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二叠纪末生物大灭绝事件研究进展综述

侯海海[1)]，何倩[1)]，刘书君[2)]，高莲凤[1)]，王崇敬[1)]

1)辽宁工程技术大学矿业学院，辽宁阜新，123000；

2)太原理工大学地球科学与测绘工程学院，太原，030021

内容提要：二叠纪末生物大灭绝(The end-Permian mass extinction，EPME)作为全球地质历史时期最大的灭绝事件，导致了约75%的陆生物种和约81%的海生物种的灭绝，全球范围内的陆生植被、昆虫和陆地四足脊椎动物历经了快速和毁灭性的打击，显著灭绝的海洋物种包括蜓 、三叶虫、棘皮动物和珊瑚等，大部分灭绝或者被替代的物种包括腕足类、双壳类、放射虫、有孔虫和菊石等，EPME 生物灭绝具有区域性、选择性和阶段性等特点。西伯利亚大火成岩省(the Siberian large ignous province, SLIP)的爆发与 EPME 时间高度耦合，SLIP 及其连带的一系列次生事件被认为是 EPME 的主要驱动力，同时也是滞缓生物复苏的主要因素。海洋缺氧、海水升温等部分次生事件的持续时间、强度和区域分布仍存争议，且单一次生事件不能独立支撑 EPME，EPME 是多个因素综合叠加作用的结果。SLIP 爆发促使埋藏在内陆盆地和大陆架沉积物中的温室气体向大气圈大量释放，全球气候快速变暖导致陆地危机先行发生，极端干旱天气促进了森林野火的频发和陆地生态系统的崩溃；大陆风化加剧使得大量碎屑注入海洋造成严重的富营养化、海底生物缺氧、海洋酸化和海洋古生产力紊乱等，致使海洋灭绝事件的发生，陆地灭绝的滞后性导致陆地危机的结束时间晚于海洋灭绝事件。二叠纪末全球性的环境突变对地球生态系统产生了巨大的影响，通过综述 EPME 演变过程，深入探讨引起生物大灭绝的原因，对了解二叠纪末全球生态系统崩溃和预测今后类似地质事件的发生具有重要意义。

关键词：生物大灭绝；二叠纪—三叠纪之交；西伯利亚火成岩省；古环境演化

二叠纪末全球存在两次独立的大灭绝事件(Jin Yugan et al., 1994; Stanley and Yang Xiangling, 1994)，一次发生在瓜德鲁普世末期(约 260 Ma)；另一次始于 251.941 Ma，结束于 251.880 Ma(Burgess et al., 2014)，跨越了二叠纪—三叠纪之交(Permain—Triassic boundary，PTB)，称为二叠纪末生物大灭绝事件(End-Permian mass extinction，EPME)。EPME 在显生宙地质历史时期的 5 次生物大灭绝事件中当属最为严重(Jin Yugan et al.，2000；Shen Shuzhong et al.，2011；Song Haijun et al.，2021a)，在 PTB 处约有 81%的海生物种和 75%的陆生物种消失(Stanley and Yang Xiangling，1994；沈树忠和张华，2017；Fan Junxuan et al.，2020；Li Menghan et al.，2021；Dal Corso et al，2022)，显著灭绝的物种包括蜓 、三叶虫、棘皮动物和珊瑚等，大部分灭绝或者被替代的物种包括腕足类、双壳类、放射虫、有孔虫和菊石等(He Weihong et al.，2015；Shen Shuzhong et al.，2019；Liu Xiaokang et al.，2020；Dal Corso et al，2022)。在此次大灭绝事件中，陆地和海洋生态系统都经历了异常缓慢和曲折的复苏过程(Josefina et al.，2021；Saito et al.，2023)，直到中三叠世早期海洋生态系统才繁盛如初(Zhao Xiangdong et al.，2020)。晚二叠世—早三叠世作为最典型的生物—环境协同演化案例，一直是国内外学者研究的热点。大量研究表明二叠纪末生物大灭绝是一次全球范围内的突发性灾变事件，随着研究精度的提升，其发生的持续时间也越来越精确，从大约 10 Ma(Sepkoski，1984)、大约 0.7 Ma(Jin Yugan et al.，2000)、大约 0.2 Ma(Shen Shuzhong et al.，2011)到 61 ka 左右(Burgess et al.，2014)，最新研究认为整个灭绝过程不超过 30 ka(Shen Shuzhong et al.，2019；沈树忠和张华，2017)。EPME 主要包括单幕

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作者简介：侯海海，男，1986 年生，博士，教授，主要从事“含煤岩系沉积学”教学和科研工作；Email：houhaihai@lntu.edu.cn。

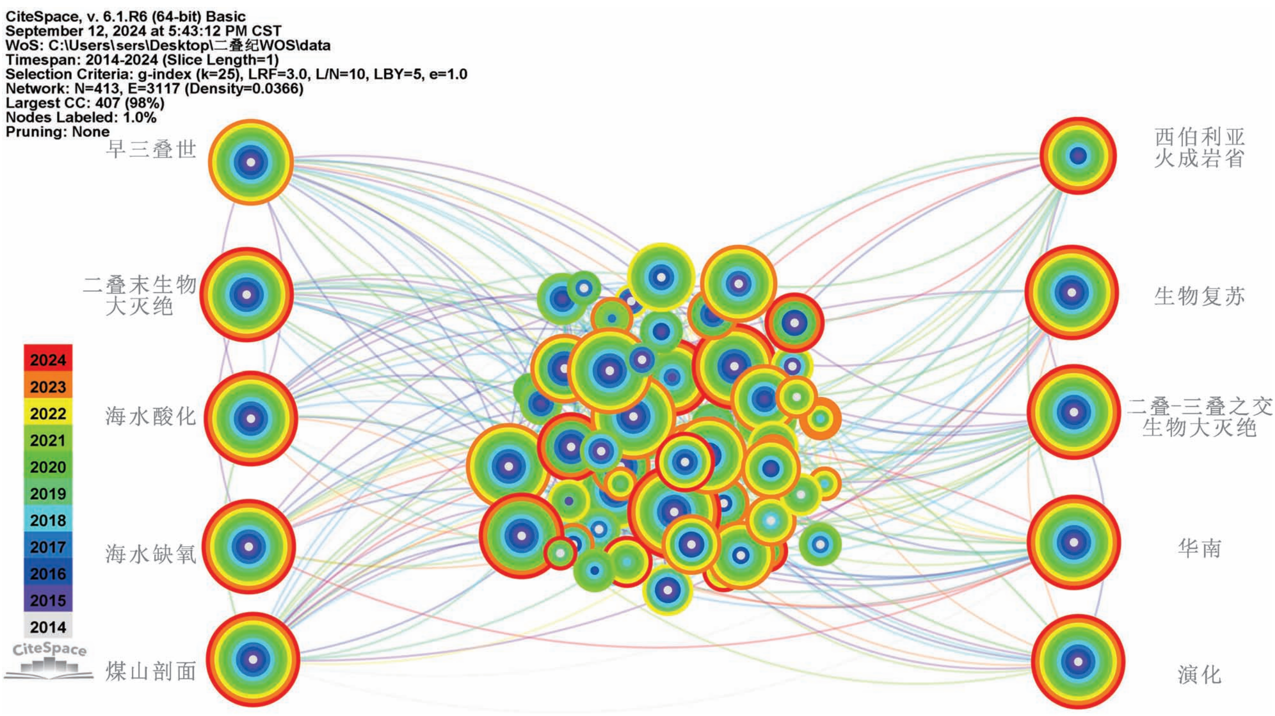

图 1 二叠纪末生物大灭绝事件关键词聚集图谱与发文时间演变图，节点代表关键词数量，两节点之间线条代表关联性，不同颜色的圆环代表图例中对应年份及发文量

Fig. 1 Keyword co-occurrence map and publication time trend of the end-Permian mass extinction event, the nodes represent the number of keywords, the lines between the two nodes represent the correlation, and the rings of different colors represent the corresponding yearand the number of publications in the legend

式、主幕式和两幕式 3 种灭绝形式，其中单幕式观点认为，对于栖息地狭窄且生理缓冲能力差的生物（如浅水台地相有孔虫）往往表现为单幕式灭绝（赵俊杰等，2022），其灭绝层位对应于全球 PTB 煤山剖面的 24e 层顶部至 25 层（Yin Hongfu et al.，2001）；主幕式观点表明生物灭绝是一个短期又持续的过程，从煤山牙形石 *Clarkina meishanensis* 带开始，一直持续到 *Isarcicella staesche* 带，分别对应于煤山剖面 25 层底部至 28 层顶部（Shen Shuzhong et al.，2011）；两幕式的观点认为，栖息地相对宽广、生理缓冲能力较强的生物需要经历两波灭绝脉冲才能完全消亡，此外部分依靠避难所得以幸存的生物往往也需要经历两波灭绝脉冲才能完全消亡（Grauvogel and Ash，2005；Shu Wenchao et al.，2023），这些生物的化石消失带主要集中在煤山剖面 25 层和 28 层这两个含有火山灰的层位，即 *Clarkina meishanensis* 带和 *Isarcicella staesche* 带（Yin Hongfu et al.，2007；Song Haijun et al.，2013）。

“二叠纪—三叠纪之交生物大灭绝”近年来受到全球学者的高度关注，已发表论文中出现的高频词汇包括西伯利亚火成岩省、海水酸化、海水缺氧、早三叠世、二叠纪末生物大灭绝、生物复苏、煤山剖面、华南等（图 1）。众多学者对这次灾难性事件的发生机制进行了大量探索和研究，研究剖面遍布全球，包括中国藏南、湖北峡口、浙江煤山、四川朝天、贵州罗甸、织金剖面、意大利 Bulla 剖面、伊朗 Abadeh 和 Kuh-e-Ali Bashi 剖面、印度 Guryul 峡谷、澳大利亚 Eveleigh 和 Bunnererong 剖面、加拿大 Buchanan 等等（图 2），但时至今日生物大灭绝的原因还未形成统一认识。目前，普遍认为持续的火山活动是 PTB 生物环境变迁的主导原因，同时期的西伯利亚大火成岩省估计喷发体积达 $3\times10^6\sim4\times10^6$ km^3，是地质历史上规模最大的陆内火山活动。最近高精度 U-Pb 放射性年龄显示西伯利亚火山 1/3 的岩浆在生物绝灭期间及之前喷发，其作用时间与生物灭绝高度重叠并具有显著相关性（Cui Ying et al.，2021；Saito et al.，2023；Shen Jun et al.，2023）。因此，由西伯利亚大火成岩省引发的一系列环境扰动被认为最可能是造成 PTB 生物灭绝的元凶（Rampino et al.，2020；万俊雨等，2023；Allen et

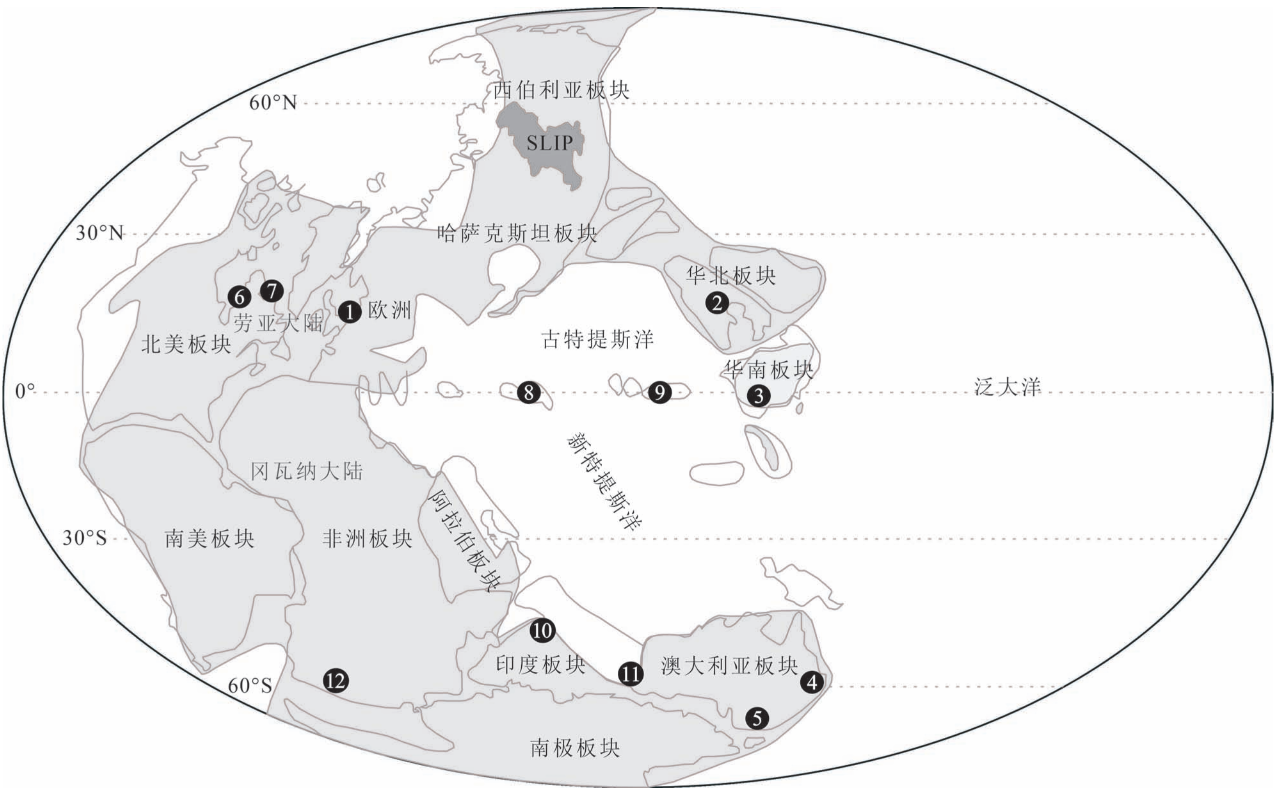

图 2 二叠纪—三叠纪之交(约 251 Ma)全球古地理重建、西伯利亚大火成岩省范围及全球剖面地点分布(据 Chu Daoliang et al. ,2021 修改)

Fig. 2 Global paleogeographic reconstruction, SLIP range and global profile location distribution at the Permian—Triassic intersection (about 251 Ma) (modified after Chu Daoliang et al. ,2021)

1—意大利 Bulla;2—华北板块:陕西铜川、河南三门峡、河南禹州;3—华南板块:湖北峡口、浙江煤山、四川朝天、贵州罗甸、贵州织金;4—澳大利亚 Eveleigh;5—澳大利亚 Bunnererong;6—加拿大 Buchanan;7—东格陵兰盆地;8—伊朗 Abadeh,Kuh-e-Ali Bashi 剖面;9—中国藏南;10—印度 Guryul 峡谷;11—澳大利亚 Perth 盆地;12—南非 Karoo 盆地

1—Bulla, Italy; 2—North China Plate: Tongchuan in Shaanxi, Sanmenxia in Henan, Yuzhou in Henan; 3—South China Plate: Xiakou in Hubei, Meishan in Zhejiang, Chaotian in Sichuan, Luodian in Guizhou, Zhijin in Guizhou; 4—Eveleigh, Australia; 5—Bunnererong, Australia; 6—Buchanan, Canada; 7—East Greenland Basin; 8—Abadeh, Kuh-e-Ali Bashi sections, Iran; 9—South Xizang (Tibet), China; 10—Guryul Valley, India; 11—Perth Basin, Australia; 12—Karoo Basin, South Africa

al. ,2023;Wu Qiong et al. ,2024)。火山喷发导致埋藏在内陆盆地和大陆架中的甲烷等温室气体大量释放,引发了全球变暖、大规模海退、水体缺氧、海洋酸化和古海水盐度异常等灾害性事件(Joachimski et al. ,2020;Wang Wenqian et al. ,2020;Wang Han et al. ,2023;Wignall and Bond,2024)。与此同时,在全球快速变暖和频繁闪电活动的影响下,高频率、高强度的野火迅速蔓延,造成大范围的燃烧(Saito et al. ,2023;Jiao Shenglin et al. ,2024),导致森林植被急剧消亡和土壤崩溃,地表径流将大量陆源碎屑带入海洋使水体条件恶化,引发了海洋生态系统的彻底崩盘(Zhang Peixin et al. ,2023b;Wignall and Bond,2024)。

但上述看似合理的解释依然存在一些问题,例如:① 西伯利亚大火成岩省火山作用持续时间超过 1 Ma,究竟哪一期火山活动与 PTB 灭绝期(30 ka)直接相关(沈树忠和张华,2017)? ② 作用于不同研究剖面的岩浆来源,是否均来自西伯利亚大火成岩省? ③ 西伯利亚火山活动是否与不同剖面 $\delta^{13}C_{carb}$、$\delta^{13}C_{org}$ 负偏位置和幅度存在时间上的高度一致性? ④ 多种同位素研究结果显示,PTB 古气温升高和海洋酸化发生时间节点与生物大规模灭绝时间不一致;⑤ 海洋生物和陆地生物灭绝在时间上是否具有一致性? 因此,要完全解释 EPME 的原因还需要更多更深入的研究。

1 PTB 生物灭绝情况

二叠纪末生物大灭绝作为全球地质历史时期最严重的一次灭绝事件,数十年来不同学者基于沉积学、古生物学、地层学及地球化学等方法对该灭绝事件进行研究发现,在 PTB 处,约有 81%的海生物种和约 75%的陆生物种灭绝(沈树忠和张华,2017;Fan Junxuan et al.,2020;Li Menghan et al.,2021),其灭绝率是全球第二大灭绝——奥陶纪末灭绝率的两倍,且远高于白垩纪末灭绝率。目前普遍认为,陆相危机产生早于海相灭绝事件(Fielding et al.,2019;Chu Daoliang et al.,2020),基于古生物数据库(Paleobiology Database,PBDB)研究表明,EPME 的全球加权平均属灭绝率约为 59%,其中陆地低纬度地区灭绝强度约 53%,高纬度地区灭绝强度约为 68%,灭绝强度从低纬度到高纬度增加了将近 15%,其危机的产生时间相对于海相危机更早且持续时间极长(Fielding et al.,2019;Gastaldo et al.,2020;Davydov et al.,2021;Fielding et al.,2021;Viglietti et al.,2021)。前人研究认为陆相危机早于海相,但结束晚于海相危机(Wu Qiong et al.,2024)。

无论陆相还是海相地层,其灭绝机制都十分复杂,陆相的弹性和复杂性决定了它灭绝的滞后性,而其灭绝的滞后性又显著影响着海相灭绝的进程,因此不能仅用两者同时发生来简单概括这一旷日持久的大灭绝事件。不同区域、不同地层的海相和陆相生物呈现的灭绝形式不同,且海洋、陆地生物的灭绝模式、顺序和二叠纪末生物大灭绝的原因尚未完全厘清。

1.1 海洋生物灭绝

二叠纪末期—三叠世早期海洋生物演化可分为 3 个阶段,第一个阶段是瓜德鲁普世末期海洋生物灭绝,又称瓜德鲁普世—乐平世之交(GLB)生物灭绝事件,第二个阶段是 PTB 海洋生物灭绝,第三个阶段是早三叠世海洋生物的初步复苏。

瓜德鲁普世末期,全球有将近 34%的海洋无脊椎生物消亡。GLB 生物大灭绝主要表现为碳酸盐生产者(如䗴、钙藻、有孔虫、珊瑚、巨型双壳等)的显著消亡以及微生物的繁盛取代(黄俊亚等,2019;Rampino and Shen Shuzhong,2021;Chen Fayao et al.,2021)。GLB 生物灭绝具有选择性和阶段性的特点,选择性体现在该时期浅海底栖生物各个生物门类、属种的分异程度不同,且在不同时间内灭绝程度也不尽相同(宋海军和童金南,2016;刘宣威等,2023)。阶段性可根据牙形石带划分的灭绝相对时间表征,窄盐度的浅海珊瑚类(*J. postserrata* 带)和有孔虫(*J. altudaensis* 带)率先灭绝,随后是腕足(*J. xuanhanensis* 带)、牙形石、放射虫和浅海钙藻类的大型消亡(刘宣威等,2023)。另外,底栖无脊椎动物的灭绝也使蓝藻细菌得以扩张(Zhang Guijie et al.,2021a;Wignall and Bond,2024)。总体上,自 GLB 开始,地球内部动力十分不稳定,生活范围广且生存水体较深的菊石类发生了全球性的灭绝高峰,这是长兴阶晚期菊石类强烈绝灭事件的预兆(陈军和徐义刚,2017)。目前,认为深海大洋最小含氧带扩张、深层硫化、升温和缺氧的海水上涌至斜坡带极有可能是造成浅海生物灭绝危机的主导因素(陈军和徐义刚,2017;刘宣威等,2023),峨眉山大火成岩省和 GLB 界线层位的碳同位素值负偏具时间耦合关系,但由于该处碳同位素负偏并不具有全球性,因此,暂未明确两者的相关性。

PTB 海洋生物灭绝标志着持续了 2 亿多年“古生代演化动物群”向“现代演化动物群”转变(Sepkoski et al.,1981;丁奕和张立军,2023)。突发性的古海洋异常事件使晚二叠世末期海洋生态系统面临着前所未有的崩盘,81%的海洋物种在这一时期消失(Fan Junxuan et al.,2020;Li Menghan et al.,2021),如三叶虫、四射珊瑚、横板珊瑚、䗴类有孔虫等;然而仍有部分物种在经受惨烈灭绝事件后得以幸存,如海百合、腕足动物、菊石、棘皮动物、苔藓虫等(图 3)(赵俊杰等,2022;Wang Han et al.,2023)。不同门类的海洋生物在代谢速率、生存环境和面对环境突变的缓冲能力等多方面存在诸多差别,这使得海洋生物的灭绝率呈现出显著迥异,具体表现为 PTB 海洋生物灭绝的选择性和不等时性(宋海军和童金南,2016;赵俊杰等,2022)。按照生活环境和生理抗环境压力的不同,可以将 PTB 海洋生物的灭绝分为两类,一类是栖息地较为狭窄的生物,其灭绝率偏高且灭绝形式一般为单幕式,如生活在海洋表层的浮游放射虫、透光带内的钙藻、温暖浅水中的䗴类底栖生物,包括有孔虫、海绵、四射珊瑚等,对应着第一次灭绝脉冲;第二类是栖息地相对宽广的生物,这类生物从浅海至深水盆地均有分布,其灭绝率相对较低且灭绝形式一般为两幕式,如非䗴有孔虫、介形虫、底栖腕足动物、软体动物(底栖双壳类、腹足类、菊石)和牙形石等,对应着第二次灭绝脉冲(图 3)(Wang Han et al.,2023)。其中,非䗴有孔虫、介形虫和底栖腕足动物灭绝率较高,而软体动物和牙形

石相对较低,如长兴期末腕足动物的科灭绝率为73%,属灭绝率81%左右,华夏双壳类动物群53.4%的属和96.5%的种灭绝。

二叠纪末生物大灭绝发生后不久,海侵及海洋深水区缺氧使得早三叠世的印度阶出现了非连续的海洋生物恢复期,如较深水区的菊石在格里斯巴赫阶早期开始低水平的复苏,但水体条件的反复改变使得残存的菊石群落彻底衰亡。早三叠世奥伦尼克阶又发生了全球性灾难事件,即史密斯亚阶/史帕斯亚阶界线事件(SSB 事件)。这一时期海洋动物群和生态系统也发生了重大变迁,包括全球热量的最大化(吴奎等,2022)、牙形石、有孔虫、腕足类及双壳类等海洋生物多样性的减少以及小型化现象的出现(Chen Bo et al.,2013;李飞洋等,2022),甚至有个别种类的牙形石、菊石、放射虫、有孔虫以及头足类等生物出现返祖现象(吴奎等,2022)。在二叠纪末生物大灭绝事件之后 8~9 Ma(安尼阶中期至晚期),海洋脊椎动物群落缓慢复苏,海洋生态系统稳定性在史帕斯亚阶达到较高的水平,海洋生态系统检测出了显著实质性的生态环境改善迹象(Chen Zhongqiang and Benton, 2012; Zhang Hua et al., 2016),海洋生态系统的复苏进程加快,并且在陆地群落恢复中也出现了类似的模式(Romano et al., 2020)。海水含氧度、海水温度、海水酸碱度和火山活动是影响早三叠世生态复苏漫长曲折的潜在因素,在 PTB 海水仍处于高温状态并伴随着持续上升的趋势,长时间的高温阻碍了早三叠世海洋生物的复苏(崔亚圣等,2023);PTB、早三叠世史密斯亚期—史帕斯亚期之交以及早—中三叠世之交均出现了不同程度的海水酸化现象(Zhao Xiangdong et al., 2020;Song Haijun et al.,2021b),延迟了海洋生物的复苏,随着西伯利亚火山喷发的相对减弱,在早史帕斯亚阶时期生态获得了极大程度的稳步复苏(王向东,2019)。

1.2 陆地生物灭绝

1.2.1 陆地植物

晚二叠世是否发生过陆地植物大灭绝目前仍然存在争议,部分学者指出 PTB 陆地存在从古植代向中植代演替这一渐变的过程,这种类似于突变灭绝的事件,被归咎于不同植物区系之间演替速率不同(Nowak et al.,2019;Yang Wan et al.,2021)。但目前更多证据表明 PTB 陆地植物的确发生了全球性的灾难事件而并非渐变演化(Dal Corso et al.,2020;Zhang Peixin et al.,2023a),如在全球范围内早—中三叠世存在着“煤缺失”(图 3),直至三叠世末成煤植物出现才得以恢复(Dal Corso et al.,2020;Zhang Peixin et al.,2023a);PTB 存在繁盛的真菌孢子和随之急剧降低的植物孢粉含量,以及植物孢粉中木本属种显著降低。基于上述证据,许多学者证实 PTB 在不同的地域和气候区均发生了陆生植物群落的快速灭绝/消失和植物多样性的灾难性下降事件(Chu Daoliang et al.,2020;Feng Zhuo et al.,2020;Gastaldo et al.,2020;Shu Wenchao et al.,2023;Shao Longyi et al.,2023)。

PTB 陆地植物历经了快速的种类演替和显著的灭绝事件。首先,在全球范围内发生了不同强度和时限的古植代向中植代演替,主要表现为喜湿孢子类植物向耐旱性强裸子植物快速转化(Gastaldo et al.,2020;Shu Wenchao et al.,2023)。另外,晚二叠世末在全球纬度上均存在着不同程度的植物灭绝事件,以植物丰度、多样性急剧降低和煤层缺失为标志。二叠纪全球植物可分为低纬度华夏植物区、中—低纬度欧美植物区、北半球中—高纬安加拉植物区、南半球中—高纬冈瓦纳植物区。其中,北半球中—低纬度植物种灭绝率高达 86%,如跨越赤道—北半球低纬度的华南盆地,植物的灭绝危机事件主幕发生在晚二叠世末期,华南植物宏观化石记录显示,PTB 陆生植物群落崩溃以及多样性显著下降(Hua Fanghui et al., 2024; Shao Longyi et al., 2023),石松、蕨类、种子蕨类和苏铁等成煤植物迅速消失,植物种减少 95%,植物属减少 50%(Zhang Hua et al., 2016; Chu Daoliang et al., 2020; Feng Zhuo et al.,2020);晚二叠世早期的北半球低纬度华北盆地,以蕨类植物和大羽羊齿植物群为主的华夏植物区系灭绝并被以针叶树和种子蕨等裸子植物为主的欧美型 *Zechstein* 植物区系取代(Lu Jing et al.,2020;Shu Wenchao et al.,2023),由植物宏观化石推断出华北盆地 54%植物属及 88%植物种灭绝(Chu Daoliang et al.,2019),且暂未发现早三叠世的残存植物群(Xu Xiaotao et al.,2022)。PTB 南半球的中—高纬度地区也存在植物群落快速演替、植物多样性降低、煤层缺失以及真菌、细菌和浮游藻类的大量繁殖等现象,如图 2 中纬度的 Karoo 盆地和印度地区陆地植被数量急剧减少,且存在大量的藻类遗体(Gastaldo et al.,2020);高纬度的澳大利亚地区舌羊齿植物灭绝后被蕨类植物和裸子植物快速取代(Vajda et al.,2020;Mays et al.,2021)。而在北半球高纬度的西伯利亚地区,晚二叠世长兴期中—晚

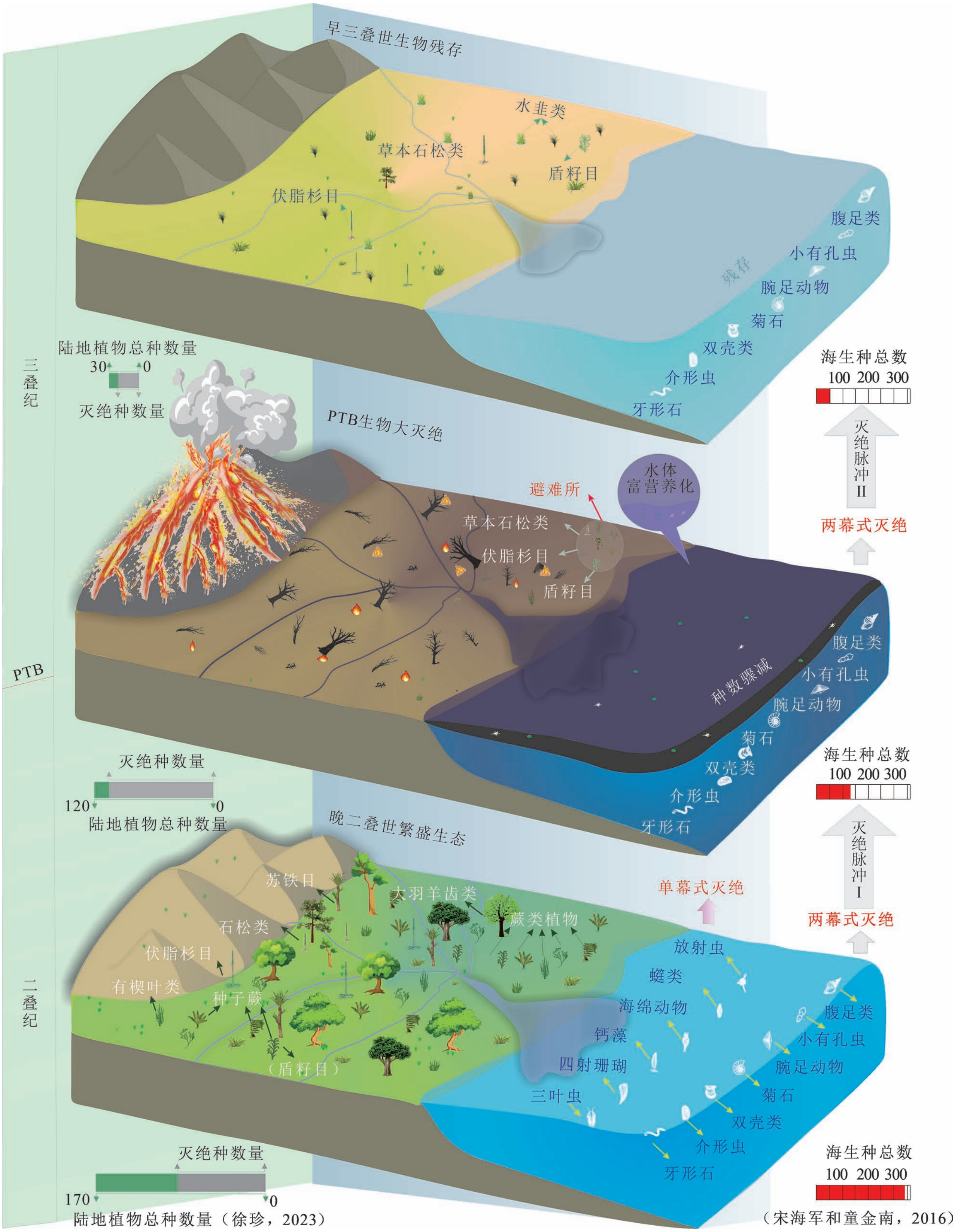

图 3 二叠纪末—早三叠纪陆生植物与海生生物灭绝危机(据 Jiao Shenglin et al. ,2023 修改)

Fig. 3 End-Permian—Early Triassic extinction crisis of terrestrial plants and marine organisms (modified from Jiao Shenglin et al. ,2023)

期科达植物灭绝后,二叠纪—三叠纪界线前后无明显大灭绝事件,陆地植物以松柏类、真蕨和种子蕨为主,草本石松等能适应干旱环境的特征植物群跨过界线延伸至早三叠世(图 3)(Davydov et al. ,2021)。目前,整体上有关北半球高纬度地区的物种灭绝数据较其他地区而言偏少,要从全球角度解释二叠纪末生物大灭绝的原因还需要更多不同纬度剖面数据的深入分析和解译。

华北盆地和欧美地区在 PTB 存在避难所,使得晚二叠世部分植物群分子如 *Voltzia*、*Peltaspermum* 能得以保留并在早三叠世复苏(图 3)(Grauvogel and Ash,2005;Shu Wenchao et al. ,2023;Peng et al. ,2025)。在早三叠世最早期 *Griesbachian* 期也存在灭绝事件,以晚二叠世残存分子的消失为标志,早三叠世全球仅在大陆边缘和高纬度地区保存以草本石松为主的植物群,植物区系弱化(图 3)(Feng Zhuo et al. ,2020;Xu Xiaotao et al. ,2022)。

1.2.2　陆地动物

二叠纪最有代表性的陆生动物是四足类脊椎动物,它在二叠纪的灭绝率达到 89%(Viglietti et al. ,2021),其中以 *Dicynodon* 占主导地位的动物群被以大量 *Lystrosaurus* 脊椎动物群替代。此外,地质历史时期唯一的昆虫大灭绝事件也记录于此,约有 30% 的昆虫目、50% 的昆虫科和 83% 的昆虫属消失(Labandeira and Sepkoski,1993)。由于早三叠世陆地生态系统极度退化,PTB 灭绝后新陆地生态系统的重建似乎比海洋稍晚,即二叠纪末生物大灭绝后 10 Ma,晚三叠世卡尼阶时期湖泊、森林等陆地生态系统才明显恢复,陆地生物重新从荒芜走向繁盛(Zhao Xiangdong et al. ,2020)。

2　PTB 生物灭绝原因

国内外学者一致认为西伯利亚大火成岩省的喷发是引起 PTB 生物灭绝的主要原因(Davydov et al. ,2021;Kaiho et al. ,2021;Zhang Hua et al. ,2021)。高精度 U-Pb 地质年代学研究结果表明,西伯利亚火山活动与生物大灭绝具有同频性和相关性(Cui Ying et al. ,2021;Saito et al. ,2023;Shen Jun et al. ,2023),火山大规模喷发引起的一系列连带性和次生性的灾难事件都可能是引发生物大灭绝的重要因素,如温室效应(Chen Jun et al. ,2020;Joachimski et al. ,2020;Wang Wenqian et al. ,2020)、全球性频发的大规模野火事件(Vajda et al. ,2020;Cai Yaofeng et al. ,2021a;Jiao Shenglin et al. ,2023)、大陆强烈风化剥蚀(Biswas et al. ,2020;Lu Jing et al. ,2020;Kaiho et al. ,2021;Shen Jun et al. ,2022),海水缺氧(Fang Ziyao et al. ,2021;Newby et al. ,2021)、海水酸化(Jurikova et al. ,2020;Song Haijun et al. ,2021b)、海水升温(崔亚圣等,2022;吴奎等,2022)和富营养化等(Liu Dongyan et al. ,2022)。在西伯利亚火山大规模爆发期间,岩浆侵入西西伯利亚煤田,导致热成因甲烷、二氧化碳、水蒸气、二氧化硫以及有毒气体巨量排放(Zhang Hua et al. ,2021;Zhang Peixin et al. ,2023b)。火山喷发后大气圈中 CO_2 含量急剧升高,最高时甚至达到了原先的 6 倍(Cui Ying et al. ,2021;Wu Yuyang et al. ,2021)。大量温室气体致使全球迅速变暖;水蒸气进入平流层促使闪电事件频发,在极端干旱天气和闪电活动的加持下(Zhang Peixin et al. ,2023a),野火事件在全球范围内频发;酸性气体的大量存在导致全球性酸雨气候的形成(Saito et al. ,2023)。上述事件之间存在着关联性和双向性,一方面,野火大规模频发使得陆地植被大面积消失和土壤表层结构受损,大量酸雨促使全球性陆地风化作用迅速增强,陆地土壤大规模侵蚀,释放出更多^{13}C 损耗的碳,导致碳同位素出现负增长(Zhang Guijie et al. ,2021b)。同时,大量^{12}C 输入地球表层系统(谢树成,2018),造成全球温室气体浓度急剧升高,纬向温度梯度减小(Joachimski et al. ,2020),又进一步促进野火频发(Yan Zhiming et al. ,2019)。另一方面,地貌和沉积物扰动,暴露侵蚀作用增强,大陆风化作用将地表巨量的离子和营养盐输送至海洋(Lu Jing et al. ,2020),引起了各类环境和生物危机,如海洋循环能力减弱、海水富营养化和酸化、海水温度升高、透光带深度变深、海水$^{87}Sr/^{86}Sr$ 幕式增高、海洋系统出现分层、海水缺氧、海洋中溶解氧含量降低和氧含量最小层的扩张、海水古盐度异常等(雷丽丹,2017;Chen Jitao et al. ,2022;Wang Han et al. ,2023),各类因素的叠合作用导致了海洋生物大灭绝。灭绝事件后微生物爆发释放毒素并造成的缺氧环境,抑制了淡水动物群复苏并延迟陆地生态系统恢复达数十万年之久(Mays et al. ,2021)。

2.1　二叠纪古气候演化

基于全球气候演变,二叠纪代表了从晚古生代的“冰室”环境向中生代三叠纪早期“温室”环境转换(仲钰天等,2023;王永达等,2024),古生代晚期较高水平 CO_2 为主导的温室气候基本上贯穿了整个中生代,这些变化根本上可能受泛大陆聚合裂解

活动及大规模的海平面升降波动等因素影响(付修根等,2020;田力等,2023)。气候变暖被视为导致海洋缺氧和相关海洋生物栖息地丧失的关键因素(Gliwa et al.,2022)。研究表明,气候的升温与生物集群灭绝呈正相关,当温度变化幅度>5.2℃(平均持续时间为9.71 Ma)及变化速率>10℃/Ma时,就会导致生物集群灭绝(Song Haijun et al.,2021a)。目前,主要借助生物骨骼(牙形石)的氧同位素来研究气候升温事件(Chen Jun et al., 2020; Wang Wenqian et al.,2020;崔亚圣等,2022),如华南海相剖面:PTB牙形石氧同位素分析结果认为二叠纪晚期大气温度显著上升,并在生物灭绝期间达到最高峰值(Joachimski et al.,2020),炎热干旱的高温气候一直持续到早三叠世(Sun Yadong et al.,2012;Cao Cheng et al.,2022);华南、藏南和伊朗剖面的PTB牙形石氧同位素分析结果显示(图2),即使这些剖面所处地区、相带、纬度条件都不同,它们在PTB均出现了氧同位素负漂移的现象,且气温大幅度变暖的时间和幅度高度相似,因此可认为PTB发生的气候变暖具有全球性(崔亚圣等,2022)。此外,还有学者根据化学蚀变指数(CIA)对古气候温度进行估算,如华北陆相剖面CIA估算结果显示,在二叠纪末植物灭绝(EPPE)之前,铜川石川河的平均温度(从11.6℃至16.5℃)和三门峡义马的平均温度(从9.3℃至18.4℃)迅速上升(图2)(Yang Jianghai et al.,2014)。二叠纪末出现最高温度的时期与生物灭绝时期相吻合,这表明生物灭绝事件与气温升高具一定相关性(Liu Feng et al.,2020;Song Haijun et al.,2020),也进一步验证了二叠纪末温度急剧上升导致陆地生物灭绝的假说(Cao Changqun et al.,2019)。

早三叠世经历了极端的气候扰动。西伯利亚大火成岩省在早三叠世印度阶时期的二次喷发,导致全球气候长期变暖,各气候带南移,使得该时期的气候普遍干旱及沙漠持续规模性扩张(Lu Jing et al.,2020)。同时,干旱的气候改变了降水和蒸发模式,使得南温带更加潮湿,南半球高纬度地区愈加温暖(Liu Feng et al.,2020;Romano et al.,2020)。早三叠世期间发生的多次温室危机对生物的恢复速度与方式有重要的影响:温度较低时生物体延迟复苏,温度较高时生物加速灭绝(崔亚圣等,2022),因此,早三叠世间歇性的气候动荡是影响生物复苏的重要因素(邢智峰等,2022;Saito et al.,2023)。

2.1.1 二叠纪末大气 CO_2 浓度

二叠纪晚期至三叠纪早期,西伯利亚火山大规模持续性喷发(Cui Ying et al.,2021),大气中氧含量快速降低,而二氧化碳含量成倍骤升(碳同位素负偏出现之后的0.044 Ma)。基于碳酸盐岩结核研究发现,晚二叠世(长兴期)至早三叠世(格里斯巴赫阶)大气中 CO_2 含量增加了4倍(Joachimski et al.,2022),在二叠纪末最高甚至达到原先水平的6倍之多(Wu Yuyang et al.,2021),比显生宙时期的其他时间(包括今天)都高得多(Wu Yuyang et al., 2021;Wang Han et al.,2023),直至早三叠世,CO_2 浓度也一直维持在较高水平(Jurikova et al.,2020)。

$\delta^{13}C_{carb}$ 记录海洋无机碳,$\delta^{13}C_{org}$ 记录陆源有机碳,两者配对分析可为碳循环、生物灭绝率和古氧化还原条件研究提供依据(Ge Yuzhu,2021;侯海海等,2023)。PTB全球不同地区剖面的碳同位素均存在显著负偏,这印证了该时期 CO_2 含量发生过剧变(图2,图4)。二叠纪末生物大灭绝与全球碳同位素负偏在时间上具有一致性,如PTB的华南峡口段和朝天均显示 $\delta^{13}C_{carb}$ 和 $\delta^{13}C_{org}$ 两次下降段,且两次降低时间与放射虫两个阶段的消亡时间相契合(Zhang Guijie et al.,2021b),但最新研究表明,不同剖面中放射虫的灭绝时间/阶段因古地理环境差异而有所不同(He Weihong et al.,2025);华北盆地禹州煤田晚二叠世长兴阶至早三叠世印度阶的 $\delta^{13}C_{org}$ 记录显示,在长兴期孙家沟组存在两次有机碳同位素负偏,第一次发生在长兴期中期(CIE-I,2.2‰),第二次较大的偏移在长兴期末期(CIE-II,2.7‰),且此次偏移与化学指数(CIA)值和植物灭绝的峰值一致(Lu Jing et al.,2020);中国西南整个宣威组的 $\delta^{13}C_{org}$ 值稳定在−24‰左右,上覆卡以头组迅速下降4‰~8‰,其最小值达到−30‰左右,该有机碳同位素的负偏与生态系统的崩塌具有同时性(Cai Yaofeng et al.,2021b;Wang Xiangdong et al.,2021)。此外,基于煤山剖面PTB牙形石的钙同位素分析,也发现了同样的规律性变化,即在灭绝层位上下,$\delta^{44/40}Ca$ 与 $\delta^{13}C_{carb}$ 同步负偏。这也更加印证了大规模火山活动能释放出大量 CO_2,高 CO_2 浓度会导致全球迅速变暖,并加速全球海洋酸化和缺氧的发展,促使海洋生物灭绝(Wignall and Bond,2024)。

2.1.2 二叠纪末大气 O_2 浓度

煤岩学证据(煤中惰质组)和地球化学指标(如碳酸盐岩沉积物中Ce异常、页岩中的碳磷比和黄

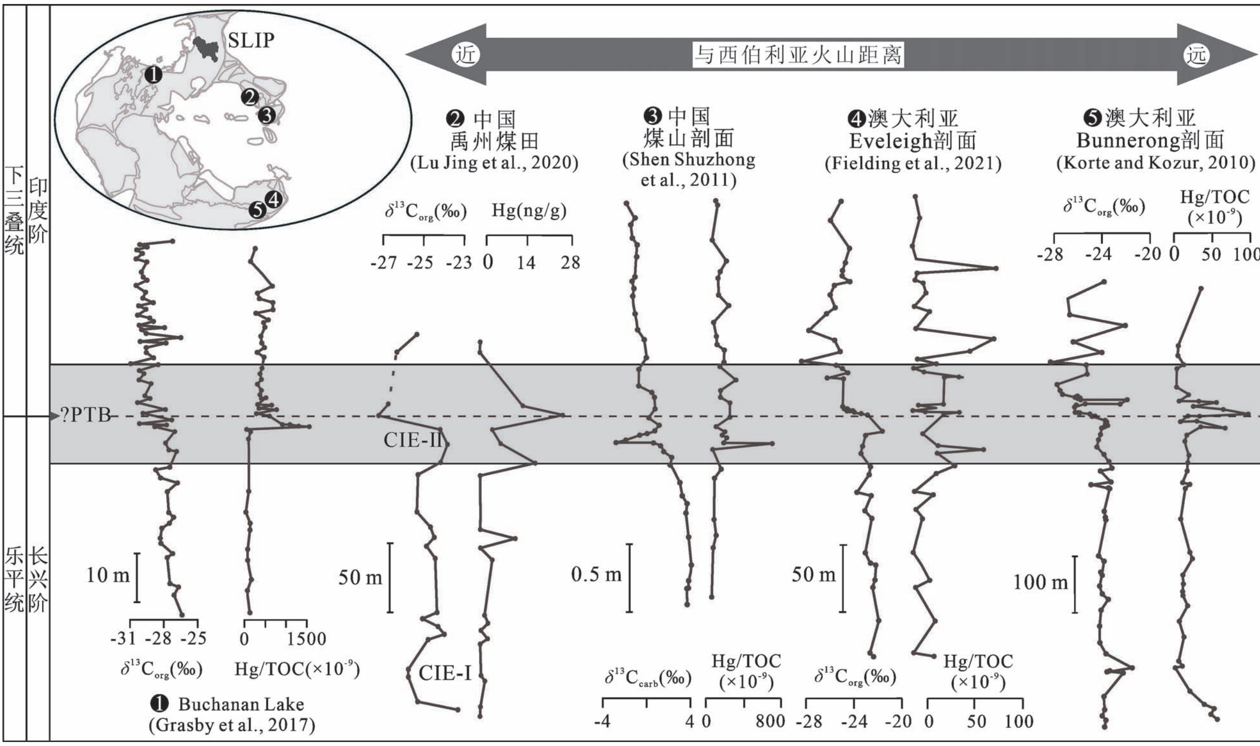

图 4 全球典型 PTB 剖面碳同位素负偏、汞同位素负偏和汞与有机质比值对比

Fig. 4 Negative bias comparison of carbon and mercury isotopes in global typical PTB profiles

铁矿颗粒中的 Se/Co 值等)是厘定古大气氧含量的有效方法(Berner,2006;Glasspool and Scott,2010;Mills et al.,2023)。基于上述方法,部分学者发现 PTB 大气氧浓度相对较低,且有机物的埋藏和氧气浓度在整个二叠纪末期稳步下降(Graham et al.,1995)。这可能归因于 PTB 陆地生态环境系统遭到破坏,大规模的森林野火使生物固碳快速向大气释放,进而引起大气 CO_2 含量(PTB 大火释放并叠加火山喷发的大量温室气体等)升高,燃烧消耗导致大气氧含量降低(Song Haijun et al.,2014)。二叠纪末至三叠纪初较低的大气氧含量被认为是促使生物灭绝的原因(Sheldon and Retallack,2002)。

然而,也有学者发现 PTB 大气 O_2 浓度并不处于低值状态,且认为大气缺氧不是造成二叠纪末期海洋广泛贫氧和生物大灭绝的主要驱动力。英国学者借助惰质组含量模拟出显生宙以来大气中氧气变化趋势(Mills et al.,2023),泥盆纪晚期大气氧气含量从 13%急剧上升,石炭纪—二叠纪期间氧气浓度水平处于高位,早二叠世(乌拉尔统)中晚期达到峰值阶段 28%~30%,中二叠世瓜德鲁普统时期大气 O_2 浓度适度下降(Glasspool et al.,2015),晚二叠世 O_2 浓度水平降为 26%左右,直到早三叠世全球大气氧含量才发生急剧下降,自侏罗纪起至今一直保持着高氧气水平(图 5)。该趋势在其他研究中得到了验证,如借助同样手段厘定出云南宣威晚二叠世的大气氧含量为 28%(Shao Longyi et al.,2012),华北南部的平顶山盆地下二叠统山西组古大气含氧量为 24.29%(Shao Longyi et al.,2023)。这说明晚二叠世古大气并没有出现明显的缺氧现象(图 5)(Glasspool and Scott,2010;Yan Zhiming et al.,2019),因此,O_2 浓度的变化是否是致使二叠纪末期至三叠纪早期动物多样性丧失的主要诱因还有待考证。

2.2　二叠纪末野火事件

目前普遍认为野火不仅是引发 PTB 陆地植被危机的重要因素,也是助推海洋生态覆灭的潜在因素(Lu Jing et al.,2020;Zhang Peixin et al.,2023b;Hua Fanghui et al.,2024)。西伯利亚火山活动是致使 PTB 全球性野火的主要驱动力,首先,火山大规模喷发释放的巨量 CO_2 引发了全球快速变暖,干旱的气候成为野火燃烧的助推剂(Jiao Shenglin et al.,2023);其次,喷发释放的大量水蒸气到达对流层增加了闪电发生的概率(Miller and Baranyi,2021),为野火事件的发生提供点火契机(吕大炜等,2024)。

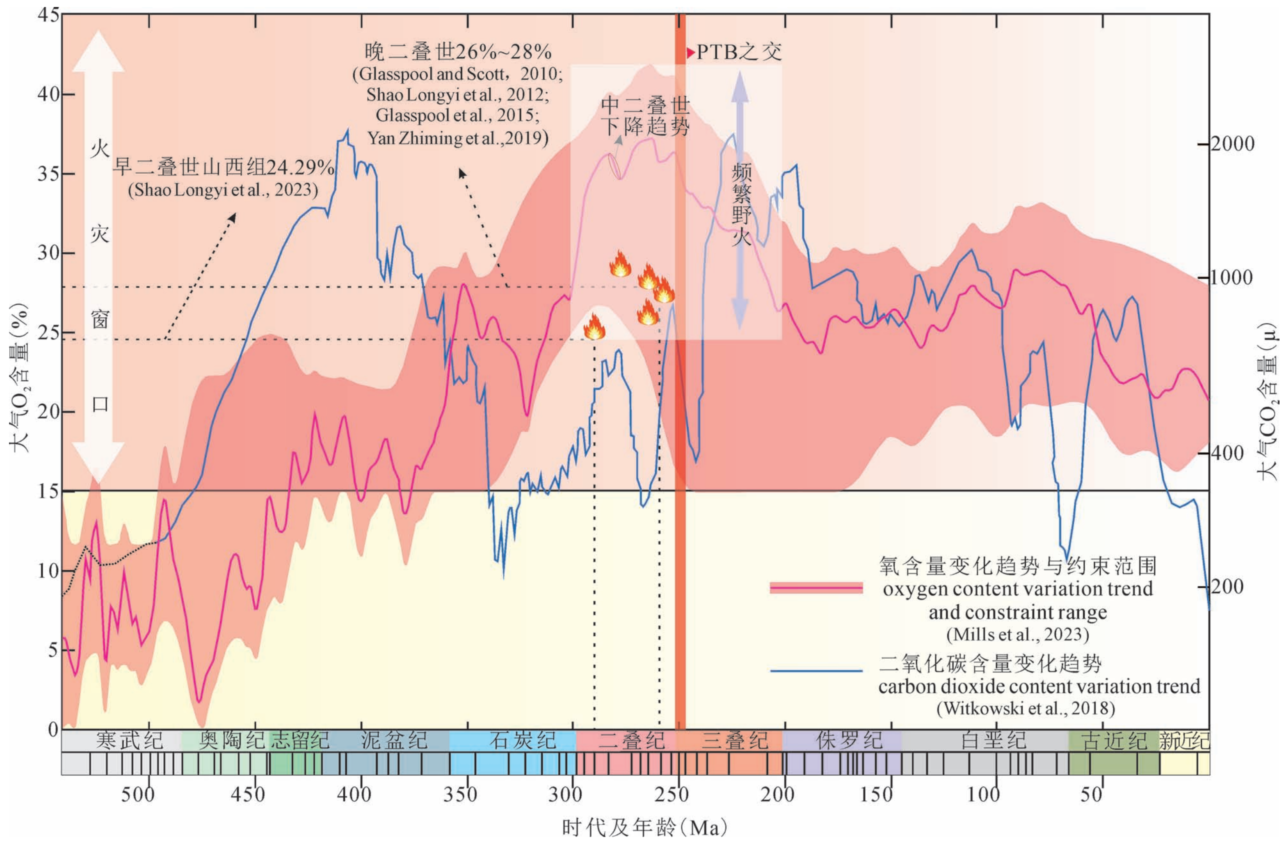

图 5 显生宙以来大气氧含量和二氧化碳含量变化趋势图

Fig. 5 Changes in atmospheric oxygen and carbon dioxide contents since Phanerozoic Eon

频发的野火叠加酸雨等灾害事件严重摧毁了陆地植被系统,植被的衰退会使地表土壤失去保护层,加剧土壤的剥蚀,生物质燃烧后产生的大量氮、磷元素会随着地表径流进入河流、湖泊和海洋,造成水体的富营养化,破坏水生生态系统。木炭化石和多环芳烃(PAHs)可用来反映森林野火燃烧事件或热事件,是古野火燃烧的直接证据(Brown et al. ,2012;Kaiho et al. , 2021; 杜建峰等, 2022; Jiao Shenglin et al. , 2024)。国内外学者对 PTB 不同地区剖面中的野火指标进行研究,证实了 PTB 在全球范围内存在频繁且大规模的野火(图 2,图 5),如中国西南部(Feng Zhuo et al. ,2020;Cai Yaofeng et al. ,2021b),中国西北和北部(Song Yi et al. ,2022;Zhang Peixin et al. , 2023b)、中欧(Uhl et al. ,2014),加拿大(Grasby et al. ,2011)、巴西(Kauffmann et al. , 2016),印度(Srikanta et al. ,2020)和澳大利亚西部(Vajda et al. ,2020)。

PTB 野火事件与生物大灭绝关联密切(周文凤,2017;Jiao Shenglin et al. ,2024)。二叠纪末期第一幕野火事件的发生始于海洋宏体生物灭绝前长兴阶 *Clarkina yini* 带,对应于煤山剖面 24 层,即稍微早于第一幕生物大灭绝对应的煤山剖面 25 层(Yin Hongfu et al. , 2007),一直持续到长兴阶的 *Hindeodus Changxingensis* 带,对应于煤山剖面 26 层(Yin Hongfu et al. ,2007;周文凤,2017)。在晚二叠世末期碳同位素负偏和 PAHs 均达到最大值(Cao Changqun et al. ,2009),指示着高频森林火灾的存在,这与当时陆地严重的生态系统危机相吻合(Jiao Shenglin et al. ,2024)。在第一幕生物大灭绝事件后,古环境干旱、陆地植被萧条、大气湿度降低,使得陆地上没有再发生较强的大火事件,只出现了受季节干湿气候交替引起的阶段性大火(Cao Changqun et al. ,2009),野火的发生由高频高强度转变为低频低强度,碳同位素发生小幅度负偏,直至第二幕野火事件的发生达到负偏最大值。第二幕野火事件发生在早三叠世印度阶 *Isaricella isarcica*(Song Haijun et al. ,2013),对应于煤山剖面 29~30 层(Yin Hongfu et al. ,2007),稍晚于第二幕生物大灭绝对应的煤山剖面 28 层,PAHs 的浓度急剧升高,森林野火事件达到第二幕高峰,加剧了陆生生态系统的崩溃。

2.3　二叠纪末风化事件

西伯利亚火山活动和古特提斯演化是引发二叠纪末强烈风化作用的主要驱动力(Biswas et al.,2020;田力等,2023),前者引发了温室效应、大规模野火和酸雨等灾害事件,导致了陆生生态的崩溃和土壤表层结构的破坏,加剧了陆地风化的速率和强度,后者通过造山活动抬升大陆平均海拔,增加了风化作用面积,强烈的风化作用导致近岸水体的富营养化并降低了水体溶氧度和携氧能力,营养物质的激增促使了蓝细菌的繁殖,全球变暖伴随巨大的生物泵作用使得洋流循环趋于停滞,造成了海洋分层、缺氧,最终导致了海洋生物的覆灭(宋海军等,2012;Biswas et al.,2020)。

目前,主要借助汞含量及其同位素、锶同位素、锂同位素、有机碳同位素、化学蚀变指数 CIA 和粘土矿物等指标推断风化作用强度及其演变特征(Kaiho et al.,2021;Shen Jun et al.,2022;吴奎等,2022;龚清等,2024),如二叠纪末生物大灭绝前夕直至早三叠世初期,海水 δ^7Li 值发生负偏,表明全球性大陆风化作用快速增强(Sun He et al.,2018),PTB 土壤侵蚀率在 2 Ma 内持续增强,严重影响了海洋沉积率并使得海洋生产力在近 1 ka 内迅速崩溃(Stüeken et al.,2015);华南盆地和意大利多环芳烃和汞同位素证据表明(图 2),由火山喷发导致的风化剥蚀先触发了陆地生态系统危机,随后引发了海洋生态系统危机;贵州青岩、关刀剖面和浙江煤山剖面牙形石锶同位素的测定结果显示(图 2),早三叠世陆地的风化速率高出晚二叠世 1.9 倍(Song Haijun et al.,2015),这与前人通过 Sr 和 Nd 同位素证实早三叠世陆地风化速率大幅增强的结论一致(Sheldon,2006)。晚二叠世末^{12}C 不断地输入海洋表层系统(碳酸盐岩碳同位素持续地下降),全球变暖、海洋系统出现分层(Luo Genming et al.,2011;Xie Shucheng et al.,2017)并减少对地表的营养供应,从而抑制海洋生态的恢复(Stüeken et al.,2015;Lu Jing et al.,2020)。

2.4　二叠纪末海洋缺氧事件

基于沉积相(Wignall and Hallam,1992)、铊同位素(Newby et al.,2021)、铬同位素(Fang Ziyao et al.,2021)、铀同位素(Lau et al.,2016)、Th/U 比值(Wignall and Twitchett,1996)、水体自生草莓状黄铁矿(粒径、微晶的大小及形态、硫同位素)和黑色页岩的沉积构造(Bond and Wignall,2010;田力等,2023)等多种证据分析,众多学者证实了在二叠纪末期的确存在着全球性的海洋缺氧事件。二叠纪末期海洋缺氧始于距离生物大绝灭事件约 2 Ma 前的长兴阶晚期(Wignall and Twitchett,2002),并被认为是生物大灭绝的前兆(Nielsen and Shen Yannan,2004),同期还伴随着区域性海洋中层硫化海水向表层扩张过程(Clarkson et al.,2016)。二叠纪末生物大灭绝事件发生的前夕,陆源输入的增大导致海洋循环能力减弱(Hotinski et al.,2001;Algeo et al.,2010)、海水缺氧、海洋中溶解氧含量降低和深海大洋最小含氧带扩张等(Joachimski et al.,2012;Sun Yadong et al.,2012;Chen Bo et al.,2013)。此外,PTB 海侵过程也引起了海洋环境缺氧事件的发生(吴亚生等,2006;周文凤,2017)。PTB 有毒的、高温的、缺氧的、甚至是硫化的海洋环境造成了海洋生物多样性的降低(Wang Xiangdong et al.,2019)。

二叠纪末期全球多个剖面均有海洋缺氧的记录(图 6),如秦岭洋、古特提斯洋、华南盆地、冈瓦纳大陆边缘以及北美板块等高纬地区(Wignall and Twitchett,2002;Yan Zhiming et al.,2019;Fang Ziyao et al.,2021;Chen Jitao et al.,2022)。PTB 大灭绝前后,煤山地区海水环境持续缺氧(Li Guoshan et al.,2016)。贵州罗甸大文剖面中的 δ^{238}U 在 PTB 地层突然下降(图 2),意味着海洋缺氧程度的增加(Brennecka et al.,2011;Lau et al.,2016)。PTB 华南(古特提斯东部)峡口剖面碳酸盐岩斜坡的铬同位素负偏一直持续到早三叠世(图 2),印证了古特提斯东部快速扩张的海洋缺氧事件(Fang Ziyao et al.,2021)。华南嘉荣剖面早三叠世史密斯—早史帕斯亚期之交的高分辨率碳同位素记录表明,全球史密斯期碳同位素负偏与全球海侵和海洋缺氧具有良好的耦合关系,史密斯期碳同位素负偏的最低点与生物多样性的严重消亡相吻合(Zhang Guijie et al.,2021a),这与“海洋缺氧带扩张高峰期对应着生物大灭绝高峰期”观点一致(Isozaki,1997)。在高纬度地区的东格陵兰岛盆地(图 2),丰富的草莓状黄铁矿显示出硫化、缺氧环境在晚二叠世—早三叠世的反复出现(Nielsen et al.,2010)。加拿大 Buchanan Lake 生物绝灭层位上发现了随着气体输送而沉降的木炭和漂珠(图 2),它们是煤层受西伯利亚玄武质岩浆高温燃烧后的产物,而木炭等物质的大量沉积造成了当地水体的区域性缺氧(沈文杰等,2012)。

然而部分学者认为缺氧环境在浅海区域的分布和持续时间相对有限,并非全球性的持续性事件

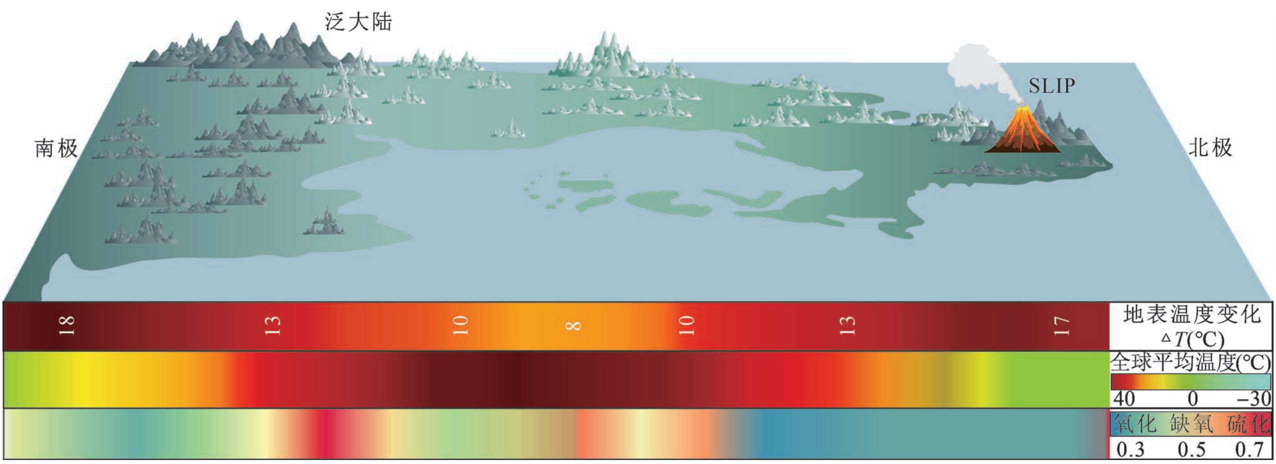

图 6 PTB 全球纬度下的地表温度(据 Witkowski et al. ,2018 修改)、全球平均温度变化特征(据 van der Meer et al. ,2022 修改)和海水氧化还原程度(据 Emmings et al. ,2022 修改)模式图(据 Wu Qiong et al. ,2024 修改)

Fig. 6 Model maps of surface temperature(modified from Witkowski et al. ,2018), global mean temperature (modified from van der Meer et al. ,2022) and seawater REDOX degree (modified from Emmings et al. ,2022) at PTB global latitudes (modified from Wu Qiong et al. ,2024)

(雷丽丹,2017;丁奕和张立军,2023)。如 PTB 的两幕式缺氧事件只在古特提斯洋和新特提斯洋地区发现(Algeo et al. ,2011)。海洋缺氧在部分区域的时间序列上存在较大差异性,与生物灭绝的时间并不能一一对应(Proemse et al. ,2013;雷丽丹,2017)。潘多拉大洋黄铁矿铊同位素研究结果表明,PTB 曾短暂出现气候变冷和海洋氧化状态(Newby et al. ,2021)。二叠纪末生物大灭绝前后煤山剖面确实存在氧水平波动(图 2),但并不是持续缺氧状态,而是呈现缺氧/贫氧──→富氧/有氧的周期性变化,这侧面反映长期缺氧极可能不是二叠纪末生物大灭绝的主要驱动(丁奕和张立军,2023)。因此,虽然 PTB 海洋缺氧事件的确存在,但缺氧的影响范围与环境演变存在何种规律,以及缺氧事件在生物灭绝中是否占主导地位都尚待厘清。

2.5 二叠纪末海水升温事件

在西伯利亚火山喷发、全球变暖、陆源碎屑输入增多和溶解 Ni 元素突然增加等综合因素影响下(Black et al. ,2015;Jurikova et al. ,2020),二叠纪末期海洋表层温度升高(Chen Jun et al. ,2020),在低纬度地区增幅可达 8~10℃,海水高温度一直持续到早三叠世(Sun Yadong et al. , 2012; Joachimski et al. ,2020),海洋生物地球化学过程发生改变,并逐渐演化为海洋环境剧变,继而导致二叠纪末生物大灭绝的发生。

地球化学研究是还原古海水温度的有效手段(如牙形石同位素)(Joachimski et al. ,2012;崔亚圣等,2022;吴奎等,2022)。学者通过研究古生物化石氧同位素发现,二叠纪末期不同剖面均存在海水升温现象。浙江长兴煤山剖面、四川广元上寺剖面、藏南和伊朗地区牙形石氧同位素测定结果表明(图 2),在二叠纪末生物灭绝前期上述剖面均出现了显著快速的负偏,证实了二叠纪末海水温度的快速升高,海水温度升幅可达 8℃(Joachimski et al. ,2012;崔亚圣等,2022);利用牙形石氧同位素重建四川来宾地区 GLB 界线处的古海水温度变化趋势,古海水温度呈升—降—升 3 个阶段的变化趋势(Chen Bo et al. ,2011;陈军和徐义刚,2017);基于晚二叠世到中三叠世早期华南多条剖面的牙形石磷灰石的氧同位素研究,认为早三叠世长期处于高温干旱气候且海水温度持续波动上升,海洋表层海水最高温度可能超过 40℃(Sun Yadong et al. ,2012;吴奎等,2022)。利用腕足动物 $\delta^{18}O$ 变化重建出意大利 Dolomites 地区和西藏札达姜叶玛剖面在晚二叠世高精度古海水温度波动变化过程,发现在生物大规模灭绝前,海洋酸化现象和海洋表面温度升高已明显发生,海洋升温最高值出现在生物大灭绝前,并在生物灭绝期间温度持续升高(Brand et al. ,2012;Garbelli et al. ,2016)。二叠纪末生物大灭绝后,海水温度在整个早三叠世持续波动上升,海水温度快速上升与早三叠世生物复苏的滞后有一定对应关系(Joachimski et al. ,2012;崔亚圣等,2022)。

2.6　二叠纪末海洋酸化事件

二叠纪末大规模火山作用导致大量 CO_2、SO_2 释放,影响了海洋 C—S 循环。这导致海洋表面 pH 值显著下降,进一步加剧了全球海洋的缺氧和酸化,引发了海洋化学和物理环境的变化,并严重影响了海洋生物的代谢过程和生态系统的稳定性(Payne et al. ,2010;Cui Ying et al. ,2021)。

硼、钙等同位素作为可靠的地球化学指标常用于估算古水体的 pH 值,此外还有部分生物的生理结构变化也可指示水体特征(陈军和徐义刚,2017;Wignall and Bond,2024)。华南煤山剖面 PTB 牙形石的 $\delta^{44/40}$Ca 在第一幕灭绝线附近出现一次幅度约 0.3‰的快速负偏,海水 $\delta^{44/40}$Ca 值的变化与 $\delta^{13}C_{carb}$(3‰~5‰的快速负偏)同步,指示了海洋酸化事件(Hinojosa et al. ,2012)。基于硼同位素定量模拟实验结果,在煤山剖面第一幕生物大灭绝线附近(长兴阶 *Clarkina meishanensis* 带),硼同位素所指示的海水 pH 相对稳定无明显降低(Clarkson et al. ,2015),但在第二幕生物大灭绝线附近,海水迅速酸化,导致钙质生物的钙化速率显著降低(Gao Kunshan et al. ,1993),造成海洋中钙质壳体生物灭绝。华南大贵州滩剖面钙同位素在第一幕灭绝线附近出现负偏且与碳同位素负偏同步,反映了一次海洋酸化事件(Payne et al. ,2010),这在后人研究中得到了验证,如华南 PTB 剖面出现了 3 次钙同位素的负偏,第一次与碳酸盐岩碳同位素的负偏相耦合,后两次与碳同位素正偏一致(Song Haijun et al. ,2021b)。特提斯陆架腕足类化石贝壳的硼同位素记录表明,随着二叠纪末期大规模灭绝的开始,海水 pH 值大幅下降引发了造礁生物的大规模灭绝,海洋酸化携同海水升温被认为是海洋生物灭绝的主要贡献因素(Martindale et al. , 2019; Jurikova et al. ,2020)。加拿大北极地区 Sverdrup 盆地(距离西伯利亚大火成岩省约 2×10^4 km)的深水相剖面,PTB 生物大绝灭层中 Mo 同位素发生显著正偏,表明水体缺氧硫化(Proemse et al. ,2013)。浙江煤山剖面透光层和澳大利亚 Perth 盆地剖面均发现了绿硫细菌的生物标志化合物(图 2),表明二叠纪—三叠纪过渡时期两个剖面浅水海洋透光层水体富集 H_2S,缺氧硫化程度严重(Grice et al. ,2005)。华南盆地海洋深水区硫化环境逐渐向铁化环境转变(雷丽丹,2017),早三叠世透光带硫化区域向较深水扩张(周文凤,2017),持续或间歇性的硫化环境成为生物大灭绝之后海洋生命迟缓复苏的主导因素之一(张桂洁,2016)。

2.7　二叠纪末海平面波动事件

受西伯利亚火山释放高水平 CO_2 引起的温室效应、冰川融化和米兰科维奇旋回等因素的影响(Miller et al. ,2020),瓜德鲁普统晚期和 PTB 海平面波动频繁,海退—海侵变化旋回始于瓜德鲁普统卡匹敦阶晚期的全球性海退,于早三叠世初期由海退转为全球性迅速的海侵过程(邱振等,2014;Cao Ying et al. ,2019;黄俊亚等,2019;易雨昊等,2024)。瓜德鲁普统卡匹敦阶晚期,板块作用驱动下的构造型全球海平面变化事件,使海平面持续下降达到了显生宙海平面的最低值(Haq and Schutter,2008),即全球范围内发生了显著、急剧的大规模海退,导致了皱壁珊瑚、腕足类和大型蜓类灭绝(Shen Shuzhong and Shi Guangrong,2009;Rampino and Shen Shuzhong,2021;Chen Fayao et al. ,2021),并造成全球范围内地层的普遍缺失(沈树忠等,2019)。中二叠世的大规模海退事件一直持续到晚二叠世末期(张桂洁,2016;万俊雨等,2023),随后在乐平统吴家坪阶早期发生快速海侵,海平面快速上升,期间出现了菊石和牙形石的灭绝高峰(Wang Yue and Jin Yugan,2000)。长兴阶末期,PTB 海退事件开始,对应浙江煤山剖面 24e 层底部的一个Ⅱ型层序界面(Yin Hongfu et al. ,2014)。此次海退事件导致了珊瑚分异度和丰度的急剧减少(沈树忠等,2019)、部分生物的灭绝以及残余生物的小型化现象(He Weihong et al. ,2015;李飞洋等,2022),大规模生物灭绝事件主要发生在 PTB 海侵阶段(Hallam and Wignall,1999;Fan Junxuan et al. ,2020;Li Menghan et al. ,2021)。

部分学者认为海平面波动难以独立用于解释大规模生物快速灭绝机制(吴亚生等,2006;宋海军和童金南,2016),其一,在显生宙其他时期也曾多次出现过类似海侵—海退现象,但它们并未伴随生物灭绝事件。其二,海洋生物及其幼体都具有适应海平面升降的能力,因此,海平面波动对大部分海洋生物并无致命影响。也有学者认为二叠纪晚期海平面下降及 PTB 海侵作用引起的海洋贫氧事件是导致二叠纪末期生物大灭绝的主要原因之一(周文凤,2017;Wang Han et al. ,2023)。此外,晚二叠世海平面强烈波动,海水跨越淡水与咸水之间的界限,水体的反常变化及其引发的古盐度异常可能在 PTB 生物圈中发挥了不可小觑的作用(Zheng Binsong et al. ,2021)。

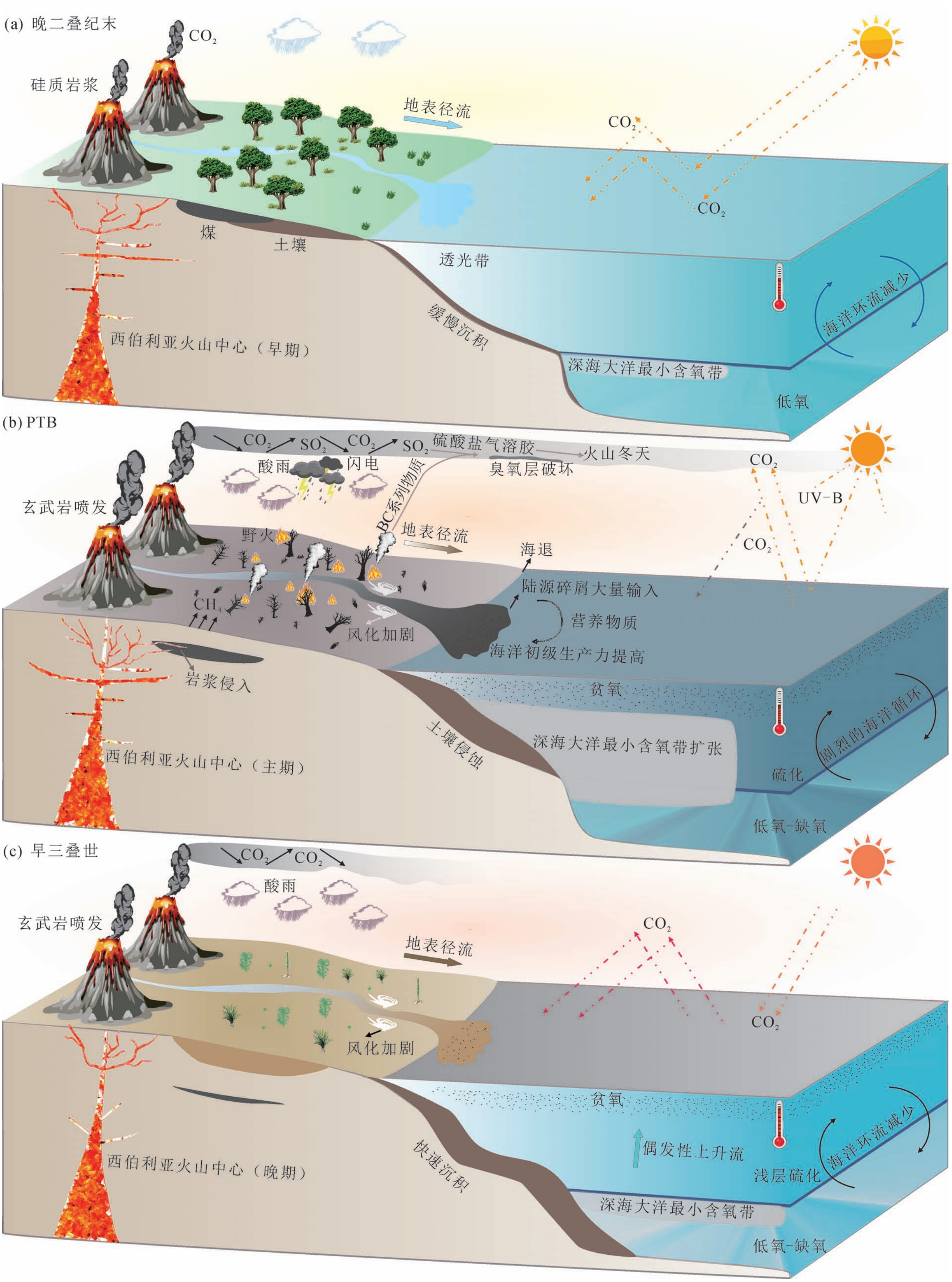

图 7 二叠纪末生物大灭绝综合模式：(a) 灭绝前夕繁荣生态；(b) 二叠纪末生物大灭绝；(c) 早三叠世生物萧条

Fig. 7 Integrated model of mass extinction at the End-Permian: (a) prosperous ecology on the verge of extinction; (b) the End-Permian mass extinction; (c) Early Triassic biotic impoverishment

3 PTB 生物灭绝模式

二叠纪末期陆相古生态环境紊乱的原因很可能是西伯利亚火山活动的爆发与古大气环境、古火灾事件以及生物圈多重因素等共同作用叠加的结果。二叠纪末生物大灭绝前,陆地生态系统和海洋生态系统都是一片繁荣的景象(图 7a)。

在二叠纪—三叠纪之交,西伯利亚火山大面积喷发,大量的二氧化碳快速释放引起陆地酸化;岩浆侵入西西伯利亚煤田,释放大量热源性二氧化碳以及热成因甲烷,从而引发强烈的全球变暖,地表温度上升幅度约为 8~18℃,其中赤道地区地表温度在原有高温的基础上升高了 8℃,且此时赤道平均温度高达 40℃,两极地区地表温度变化幅度均超过了 17℃,此时两极的平均温度均超过了 30℃(图 6);大量酸性气体导致全球性酸雨气候的形成,进而促使全球性陆地风化作用迅速增强,陆地土壤大规模侵蚀;在大陆气候极度干旱以及闪电活动的加持下,陆地野火大规模频发,森林植被体系毁坏、水土流失加剧、生物多样性下降、辐射加剧,最终导致陆相生态系统破坏甚至崩溃。除此之外,由于火山大规模喷发,大量 SO_2 的排放和大气中硫酸盐气溶胶的形成会致使全球变冷,称“火山冬季”(又称快速变冷),它的影响可持续几年至几十年,部分学者认为其与灭绝事件有所关联,但此观点仍需实质性数据支持。由于陆地生态的崩溃,陆地地表径流向海洋输送营养物质量增加,海水溶氧度降低、海洋表层生产力提高、海洋透光带硫化、深海大洋最小含氧带扩张、海洋持续低氧—缺氧(碳排放活动伴随着有机碳埋藏,从而促进海洋广泛的缺氧环境)、海洋循环加剧,其中,北半球海水多处于氧化状态,北极虽有硫化现象,但硫化现象更多出现在赤道附近和南半球低纬度,此外,南半球高纬度和赤道地区大多处于缺氧状态(图 6)。陆地和海洋生态系统快速崩溃,最终导致了 EPME 的发生(图 7b)。

三叠纪早期,西伯利亚火山喷发进入相对微弱的晚期阶段,但仍对陆地环境有着巨大的影响:化学风化率持续增强、生态地貌侵蚀加剧,基岩侵蚀率在该阶段达到了高峰。沉积物快速堆积,陆源营养物质流量增加,刺激海洋生产力提升并增大了有机碳的埋藏量。伴随着全球变暖减轻,海洋生态系统出现了最初的生物恢复期,但海水温度升高、浅层水体硫化、深部缺氧水体上涌、海洋环流减少,浅海环境发生氧化还原变化始终影响着早三叠世的海洋生态系统(图 7c)。

4 结论和展望

二叠纪末生物大灭绝(EPME)作为全球地质历史时期最高级别的灭绝事件,导致了约 75%的陆生物种和约 81%的海生物种的灭绝。国内外学者一致认为,西伯利亚火成岩省(SLIP)的爆发是导致 EPME 的直接诱因,火山喷发引起的全球升温、古野火频发、风化作用加剧、海水富营养化、海平面波动、海水缺氧、海洋升温和海水酸化等一系列次生事件的叠加极有可能是促使 EPME 的直接原因,但各个次生事件影响占比仍有待商榷。前人的研究虽然已经取得了长足的进步,但二叠纪末期生物大灭绝事件还存在不少争议,需要进行深入剖析和研究,具体表现在以下几个方面:

(1)不同纬度地区的多种同位素数据仍需进一步丰富,以佐证火山作用、海洋酸化、氧化范围以及风化作用类型等诸多疑团。目前,有关 PTB 物种灭绝数据的研究主要集中在华南盆地,缺乏高纬度地区的灭绝数据,要从全球角度解释二叠纪末生物大灭绝的原因还需要更多不同纬度陆相、海陆过渡相和海相剖面数据的深入分析和解译。

(2)基于地层、古生物和沉积记录大数据,建立高精度的深时全球生物多样性重建和分析方法,并将全球生物多样性变化、地质历史时期温度变化以及碳同位素变化归纳到同一框架之中,进一步探索二叠纪—三叠纪之交(PTB)气候变化和生物协同演化关系。

(3)西伯利亚火成岩省(SLIP)喷发期次、不同生物类群自适应性差异和生物选择性灭绝内在联系需进一步研究。不同区域、不同地层的海相和陆相生物呈现显著的选择性灭绝,但海、陆生物的灭绝模式、顺序与 SLIP 喷发之间的内在机制仍有待进一步研究。

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A review of the mass extinction at the End-Permian

HOU Haihai[1), HE Qian[1)], LIU Shujun[2)], GAO Lianfeng[1)], WANG Chongjing[1)]

1) *College of Mining, Liaoning Technical University, Fuxin, Liaoning*, 123000;

2) *College of Geological and Surveying Engineering, Taiyuan University of Technology, Taiyuan*, 030021

Objectives: As the most severe of the five major global extinction events in geological history, the Late Permian mass extinction led to the loss of approximately 81% of marine species and 75% of terrestrial species in the ecosystem. A systematic review of the extinction patterns and mechanisms at the Permian—Triassic boundary (PTB) holds significant practical importance for predicting the recurrence of large-scale extinction events.

Methods: An analysis of the evolution of terrestrial plants, tetrapods, and marine organisms at the end of the Permian was conducted based on paleontological data from multiple global sections. Regarding the causes of the end-Permian mass extinction, factors such as ocean acidification, marine anoxia, ocean warming, sea-level fluctuations, ancient wildfire events, and weathering conditions were discussed.

Results: The SLIP outbreak promoted the release of a large amount of greenhouse gases buried in the sediments of inland basins and continental shelves into the atmosphere, and the rapid global warming led to the land crisis in advance. Extreme dry weather promoted the frequent forest wildfires and the collapse of terrestrial ecosystems. The intensification of continental weathering caused a large number of debris to be injected into the ocean, resulting in serious eutrophication, hypoxia of submarine organisms, ocean acidification and disturbance of marine paleoproductivity, etc., resulting in the occurrence of marine extinction events. However, the lag of terrestrial extinction led to the end of the terrestrial crisis later than the marine extinction event.

Conclusions: The extinction of EPME species was characterized by regional, selective and phased extinction. The eruption of the Siberian Igneous Province (SLIP) is highly coupled with the EPME time, and SLIP and its associated series of secondary events are considered to be the main driving force of EPME and the main factor of delayed biological recovery. The duration, intensity and regional distribution of some secondary events, such as ocean hypoxia and sea water warming, are still controversial, and a single secondary event cannot independently support EPME, which is the result of the comprehensive superposition of multiple factors.

Keywords: mass extinction; Permian—Triassic boundary; Siberian igneous Province; paleoenvironmental evolution

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First author: HOU Haihai, male, born in 1986, Ph. D., professor, is mainly engaged in teaching andresearching of sedimentology related in coal-bearing strata; Email: houhaihai@ lntu. edu. cn

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