>Tellina</i> , <i>Astarte</i> , <i>Glyptoleda</i> , <i>Nuculana</i> , <i>Phaenodesmia</i> , <i>Polidevcia</i> , <i>Solemya</i> , <i>Grammatodon</i> , <i>Parallelodon</i> , <i>Septifer</i> , <i>Avicula</i> , <i>Enantiostreon</i> , <i>Isognomon</i> , <i>Lopha</i> , <i>Pinna</i> , <i>Anomia</i> , <i>Limatula</i> , <i>Plagios-toma</i> , <i>Pseudomonotis</i>

注:下划线表示未在中三叠世 Anisian 期出现。

的双壳类属属于古生代的类型 (Fraiser and Bot-tjer, 2007b)。本研究表明,二叠纪的残存属占据了整个早三叠世双壳类属的主导地位,但其所占比例逐渐降低。过渡层、Griesbachian 期和 Dienerian 期,二叠纪属所占比例较高,分别为 77.3%、65% 和 67%,到了 Smithian 期和 Spathian 期,二叠纪属所占比例降低,分别为 51.2% 和 50.0%,Anisian 期二叠纪的属仅占 33.7%,指示双壳类的逐步复苏过程。另外,与二叠纪有关的避难属 (Lazarus taxa) 则有 19 属,大部分直到中一晚三叠世才重新出现。避难属反映了地史时期化石记录的不完备性,其最初被认为是迁移到了不为人知的避难所中。近年来,多被归因于生物居群数量少而未能保存为化石 (Twitchett, 2001),或者由于个体较小而被忽略 (Hautmann *et al.*, 2011)。

## 4 讨论

在二叠纪—三叠纪之交生物大灭绝的第一幕灭绝中,全球双壳类遭受了中等程度的属级灭绝,灭绝率为 54.3%,这与华南地区的 67.2% (李玲, 1995) 或 53.4% (方宗杰, 2004) 的值相比差异不显著 ( $Z$  检验,  $p > 0.05$ )。不同亚纲双壳类的灭绝率也有所差异, Heteroconchia 亚纲为 74.2%, Palaeotaxodonta 亚纲为 20.0%, Pteriomorphia 亚纲为 50.0%, 其中 Palaeotaxodonta 亚纲比其他两亚纲低 (图 4)。在早三叠世初期的第二幕灭绝中,双壳类表现出了 13.6% 的属级灭绝率,因其接近于背景值,曾被认为是 Griesbachian 期早—中期之间的次级灭绝 (陈金华, 2004),也可能仅为背景灭绝 (Huang *et al.*, 2014)。

经历了二叠纪—三叠纪之交的生物灭绝后,双

壳类的分异度在 Griesbachian 期和 Dienerian 期缓慢增长,二叠纪残存类型占据了主导地位。Griesbachian 期以 *Claraia* 为代表的机会分子广泛分布于各个相区 (殷鸿福, 1983),但是双壳类在环境好转的孤立碳酸盐台地相区表现出了较早的复苏 (Hautmann *et al.*, 2011)。笔者发现 Dienerian 期的双壳类分异度低于 Griesbachian 期,但是只有 1 个属灭绝,灭绝率只有 3.3%,双壳类面貌发生了显著的变化,即由以 *Claraia* 主导的群落转变为了以 *Eumorphotis* 占主导的群落,这可能与该时期海水温度转凉 (Sun *et al.*, 2012; Romano *et al.*, 2013)、海洋缺氧程度降低等环境好转 (Song *et al.*, 2012; Grasby *et al.*, 2013) 有关 (图 4)。

Smithian-Spathian 期之交的生物灭绝事件得到了较多的关注 (Hallam and Wignall, 1997; Galfetti *et al.*, 2007b),牙形石和菊石表现出显著的灭绝 (Orchard, 2007; Brayard *et al.*, 2009; Stanley, 2009),陆相植被优势分子也发生了完全转变 (Galfetti *et al.*, 2007b; Hermann *et al.*, 2012; Saito *et al.*, 2013),同时伴随着全球海水温度的转变 (Sun *et al.*, 2012; Romano *et al.*, 2013)。双壳类曾被认为在这次事件中遭受了一次小的灭绝, *Claraia* 属即在该次事件中灭绝, *Eumorphotis* 属则遭到重创 (Hallam and Wignall, 1997)。本研究表明双壳类属遭受了较低的灭绝 (14.0%),灭绝程度相当于二叠纪—三叠纪之交生物灭绝的第二幕灭绝 (13.6%),外栖活动类、外栖固着类和内栖浅掘穴类的灭绝率分别是 20.0%、16.7% 和 9.1%,表栖类的灭绝率 (17.6%) 高于内栖类 (7.7%)。双壳类的这种灭绝表现可能与 Smithian 晚期的海水高温、海洋缺氧等综合环境因素 (图 4) 有关,其中海洋缺氧更影响内栖类,而海水高温更影响外栖类,考虑到外栖双壳类和

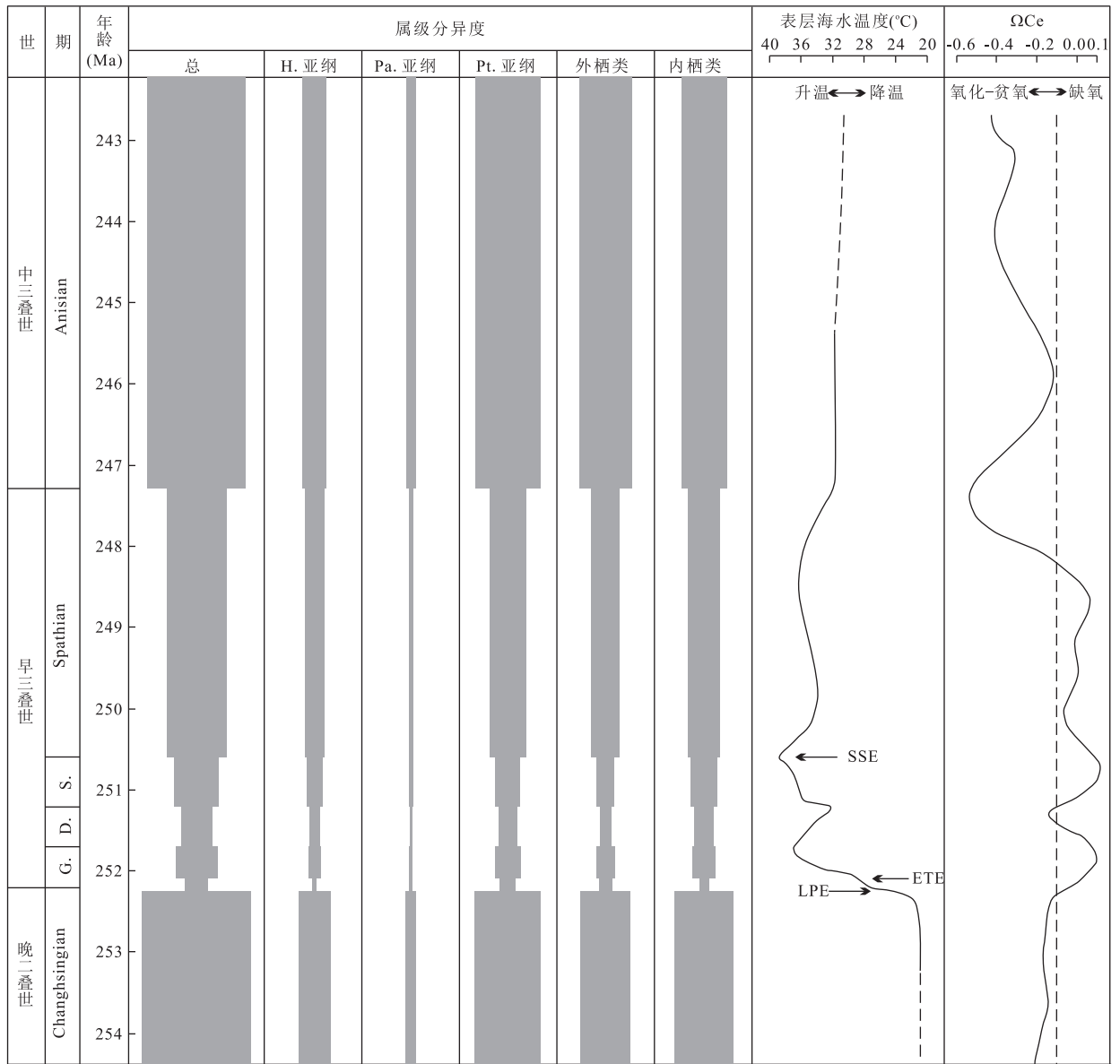


图 4 二叠纪—三叠纪之交双壳类分异度演化与海洋环境变化对比

Fig.4 Correlation of bivalve diversity with marine environments during the Permian-Triassic

G.为 Griesbachian;D.为 Dienerian;S.为 Smithian;H.为 Heteroconchia;Pa.为 Palaeotaxodonta;Pt.为 Pteriomorphia;LPE 为 Latest Permian Extinction event;ETE 为 Earliest Triassic Extinction event;SSE 为 Smithian—Spathian Extinction event;表层海水温度数据引自 Joachimski *et al.*(2012)和 Sun *et al.*(2012);牙形石 Ce 异常数据引自 Song *et al.*(2012);年龄数据引自 Lehrmann *et al.*(2006);Ovtcharova *et al.*(2006);Galfetti *et al.*(2007a)和 Shen *et al.*(2011)

内栖双壳类的灭绝率差异并不显著( $p > 0.05$ ),缺氧和高温可能共同导致了双壳类的灭绝。

双壳类在早三叠世末期表现出了较为显著的灭绝,灭绝率可达到 20.7%,其中 Palaeotaxodonta 亚纲未遭受灭绝,Heteroconchia 亚纲和 Pteriomorphia 亚纲的灭绝率分别为 15.8%和 25.7%( $p > 0.05$ )(图 4)。值得指出的是,除内栖深掘穴类外,其他生活方式的双壳类均表现出了显著的灭绝。与此同时,牙形石和菊石在晚 Spathian 期表现出了显著的分异度

降低(Brayard *et al.*, 2009; Orchard, 2007)。在该次事件中,双壳类并没有表现出生活方式上的选择性灭绝,这次事件的原因仍然值得深入思考。

综上所述,自晚二叠世末期生物大灭绝后,双壳类在早三叠世的灭绝率仅相当于背景值,未遭受明显的灭绝,这可能与早三叠世长期的异常环境因素(如海洋缺氧、海水高温等)有关。现代双壳类的模拟实验表明,内栖类和外栖类双壳类均可以表现出对海水高温、贫氧—缺氧/硫化、高二氧化碳含量及海



洋酸化等异常环境的显著的抵抗和适应(Wilson and Elkaim, 1991; Wang and Widdows, 1993; Sobral and Widdows, 1997; Hicks and McMahon, 2002; Laudien *et al.*, 2002; Gazeau *et al.*, 2010; Talmage and Gobler, 2010; Thomsen and Melzner, 2010; Navarro *et al.*, 2013)。或许正是由于这种较高的适应能力,使得双壳类的演化要慢于游泳类别的菊石和牙形石,从而在早三叠世多次的环境事件中未遭受大的损失,同时其复苏过程变得极其缓慢。

## 5 结论

二叠纪—三叠纪之交软体动物双壳类分布广泛,化石数量丰富,全球范围内属级分异度演化动力学揭示的灭绝—残存—复苏过程可以为该时期生物与环境协同演化研究提供实证。

(1) 不同亚纲(Pteriomorphia、Palaeotaxodont和 Heteroconchia 亚纲)和不同生活方式(外栖活动类、外栖固着类、半内栖类、内栖浅掘穴类和内栖深掘穴类)的双壳类表现出一致的演化规律,属级分异度在二叠纪—三叠纪之交生物大灭绝中显著降低,直到中三叠世 Anisian 期才恢复到大灭绝之前的水平,清晰地显示出其灭绝—复苏过程。

(2) 包括长期残存分子、孑遗分子和避难分子在内的二叠纪残存类型所占的比例逐步下降,从过渡层的 77.3% 降低到了中三叠世 Anisian 期的 33.7%,反映了双壳类的缓慢复苏过程。

(3) 双壳类在整个早三叠世遭受了较低的背景灭绝,其在多次次级灭绝事件中均未遭受大的损失,指示双壳类的迟缓复苏可能与长时期的海洋缺氧和海水高温等综合环境因素有关,随着海洋环境的逐步好转,才进入较快的复苏阶段。

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