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全球古-中生代之交牙形石研究进展

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摘 要:古-中生代之交发生了许多重要的地质事件,包括"Pangea"大陆的解体、大火成岩省的喷发、晚古生代大冰期的消逝、极端高温事件、两次生物大灭绝以及迟缓的生物复苏等.牙形石作为该时期主要的标准化石,是进行地层对比以及生物与环境协同演化研究的重要依据.近些年,此阶段的牙形石相关研究取得了许多重要的进展,这些新的材料和技术手段上的突破,为人们进行高精度的地层对比、定量重建该时期地球的生物及环境演变起到了关键作用.本文系统地对该时期全球牙形石的研究,包括牙形石的生物学、地层学以及地球化学研究等进行了总结,也提出了部分亟待解决的问题.未来,随着更多技术手段的开发以及更多基础材料的发现,将加强研究人员对该时期牙形石演化的理解,必然也会在研究这段地质历史转折与突变期的古海洋、古环境、古生物过程中发挥更大的作用.

关键词:牙形石;晚二叠世;早三叠世;古环境;生物地层;地层学.

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Advance in the Study of Global Conodont during the Palaeozoic-Mesozoic Upheavals

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Abstract: Numerous geological events took place during the Palaeozoic-Mesozoic upheavals, including breakup of the Pangea supercontinent, eruptions of large igneous provinces, ending of the Late Paleozoic Ice Age, extremely hot temperatures, two mass extinctions, and delayed ecosystem recovery. As the main index fossil of this interval, conodont is an important basis for stratigraphic correlation and the co-evolution history of organisms and the environment. In recent years, significant progress has

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been achieved through the study of Permian and Early Triassic conodonts and its related researches, which plays an important role in understanding the biotic and environment evolutions. The researches about Permian and Early Triassic conodonts have been summarized in this paper, including conodont biology, stratigraphy, and geochemistry. Moreover, some issues which have remained being overlooked or un-solved are also presented. In the future, the development of more technical approaches and the discoveries of more basic materials would be favored for more deep studies on the evolution of the conodont during this interval, which will further play an indispensable role in paleo-oceanic, paleo-environmental and paleontological studies during this transitional and mutational geologic history.

Key words: conodont; Late Permian; Early Triassic; Paleo-environment; bio-stratigraphy; stratigraphy.

0　引言

牙形石(刺)是保存在沉积岩中的磷酸钙质微体化石.自19世纪60年代首次被报道以来,其相关研究得到了越来越多学科学者的关注,包括生理学、生态学、形态功能学、发育学、生物地层学、地球化学等.目前的研究表明,牙形石动物与现代的盲鳗或七鳃鳗有着最相似的形态学特征,属于无颚类脊椎动物(Donoghue *et al.*, 2000; Goudemand *et al.*, 2011).在地质历史时期,牙形石存在于寒武纪-三叠纪海相地层中(Clark, 1983; Sansom *et al.*, 1992),由于在二叠纪-早三叠世具有比其他生物演化快且分布广泛的特点,被作为该时期的主要标准化石.目前全球范围有18个以牙形石作为标准化石的全球界线层型剖面和点位("金钉子").二叠纪-早三叠世已确定"金钉子"的7个阶,全部以牙形石作为标准化石.除生物地层研究外,牙形石古环境学的研究也有重要的意义,尤其是在牙形石地球化学方面,包括氧、钙同位素以及微量元素等(Sun *et al.*, 2012b; Song *et al.*, 2012, 2015, 2021).牙形石不仅能从地球化学的角度反映环境变化,其个体的演化在二叠纪-早三叠世也出现了许多异常的现象,显示出与该时期的环境变化有明显相关性(Chen *et al.*, 2013b; Guex, 2016).可见,牙形石不仅是二叠纪-早三叠世进行全球范围内地层对比的主要依据,还是了解这段地质历史时期环境与生物的协同演变的重要依据.本文重点围绕二叠纪-早三叠世这一重大地质历史转折期的牙形石相关研究进行总结,为今后进一步的深入研究提供参考.

1　牙形石生物学研究

牙形石动物出现于寒武纪的海洋中,在地质历史上生存了近300 Ma,直到三叠纪末期的生物大灭绝之后彻底消失(Clark, 1983; Sansom *et al.*, 1992).19世纪60年代牙形石被首次报道后(Pander, 1856),其相关研究便得到了广泛的关注.早期有关牙形石生物学的研究络绎不绝,但争议也极大,认为其属于包括植物(钙藻或维管植物)、囊蠕虫、环节动物、节肢动物、触手冠类、盾皮鱼类以及不同类型的原始脊椎动物类等(Müller and Robison, 1981;Clark, 1981).虽然早期也有学者认为牙形石在其生长周期内会周期性脱落,随后长出更大的新生分子(Gross, 1954),但现在学界比较公认的说法是,牙形石是某种动物用来进食(捕食)的器官,并且其内部保留有再发育、即终生不脱落的证据(Hass, 1941, Purnell and Bitter, 1992;Purnell, 1995;Donoghue and Purnell, 1999).这些研究对古生态学研究有着极大的指示意义:(1)牙形石P_1分子的丰度可以用来指示该地区牙形石的数量;(2)牙形石分子的大小可以用来指示其年龄状态.

在个体发育的过程中,其器官经常会出现异速生长的现象,即其大小与形状不均衡发育(Mosimann, 1970; Adams *et al.*, 2013).这个现象在牙形石的研究中也得到了重视,例如在泥盆纪以及三叠纪的属种中均有相关报道(Girard and Renaud 2008; Mazza and Martinez-Perez, 2015).最近有新的研究表明牙形石在整个生长过程中因"异速生长(allometry)"出现了不同部位体型变异现象(Chen *et al.*, 2016c).而该现象的发现则是基于对中三叠世舟形牙形石分子*Paragondolella bifurcata*的横截面进行观察,同时运用形态几何学方法,最后发现该属种的青年分子具有相对更高的脊骨,底部平台更薄且窄;代表更晚成长阶段的分子则出现了脊骨相对低矮且向前升高,同时底部平台均有某种程度的向后缩短、向前变尖的现象(Chen *et al.*, 2016c).这种在其发育阶段中的异速生长现象,至少表明存在于石炭纪-三叠纪的舟形牙形石分子(Sweet, 1988; Dzik, 1991)具有更形态多变的青年个体和形态更稳定的成年个体

(更大体型个体).此外,Lambert (1994)率先建议使用"样品居群(sample population)"法来进行二叠纪舟形牙形石的鉴定工作,即根据牙形石细齿数量以及脊骨长度的变化来进行牙形石分子属种的鉴定,这种方法近来也得到了更多的肯定(Mei *et al.*, 2004; Yuan *et al.*, 2014, 2017, 2018).因此,"样品居群"在二叠纪牙形石鉴定工作上的成功应用,也反映了牙形石存在异速生长的事实.

由于研究手段以及保存形式的约束性,早期牙形石的系统分类学研究一直建立在单分子之上.直到牙形石的自然集群被报道之后(Schmidt, 1934; Scott, 1934),牙形石工作者对其才有了更深刻的认识,即每一个牙形石动物均拥有多个牙形石分子.近几年来,借助研究手段的多样化以及更多保存完好的牙形石集群标本的发现,越来越多的学者将牙形石研究转移到多分子属的相关研究上(Zhang *et al.*, 2017; Chen *et al.*, 2019a; Huang *et al.*, 2019a, 2019b; Takahashi *et al.*, 2019; Sun *et al.*, 2020, 2021; Zeng *et al.*, 2021).截至到目前,5种不同类型的多分子属已经被识别,分别包括13、14、15、17、19个分子(Agematsu *et al.*, 2008, 2014; Aldridge *et al.*, 2013; Huang *et al.*, 2019a, 2019b; Takahashi *et al.*, 2019).牙形石多分子数量的差异,可能也反映了牙形石动物获取食物能力的不同(Zhang *et al.*, 2017).对牙形石集群的研究,也促进了对牙形石动物在分类学方面的研究.目前,比较公认的观点是牙形石属于最早期的脊椎动物矿化骨骼(Donoghue, 1998; Donoghue and Sansom, 2002). Goudemand *et al.* (2011)对三维保存的早三叠世 *Novispathodus* 的齿串进行了几何学分析,发现其具有与圆口鱼滑轮形类似的舌部肌肉构造,这也进一步验证了牙形石动物是脊椎类的猜想.

作为标准化石之一,牙形石生态学的相关研究也吸引了许多学者的关注.支序分类学研究表明,牙形石动物属于无颚类脊椎动物(Goudemand *et al.*, 2011),以现生的盲鳗和七鳃鳗类为代表(Donoghue *et al.*, 2000).而现生的七鳃鳗营寄生生活,主要生存于沿海和淡水中;盲鳗则生活在海洋深层底部,偏好泥质环境,属于主动性捕食者,以某种海洋多毛类蠕虫或者死亡的海洋动物为食,多生活在冷水或者温和海水中,生活水深至少在20 m以下,有些可以深达100~300 m.由于生存在无光带的动物眼部肌肉会萎缩,而曾报道的牙形石动物眼部肌肉的存在,表明牙形石动物生存在透光带(Gabbott *et al.*, 1995; Rigo and Joachimski, 2010).晚三叠世牙形石的古生态研究也有相关报道(Rigo and Joachimski, 2010),研究表明其氧同位素值分布在18.5‰~20.8‰,相当于浅层的海水环境.同时,牙形石的形状以及纹饰不仅代表了其生长周期,也可能代表着不同类型的生活习性.例如,在二叠纪-三叠纪之交主要的牙形石类型,其一是以 *Hindeodus* 属为代表的梳形分子,其二是以 *Clarkina* 属为代表的舟形(或齿台型)分子,而有关这两属牙形石的古生态学研究一直存在争议.Orchard (1996)曾提出,*Clarkina* 是一种深水型分子而 *Hindeodus* 代表了浅水型分子.经过近20年的发展,有关 *Clarkina* 属生物相的意见逐步达到统一,认为它是一种远岸、外陆架或者盆地内部、深水型分子(Clark and Carr, 1984; Carr *et al.*, 1984; Wardlaw and Collinson, 1984; 田树刚, 1993; Orchard, 1996; Wang, 1996).然而,有关 *Hindeodus* 属生物相的设想则争议较大,比如有学者认为是近岸、浅海型(Wardlaw and Collinson, 1984; 田树刚, 1993; Orchard, 1996; Wang, 1996),也有人认为是广布型(Hatleberg and Clark, 1984; 王志浩和钟湍, 1990; Lai, 1997; Lai *et al.*, 2001).值得注意的是,Lai *et al.* (2001)根据浙江长兴煤山剖面的地层以及牙形石记录恢复的 *Hindoedus* 属和 *Clarkina* 属的生物相观点认为,前者是远洋分布型而后者属于深水游泳型.而 Chen *et al.* (2011)通过对蓬莱滩和铁桥剖面 *Clarkina* 属和 *Hindeodus* 属牙形石分子进行氧同位素测定的结果认为,相同时期 *Clarkina* 属比 *Hindeodus* 属记录了更高的氧同位素数值,表明 *Clarkina* 属所处环境的温度比 *Hindeodus* 属更低,这也从侧面印证了 Lai *et al.* (2001)的观点.同样的,最近来自阿曼和克罗地亚地区早三叠世晚期的牙形石氧同位素研究表明,早三叠世的舟形分子(*Neogondolella* 属)比同时期齿片型分子(neospathodids)记录的海水温度低大约1.7 ℃(Chen *et al.*, 2021).又例如,华南地区早三叠世的枝形牙形石(*Parachirognathus* 和 *Plativillosus*)比同时期的齿片型牙形石(*Novispathodus* 和 *Neospathodus*)有更高的海水温度记录,这也被学者认为是其生态习性不同导致其生活在不同深度的水体中造成的结果(Sun *et al.*, 2012b).

2 牙形石生物地层学研究

2.1 二叠纪牙形石生物地层

二叠纪牙形石生物地层的研究最早开始于20世纪50年代(Youngquist *et al.*, 1951),随之相关的研究数量便开始增加(Behnken, 1975; Kozur, 1978; Movshovich *et al.*, 1979; Igo, 1981; Wang and Wang, 1981),随后Kozur *et al.* (1995)对这些研究进行了一个较为系统的总结.但是,这些研究几乎均存在化石照片不足或者研究剖面信息不详细的问题.在此后经过20余年的发展之后,全球有关二叠纪牙形石的报道越来越多(Luo *et al.*, 2008a; Zhang *et al.*, 2010; 房强等, 2012; Yuan *et al.*, 2014, 2017, 2019; 叶茜和江海水, 2016; Wang *et al.*, 2016a, 2016b; Metcalfe *et al.*, 2017; Sun *et al.*, 2017).

目前,根据学者的总结(Henderson, 2016),全球范围内二叠纪可划分出40个可对比性牙形石带以及35个地方性牙形石带(图1).而这些地方性牙形石带的出现,则是由于二叠纪牙形石存在强烈的古地理分区,尤其从空谷阶到长兴阶中期(Mei and Henderson, 2001).而根据二叠纪全球牙形石的特点,前人则是将其分为3个大区:(1)北方冷水区;(2)赤道温水区;(3)环冈瓦纳冷水区(Mei *et al.*, 1999a, 1999b; Henderson and Mei, 2000a; Mei and Henderson, 2000).为了促进不同区域之间牙形石的对比,Henderson and Mei(2000b, 2000c)建立了一种"地理渐变群"的新概念.这个概念来源于在现生生物界,指由于地理位置、海拔、温度或者盐度的变化,许多类别的生物均出现了连续且渐次性的形态变化,这种现象被称之为"渐变群"(Mayr, 1942).Henderson and Mei(2007)在二叠纪和早三叠世的舟形牙形石分子研究中进行了具体的应用.

2.2 早三叠世牙形石生物地层

三叠纪的牙形石研究开始于20世纪50年代(Müller, 1956; Huckriede, 1958; Clark, 1959).目前,早三叠世的牙形石在世界各地区都有大量的报道,包括喜马拉雅地区(Sweet, 1970a, 1970b; Goel, 1977; Orchard, 1995; Orchard and Krystn, 1998; Krystyn *et al.*, 2003)、美国西部(Müller, 1956; Clark, 1959; Solien, 1979; Paull, 1982, 1983, 1988; Lucas and Orchard, 2007)、我国华南(Liang *et al.*, 2016; Lyu *et al.*, 2019)、俄罗斯(Zakharov, 2005; Shigeta *et al.*, 2009; Zakharov *et al.*, 2021)、加拿大(Orchard and Tozer, 1997a, 1997b; Orchard, 2008)、澳大利亚(Metcalfe *et al.*, 2008, 2013)、日本(Koike, 1988, 1996, 2004)、斯洛文尼亚(Chen *et al.*, 2016b)等.其中,下三叠统牙形石在我国华南地区广泛发育(Tong and Yin, 2002),因此也得到了广泛的研究,且成果丰富.该地区的牙形石工作开始于20世纪80年代(杨守仁等,1986),之后的研究越来越多,目前华南地区浙江省、安徽省、江苏省、江西省、湖南省、湖北省、贵州省、四川省、广西省等省份均有报道(Wu *et al.*, 2020).

在早三叠世,受到全球气候变化的影响,牙形石的地理分区效应降低,全球地区的牙形石带几乎可以进行对比(图2).目前,国际范围内重要的早三叠世牙形石带包括*Hindeodus parvus*带、*Isarcicella staeschei*带、*Isarcicella iasrcica*带、*Clarkina carinata* - *Clarkina planata*组合带、*Neoclarkina krystyni*带、*Neoclarkina discreta*带、*Sweetospathodus kummeli*带、*Neospathodus dieneri*带、*Neospathodus cristagalli*带、*Neospathodus pakistanensis*带、*Novispathodus waageni*带、*Discretella discreta*带、*Scythogondolella milleri*带、*Novispathodus pingdingshanensis*带、*Icriospthodus collinsoni*带、*Triassospathodus homeri*带.

2.3 牙形石相关的"金钉子"研究

自1974年以来,国际地层委员会(International Commission on Stratigraphy, 简称ICS, http://www.stratigraphy.org/)的首要任务则是建立以宇、界、系、统为全球年代地层单位的标准地质年代表.作为年代地层划分依据,显生宙以来的全球界线层型剖面和点位(global boundary stratotype section and points,俗称"金钉子")已经在全球范围内得到了大量的建立(http://www.stratigraphy.org/index.php/ics-gssps).这些"金钉子"的确定,则是以一些特定标准化石的"首现点"(first appearance datum, 简称FAD)为标准.在地层中,由于其具有演化快、分布广、数量多、易于获得的特点,牙形石经常被作为标准化石来使用.截止至目前,国际地层委员会已经通过了19枚以牙形石作为标准的"金钉子".而在二叠系-三叠系已经确认的10枚"金钉子"中,以牙形石作为标准的则有8枚(图3).同时,一些尚未确定的"金钉子"中,以牙形石作为标准化石的呼声也很

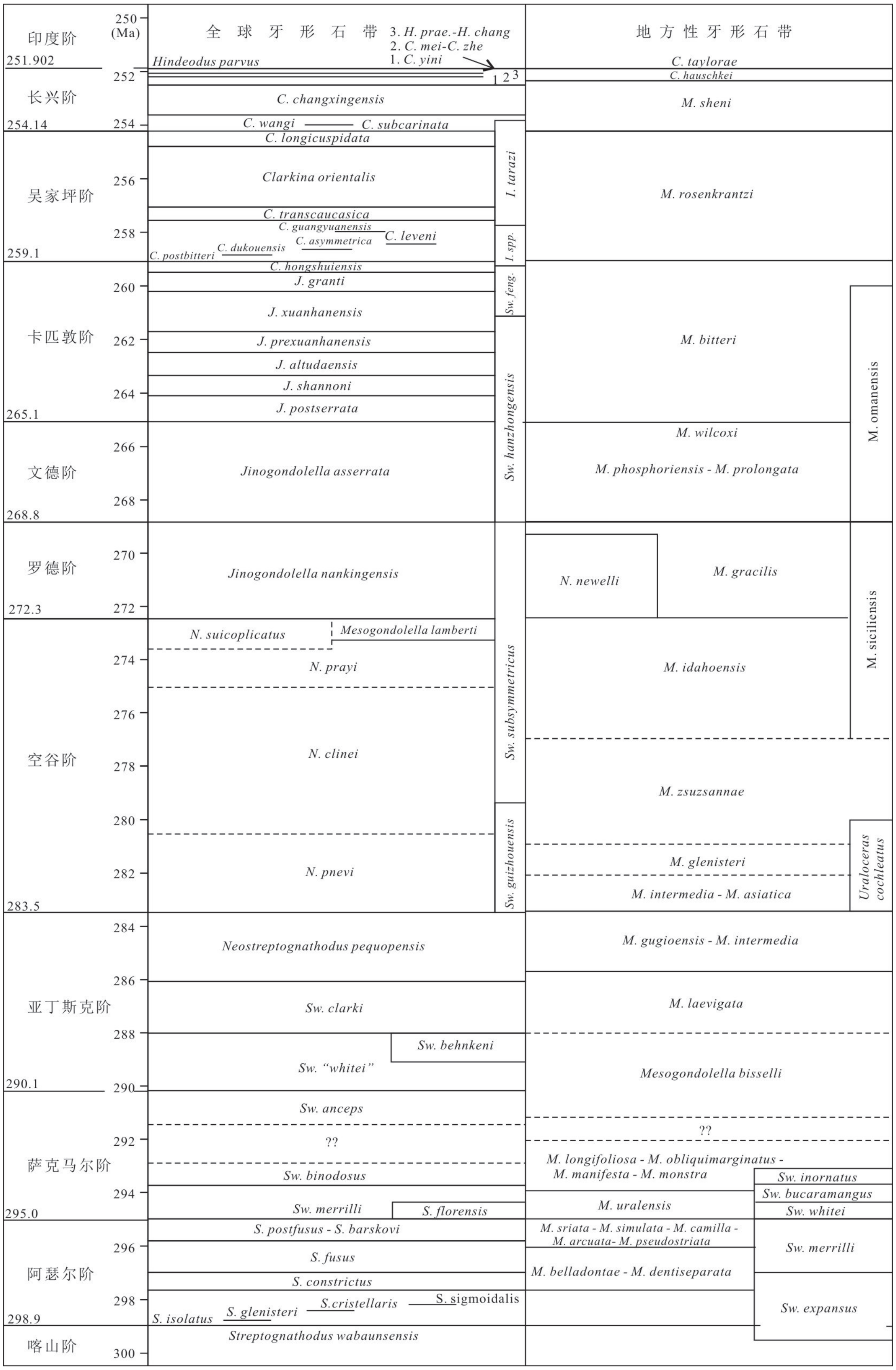

图1 二叠纪-早三叠世最早期牙形石带，包括40个可全球对比的牙形石带及35个地方性牙形石带(修改自Henderson，2016)

Fig.1 Permian-Earliest Triassic conodont zonation, including 40 global-correlative conodont zones and 35 regional conodont zones (modified from Henderson, 2016)

时代		喜马拉雅地区 Chhabra and Sahni, 1981 Sweet, 1970a	我国华南 巢湖 Zhao *et al.*, 2007	我国华南 甲戌 Chen *et al.*, 2015	美国西部 Paull, 1980	我国西藏 王志浩和王义刚, 1995	加拿大 Orchard and Tozer, 1997b Orchard and Zonneveld, 2009		俄罗斯 Siberia Dagis, 1984	俄罗斯 Primorye Markevich and Zakharov, 2004 Igo, 2009	挪威 Nakrem *et al.*, 2008	国际牙形石带 Kozur, 1993
奥伦尼克阶	史帕斯亚阶	*Ng. jubata* *Tr. homeri*	*Ns. anhuiensis* *Tr. homeri* *Nv. pingding-shanensis*	*Tr. homeri* *Ic. collinsoni* *Nv. pingding-shanensis*	*Ng. jubata* *Ic. collinsoni*	*Ng. jubata-Ns. triangularis*	*Tr. symmetricus* *Ns. triangularis* *Ic. collinsoni* *Ic. crassatus*	*Ng. regale* *Na. aff. taimy-rensis* *Ng. elongata* *Bo.* aff. *sweeti*	*Ng. jubata*		*Ng. ex. gr. regale*	*Ns. triangularis* *Tr. homeri* *Ic. collinsoni* *Tr. hungaricus*
奥伦尼克阶	史密斯亚阶	*Nv. waageni*	*Nv. waageni*: *Nv. w. wa-ageni* *Nv. w. eo-waageni*	*Par. peculiaris-Pac.* *Ds. discreta* *Nv. w. waageni* *Nv. w. eowaageni*	*Sc. milleri* *Nv. waageni*	*Sc. milleri* *Nv. waageni*	*Nv. waageni*	*Sc. mosheri*: *Sc. milleri* *Sc. phryna* *Pu. meeki* *Sc. lachry-miformis*	*Ng. milleri* *Ng. mosheri* *Nv. waageni*	*Sc. milleri* *Nv. waageni-Ns. novaeho-llandiae*	*Sc. milleri* *Sc. mosheri* *Sc.* n. sp. *Nv. waageni*	*Nv. waageni-Sc. milleri* *Nv. waageni-Pau. meeki*
印度阶	第纳尔亚阶	*Ns. pakist-anensis* *Ns. cristagalli* *Ns. dieneri* *Sw. kummeli*	*Ns. dieneri*: *Ns. dieneri* M3 *Ns. dieneri* M2 *Ns. dieneri* M1 *Sw. kummeli*	*Ns. cristagalli-Eu. costatus*	*Ns. pakist-anensis* *Sw. kummeli-Ns. cristagalli*	*Ns. pakist-anensis* *Ns. cristagalli* *Sw. kummeli*	*Ns. pakist-anensis* *Ns. dieneri*	*Bo. nepalensis* *Ns. cristagalli* *Sw. kummeli*	*Bo. nepalensis*	*Ns. dieneri-Ns. pakist-anensis*	*Ns. pakist-anensis* *Ns. dieneri*	*Bo. nepalensis* *Ns. dieneri* *Sw. kummeli*
印度阶	格里斯巴赫亚阶	*Nc. discreta* *C. krystyni* *I. isarcica* *H. parvus*	*C. krystyni* *H. typicalis*	*Nc. discreta* *C. krystyni* *H. sosioensis* *H. parvus*	*I. isarcica* *H. typicalis*	*C. carinata* *H. parvus*	*Ns. peculiaris* *C. carinata* *C. taylorae-H. parvus* *C. meishanensis*	*C.* n. sp. E *C.* n. sp. D		*C. carinata*	*C. carinata*	*C. postcarinata* *H. postparvus-H. sosioensis* / *C. carinata* *I. isarcica* *H. parvus*

图 2　早三叠世国际不同地区牙形石带

Fig.2　Early Triassic global conodont zonation

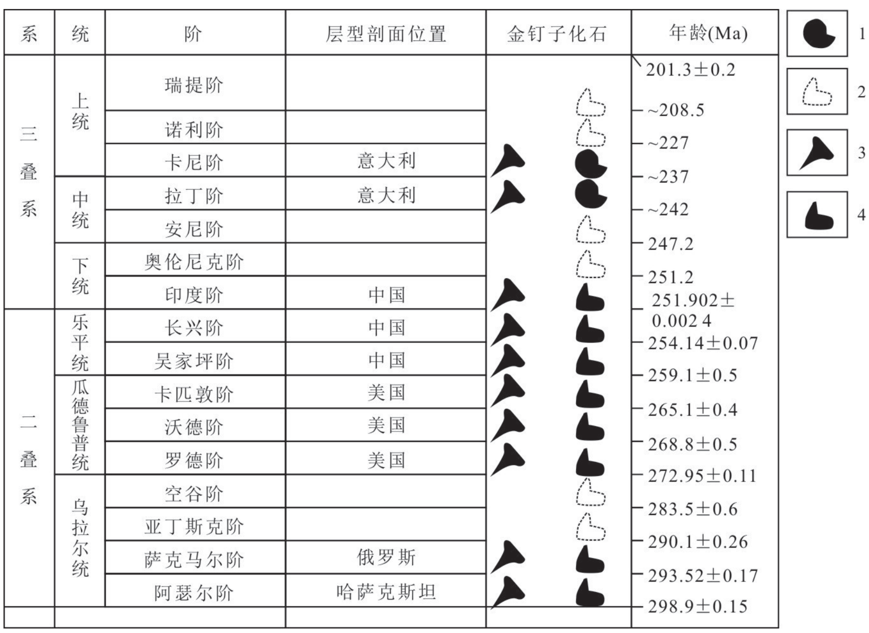

图 3　国际二叠纪-三叠纪年代地层划分及界线层型“金钉子”化石研究现状

Fig.3　Division of Permian-Triassic international chronostratigraphic units and locations of the GSSPs

1.菊石“金钉子”;2.有望以牙形石作为“金钉子”;3.已确认的金钉子;4.牙形石“金钉子”;界线年龄引自2021年5月国际年代地层表

高,如下三叠统印度阶-奥伦尼克阶界线(Tong *et al.*, 2003, 2004; Krystyn *et al.*, 2007).最近,Chen *et al.*(2020b)对位于华南南盘江地区的湾头和幼平剖面开展了多方面的详细研究,包括牙形石、菊石、磁极性、无机碳同位素、海水温度、锆石定年等,认为这两个剖面也具有以 *Chiosella timorensis* 在剖面中的首现作为安尼阶“金钉子”标志,进而作为候选层型剖面的潜力.

2.4　牙形石整体相关带研究

全球界线层型剖面中标准化石的首现点(FAD),应当是该化石在世界范围内的最早出现点(Henderson, 2006).但是,FAD是物种的演化历史、

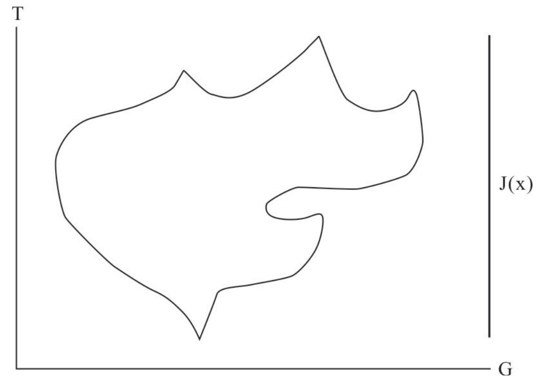

图4　物种x在时间和空间上的分布

Fig.4　Tempo and space distributions of species x

修改自Guex *et al.*(1991);J(x)表示该物种x在地层中出现的集合,G表示物种x的生存范围,T表示物种在地质历史中存在的时间范围

传播、生物相、保存、野外采集以及分类学的综合反映,因此,使用FAD去定义全球年代地层单元可能会导致许多问题(Landing *et al.*, 2013).比如,国际三叠系底界"金钉子"以*Hindeodus parvus*在华南下扬子地区浙江省长兴县煤山D剖面27层中间的首现作为标准(Yin *et al.*, 2001),因此*Hindeodus parvus*则被认为在世界范围内最早起源于煤山剖面.然而,最近却陆续有研究表明,华南地区的上寺、中寨、戴家沟剖面却存在*Hindeodus parvus*首现点与划定的二叠系-三叠系界线不一致的现象(Jiang *et al.*, 2011;Zhang *et al.*, 2014;Yuan *et al.*, 2015).而出现这种现象的原因,可以总结为以下三点:(1)生物对环境有一定的选择性,以*Hindeodus parvus*为代表的这个物种在不同的环境中出现的时间不一样(图4);(2)后期侵蚀作用或者"Signor-Lipps"效应(Signor and Lipps, 1982)的存在导致了不同剖面相同生物的不等时性出现;(3)生物的迁移需要一定的时间,相隔较远的剖面可能意味着更远的生物迁移距离,进而导致生物的首现时间不一致.

因此,在前人所报道的剖面中,经常出现两个种类的化石在不同剖面中的首现点出现矛盾的现象.例如在广西武篆剖面,Brosse *et al.*(2015)报道的*Hindeodus parvus*的首现点位于该剖面中*Hindeodus praeparvus*首现点之下,而在大文剖面,*Hindeodus parvus*的首现点则位于*Hindeodus praeparvus*首现点之上(Chen *et al.*, 2009).总之,大多数情况下使用化石首现点建立的生物间隔带会有许多矛盾的地方.而使用唯一且互相排斥的物种组合作为单元所构成的离散年代表则可以解决这个问题.这种单元彼此之间不连接,且被化石所间隔开,基于此种方法建立的整体相关带则保留了不连续的物种分布特性.

相较之下,整体相关法(unitary associated methods;Guex, 1991)是一种输出定量且确定性的、建立于离散最大相关带之上的生物带方法.目前,在PAST软件上可以专门对相关数据进行操作(Hammer, 2013).此方法涉及到的化石之间的关系包括3种:(1)共生,即两种化石在相同的地层或者相同时间形成的地层中出现;(2)叠覆,即两种化石在地层中以不同的顺序出现;(3)排斥,即两种化石在任一地层中均只出现其中一种.此外,化石的共生关系还包括实共生和虚拟共生.实共生是指这两个化石种的共生至少在一个沉积岩层中被观察到,虚拟共生则是指由于各种因素导致在沉积岩层中观察不到两个化石种的共生,但是可以从它们与其他物种在地层种的关系中推断出相互共生的关系.使用整体相关法的首要前提是识别出单个剖面中的"最大水平层(local maximal horizon)".一个独立剖面地层单元中的某个含有化石的岩层,如果其中相互共生(包括实共生以及虚拟共生)的物种集合是一个最大集合,那么该层即可被称为最大水平层.

目前,已经有多个二叠纪-早三叠世之间的牙形石记录使用整体相关带这一定量生物地层学方法进行对比(Brosse *et al.*, 2016; Chen *et al.*, 2019b;Yuan *et al.*, 2019; Wu *et al.*, 2020).在意识到依赖牙形石首现点建立间隔带可能存在一定的对比问题之后,Brosse *et al.*(2016)搜集了华南12个剖面的牙形石数据以进行整体相关带的应用,包括朝天(Ji *et al.*, 2007)、黄芝山(陈军等, 2008)、边阳(Jiang *et al.*, 2015)、中寨(Metcalfe and Nicoll, 2007)、戴家沟(Yuan *et al.*, 2015)、煤山(Jiang *et al.*, 2007)、大文(Chen *et al.*, 2009)、打讲(Jiang *et al.*, 2014)、上寺(Jiang *et al.*, 2011)、沿沟(Sun *et al.*, 2012a)、大峡口(Zhao *et al.*, 2013a)、武篆(Brosse *et al.*, 2015).由于部分化石数量较少的剖面易导致化石种之间关系的不清楚,因此其研究中先剔除了前5个剖面的牙形石数据(Brosse *et al.*, 2016).同时,由于只在单个剖面中出现的化石并没有地层对比的价值,甚至会产生更多的矛盾,因此也进行了剔除(Monnet and Bucher, 1999; Xiao *et al.*, 2018a).随后在识别各化石之间关系的过程中,也会出现一些需要更改化石实际延限的矛盾.例

如，若只是根据搜集到的7个剖面的资料，只能判断出 *Hindeodus postparvus* 与 *Clarkina taylorae* 存在共生关系．因此，综合考虑化石种的生态学特性以及在PAST软件中得到的初步结果，他们将 *Clarkina taylorae* 的顶界进行了合理的上移，最后得出了在PAST软件中没有任何矛盾的结果．由于整体相关法强调的是不同剖面之间的对比，因此得到了牙形石整体相关带之后，他们还考虑了不同整体相关带之间的侧向再现率（lateral reproductivity）．对于低侧向再现率的整体相关带需要进行合并，从而形成更高侧向连续率的整体相关带．最后，该研究在二叠系-三叠系附近共识别了6个整体相关带．这些整体相关带均由若干化石种组成，并且每一个都包含特征化石．

近来，还有几例整体相关法在古、中生代之交牙形石记录中的应用．Chen *et al.*（2019b）对Smithian牙形石整体相关带开展的研究表明，来自当时不同纬度的9个剖面，即使发育有不太一致的牙形石序列，它们依然可以被使用整体相关带来进行对比，而这其中的关键是利用整体相关法识别出了具有对比意义的牙形石属种，如几乎从不被单独用来建带的 *Neospathodus curtatus* 是其UAZ6的特征种．最近笔者对华南28条剖面中的早三叠世牙形石记录进行系统总结之后，采用整体相关法将华南早三叠世的牙形石进行了详细的划分（Wu *et al.*，2020）．结果表明，虽然牙形石整体相关带的对比分辨率可能比间隔带更高，但是整体相关带也有一定的局限性，包括该方法主要依据地层的生物学特征而容易忽略其他的地层学对比证据，以及其在定义关键的地质界线时依然具有不确定性（Wu *et al.*，2020）．值得一提的是，Yuan *et al.*（2019）在研究二叠纪牙形石过程中，统计了华南若干条乐平世剖面中的牙形石数据，随后采用整体相关法开展研究．值得注意的是，其在分析过程中未产生数据之间的矛盾，这极有可能是由于他们所采用的牙形石鉴定标准为"样品居群"法，进而减少了原始数据的误差数量，而这也进一步表明，"样品居群"法在舟形牙形石分子的鉴定过程中可能确实具有一定的指导意义．

3 牙形石地球化学研究

作为晚古生代最后一个纪，二叠纪延续了近47 Ma，这期间发生了许多重大地质事件，包括生物、环境、构造、古地磁等多方面的变化（Lucas and Shen，2018；Shen *et al.*，2019a，2020）．冈瓦纳大陆与欧美大陆发生碰撞后，形成了Pangea大陆（Scotese，2009）．在Pangea大陆形成与裂解的过程中，全球范围内发生了大量的火山活动，包括瓜德鲁普统末期华南峨眉山玄武岩喷发（Zhou *et al.*，2002；He *et al.*，2007a），二叠纪末期西伯利亚火山喷发（Ivanov *et al.*，2013；Burgess and Bowring，2015；Burgess *et al.*，2017）以及华南广泛的火山活动等（He *et al.*，2014）．另外，该时期具有显生宙以来最低的大气二氧化碳浓度、最高的氧气浓度（Berner，2006），并见证了最古老的热带雨林的演化与扩张（Cleal and Thomas，2005）以及最大海退事件（Haq and Schutter，2008）．在二叠纪-三叠纪之交发生了显生宙以来最大一次生物大灭绝事件之后（Erwin，1993，1994；Song *et al.*，2013；Stanley，2016），生态系经历了漫长的复苏，才恢复到正常的水平（Chen and Benton，2012；Song *et al.*，2018）．期间，极端高温、海洋缺氧、大陆风化作用加剧等事件也进一步表明该时期环境条件和生物演化的复杂性（Isozaki，1997；Algeo *et al.*，2011；Song *et al.*，2014）．牙形石的主要成分为磷酸钙，能够很好地保存当时海水的地球化学信息，其氧同位素以及微量元素研究，极大地帮助了人们对此复杂过程的理解（Song *et al.*，2012；Sun *et al.*，2012b）．

3.1 牙形石氧同位素对古海水温度的指示

牙形石的氧同位素数据已经广泛地被用来恢复古海水的温度（Joachimski and Buggusch，2002；Joachimski *et al.*，2009，2012；Chen *et al.*，2011，2013a；Sun *et al.*，2012b；Romano *et al.*，2013；Trotter *et al.*，2015；Huang *et al.*，2018；刘康等，2021）．涉及到的牙形石氧同位素分析方法包括传统的牙形石酸溶解法（Huang *et al.*，2016）和激光剥蚀法（周丽芹等，2012；Chen *et al.*，2016a）．前者是通过硝酸使牙形石溶解，然后将磷酸根以磷酸银的形式沉淀出来，最后通过质谱仪测试其氧同位素成分（Joachimski *et al.*，2009）；后者是使用激光原位二次离子质谱仪直接对牙形石进行氧同位素测试（Trotter *et al.*，2008）．值得注意的是，有学者提出，采用后一种方法进行实验测试时，选择使用的参考物质（references materials）需要谨慎（Sun *et al.*，2016）．

由于牙形石氧同位素测试对标本及方法的要

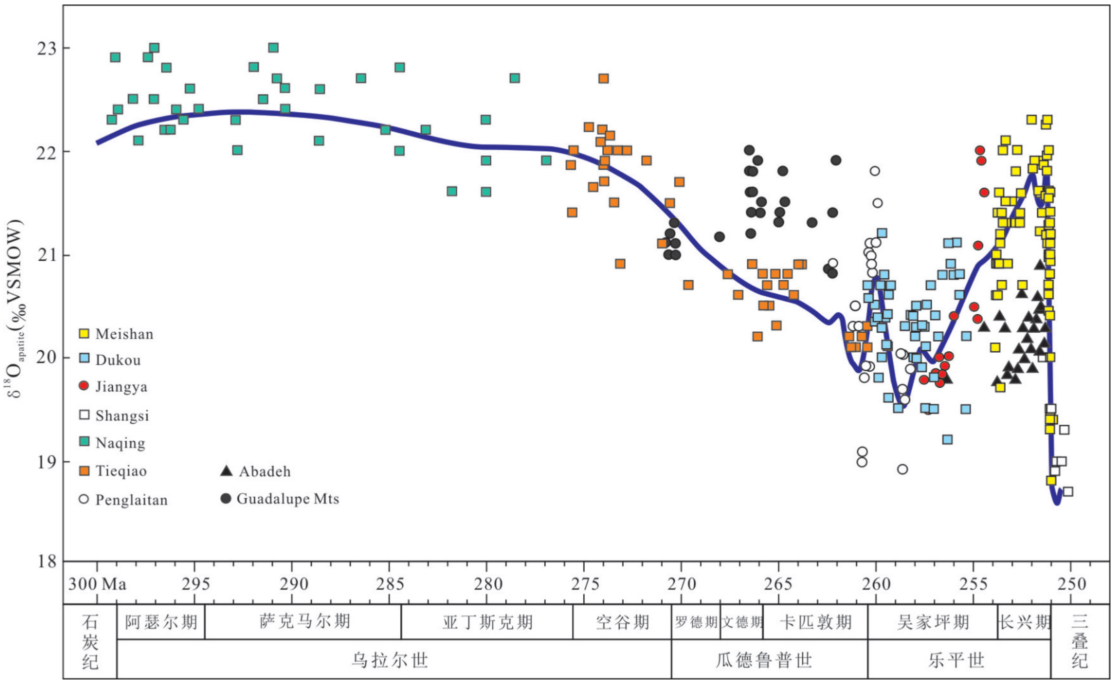

图5　二叠纪牙形石氧同位素变化曲线(修改自Chen *et al.*, 2013a)

Fig.5　Permian conodont oxygen isotopes curves (modified from Chen *et al.*, 2013a)

求较高,目前全球范围内二叠纪牙形石氧同位素的报道并不多:其一是有关瓜德鲁普统与乐平统界线附近的研究(Chen *et al.*, 2011),其二是通过对全球低纬度地区若干个剖面的研究,恢复整个二叠纪的氧同位素演化曲线,如图5所示(Chen *et al.*, 2013a).自阿瑟尔期(乌拉尔世)早期以来,牙形石的氧同位素的数值保持在22‰~23‰左右,呈现出比较平稳的趋势,直到空谷期(乌拉尔世)早期开始出现明显的下降.而前人通过古植物学的证据认为,该时间段具有明显的潮湿型气候(Hilton and Cleal, 2007).因此,早二叠世较高的牙形石氧同位素也反映出当时晚古生代冰期的扩张,在华南地区以较轻的氧同位素进入到大陆冰体而海水中氧同位素值升高的形式留下了证据.同时当时处于赤道附近的华南在早二叠世有大量的碳酸盐岩沉积,并且出现丰富的暖水型动物,如蜓、皱饰珊瑚、建礁型珊瑚(Shi and Shen, 2000; Wang *et al.*, 2006a, 2006b),表明华南当时所处位置海水的温度是极其温暖的,而根据Chen *et al.* (2013a)得到的牙形石氧同位素结果恢复的古海水温度也符合这一说法.在中二叠世,自空谷早期或中期以来,牙形石氧同位素呈现出逐渐降低的趋势,在卡匹敦晚期到最低点(图5),这种变化可能对应着8 ℃的升温,亦或是由于冰川消融而导致的200 m的海平面变化(上升).这个阶段氧同位素的变化,表明了晚古生代冰期的消融主要出现在空谷期-卡匹敦期.在瓜德鲁普统-乐平统之交,牙形石氧同位素曲线表明,在卡匹敦晚期,古海水温度出现了约4 ℃的升温,随后在界线附近出现了约6~8 ℃的降温,而最后又在吴家坪早期出现明显的升温(图5和图6).牙形石氧同位素快速变化的这个区间,与峨眉山玄武岩的喷发和当时动荡的海平面变化相耦合(Chen *et al.*, 2011).

牙形石氧同位素最为显著的变化位于二叠纪-三叠纪界线附近以及早三叠世(Joachimski *et al.*, 2012; Sun *et al.*, 2012b; Chen *et al.*, 2016a). Joachimski *et al.* (2012)率先对煤山和上寺剖面的牙形石进行了氧同位素分析,发现其值在二叠纪最晚期降低了2‰,而这也表明当时海水的温度升高了有8 ℃之多,而此次温度开始上升的时间稍早于二叠纪末期的灭绝(Joachimski *et al.*, 2012; Song *et al.*, 2013).然而,来自于华南煤山、上寺、戴家沟、凉风垭蓬莱滩剖面的激光剥蚀法牙形石氧同位素结果表明,二叠纪-三叠纪界线附近的温度上升幅度甚至达到了10 ℃,同时温度显著上升的时间则晚于第一次灭绝(Chen *et al.*, 2016a; Shen *et al.*, 2019b).最近来自伊朗和亚美尼亚地区的研究也证实,二叠纪-三叠纪之交高温事件的全球性(Joachimski *et al.*, 2020; Chen *et al.*, 2020a).

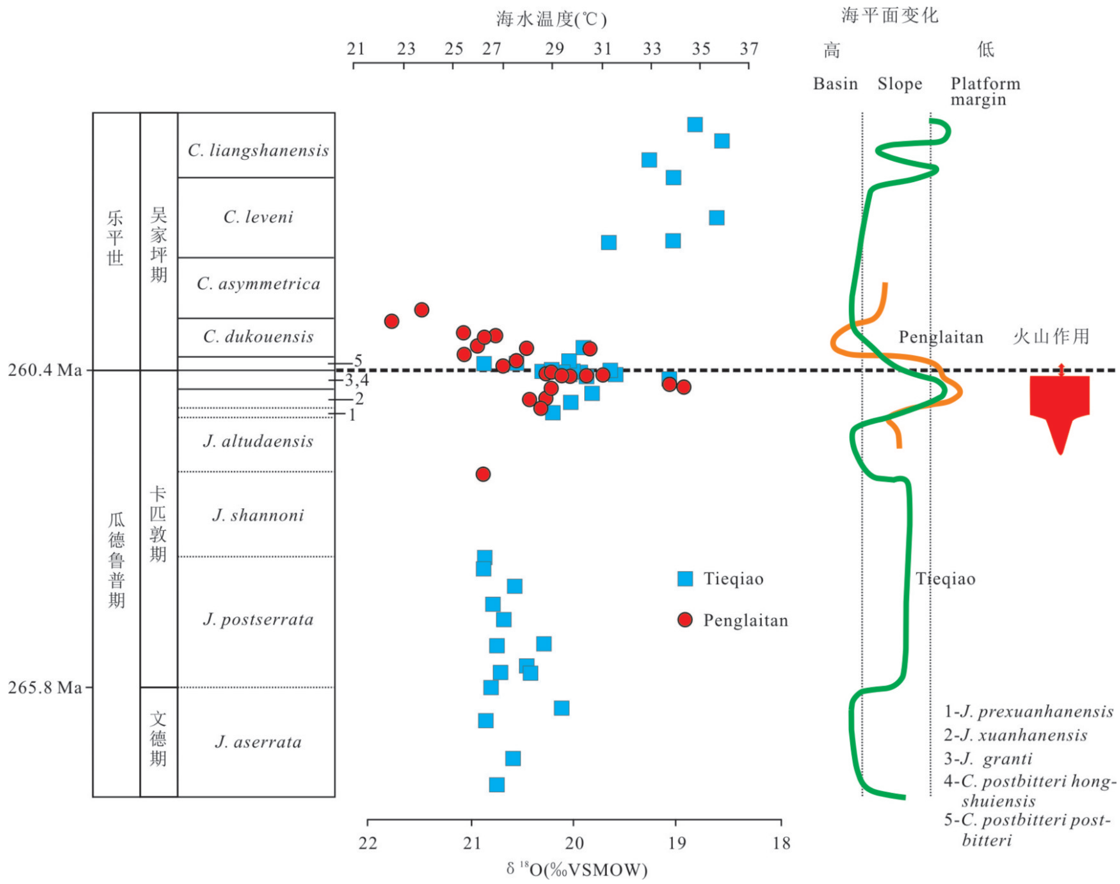

图 6　蓬莱滩、铁桥剖面牙形石氧同位素变化曲线及海平面变化(修改自 Chen *et al.*, 2011)

Fig.6　Conodont oxygen isotopes curves and sea level changes of the Penglaitan and Tieqiao sections (modified from Chen *et al.*, 2011)

在早三叠世,牙形石氧同位素研究结果显示这个阶段的古海水温度也有显著的变化,这些变化也与菊石在早三叠世全球的空间分布显示出动态的耦合关系(Brayard *et al.*, 2006).其中,最明显的变化位于以史密斯亚期-史帕斯亚期界线附近,当时浅层海水温度甚至达到 40 ℃以上,超过了二叠纪-三叠纪界线附近的最高值(Sun *et al.*, 2012b).值得注意的是,牙形石氧同位素研究结果显示早三叠世海水温度处于一个急剧变化的状态,虽然其整体温度较高,并且高温一直持续到了早三叠世晚期,但是在印度期-奥伦尼克期界线附近,海水温度存在一个明显的降温过程,而当时的游泳型生物,尤其以牙形石和菊石为代表,出现了明显的复苏迹象,表现出个体大小增加以及多样性的升高(Wu *et al.*, 2020).另外,史密斯亚期-史帕斯亚期界线极端高温之后也发生了一次明显的海水降温过程(Goudemand *et al.*, 2019).本次降温过程则被认为造成了一次显著的次级灭绝事件(Song *et al.*, 2019),造成本次降温的原因,也可能与当时逐渐升高的海平面及底部缺氧海水上涌有关(Zhang *et al.*, 2021).最近,Chen *et al.* (2021)也报道了一例早三叠世史密斯-史帕斯界线附近牙形石氧同位素的研究,但是其主要以不同属种牙形石的生态为出发点,结果表明该时期的齿台型(*Neogondolella*)牙形石分子生活水深比齿片型(neospathodids 和 *Icriospathodus*)牙形石分子更深.值得注意的是,从其恢复的结果来看,当时阿曼地区的海水温度在史密斯-史帕斯界线附近也存在高温现象,达到 40 ℃左右.

3.2　微量元素

目前,虽然有报道质疑牙形石微量元素对古海水指标的指示能力(Zhao *et al.*, 2013b; Chen *et al.*, 2015; Trotter *et al.*, 2016; Zhang *et al.*, 2016, 2017; Medici *et al.*, 2021),但是仍然有一些可靠的相关研究被报道,如前人通过牙形石 Sr 同位素(Song *et al.*, 2015)、Ce 异常(赵来时等, 2009; 陈剑波等, 2012; Song *et al.*, 2012)恢复了早三叠世大陆风化作用强度以及古海水氧化还原条件等.

3.2.1　牙形石锶同位素对陆源风化以及地层对比的指示　海水锶同位素组成主要有两个影响因素，分别为河流输入和海底洋中脊热液．其中，河流输入的锶同位素比值平均为0.711 9，而洋中脊热液中锶同位素比值平均为0.703 5．锶在海水中的停留时间约为3×10^6 a（Palmer and Edmond，1989；Hodell *et al.*，1990）．因此，锶同位素比值的变化可用于反映陆源输入的变化．陆源输入是陆地生态系统和海洋生态系统联系的纽带．

Song *et al.*（2015）通过对浙江长兴煤山剖面、贵州青岩、关刀剖面牙形石锶同位素的测定，重建了晚二叠世至晚三叠世早期$^{87}Sr/^{86}Sr$变化曲线（图7）．研究显示，早三叠世的陆地风化速率比晚二叠世增强了1.9倍，这可能与高温和植被的消失有关．直到史帕斯亚阶中晚期，锶同位素的比值才有所下降，表明当时陆地风化作用开始减弱．而前人的研究表明，在该时期陆地森林开始出现（Looy *et al.*，1999）、海水缺氧程度降低（Song *et al.*，2012）、底栖生态系统也快速复苏（Song *et al.*，2011），这些均与陆地风化作用降低有所联系．在中三叠世，锶同位素的比值逐渐降低并趋于稳定，但是依然保持在晚二叠纪水平的1.2倍左右．

另外，最近有学者对二叠纪-三叠纪之交赤道附近若干个剖面的牙形石进行了Sr同位素的研究，结果表明海水中Sr同位素快速上升比煤山剖面的生物灭绝出现得更早，而这也可以进一步表明二叠纪三叠纪之交的生物大灭绝在陆地上比海洋中出现得更早（Dudás *et al.*，2017）．同样，来自南盘江盆地碳酸盐岩台地相区的多个剖面的研究表明，在当时海洋出现生物大灭绝之前便有部分有孔虫消失，与之相伴的则是海相地层中大量硅质碎屑的沉积，进一步加强了当时陆相生态系统比海洋生态系统更早崩塌的可能性（Xiao *et al.*，2018b；Tian *et al.*，2019）．

3.2.2　Ce异常、Th/U比对海水氧化还原条件的指示　在沉积物中，Ce异常以及Th/U比均可以反映古海水的氧化还原条件．氧化条件下，可溶性的Ce^{3+}离子会被氧化，形成CeO_2沉淀在沉积物中，

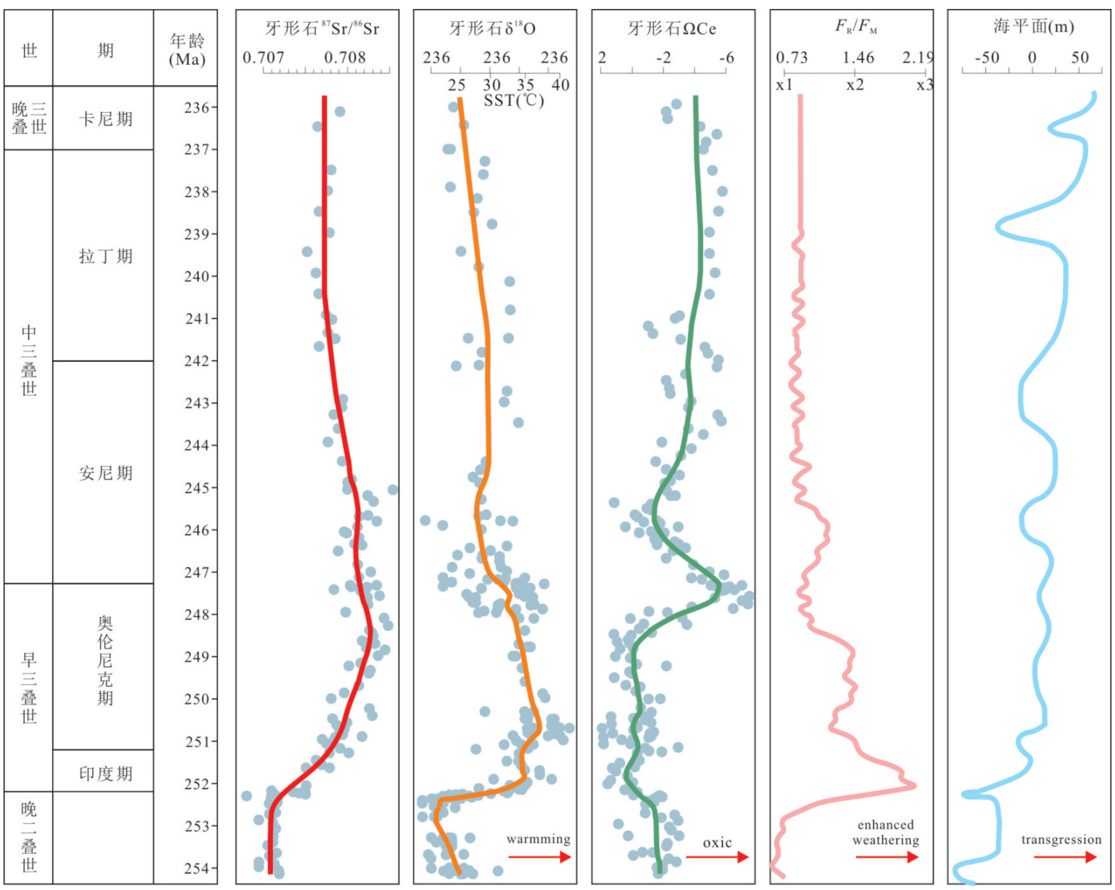

图7　早三叠世牙形石锶同位素、海水温度、氧化还原状态及海平面变化曲线(修改自Song *et al.*, 2015)

Fig.7　Sr isotpes, temperature, redox conditions of the sea water and sea level change during the Early Triassic (modified from Song *et al.*, 2015)

而其他镧系元素则不会被氧化还原条件影响而形成沉淀(Liu *et al.*, 1988).如果假定生物的磷酸盐壳体中继承了古海水的REE分布模式,那么当Ce出现明显的负异常时,表明水体处于氧化环境,而Ce与其他稀土元素含量相当时,表明水体处于还原环境.另外,U元素有两种不同的氧化还原状态,分别为＋6价以及＋4价.＋6价的U在氧化条件下是可溶并且稳定的,在缺氧条件下,＋6价的U会被还原成不可溶性的＋4价.值得注意的是,Th在水体中的溶解度是不受氧化还原条件影响的,因此在缺氧条件下,水体中Th/U比值就会升高(Wignall and Meyers, 1988).在有关早(中)三叠牙形石的研究中,前人利用Ce异常、Th/U比共识别出4个阶段(包括一次发生在中三叠世)的海洋缺氧事件:(1)长兴晚期-格利斯巴赫亚期;(2)史密斯亚期-史帕斯亚期最早期;(3)史帕斯中期;(4)安尼早期(Song *et al.*, 2012).Li *et al.*(2017)报道了江西岩沟剖面二叠纪-三叠纪界线附近牙形石的稀土元素特征,他们使用激光剥蚀法对单颗牙形石分子细齿进行质谱分析,结果表明在二叠纪末大灭绝之前牙形石出现了Ce的正异常以及U浓度降低的现象,进而得到深部海水期次性上涌而导致浅海缺氧的结论.

3.3　牙形石钙同位素对海水酸碱度的指示

牙形石的主要成分为氟磷酸钙,具有对热动力极高的耐受性,同时牙形石晶体结构致密,其钙同位素组成可以为恢复地质历史时期海水钙循环特征提供重要信息(Hinojosa *et al.*, 2012).在古中生代之交,西伯利亚火山岩省的喷发致使大气圈中二氧化碳气体含量急剧升高,甚至达到了6倍之多(Wu *et al.*, 2021).来自煤山二叠纪-三叠纪之交牙形石钙同位素的研究表明,当时的海水酸度明显升高,与当时的高浓度大气二氧化碳呈现出明显的时间相关性(Hinojosa *et al.*, 2012).最近Song *et al.*(2021)对来自华南多条剖面的牙形石样品进行了钙同位素研究,不仅证实了二叠纪-三叠纪之交海水酸化这一观点,还发现海水分别在早三叠世史密斯-史帕斯亚期之交以及早-中三叠世之交出现了不同程度的酸化现象.值得一提的是,近来相关研究表明,早三叠世Smithian/Spathian之交的海洋酸化事件也明显影响到了碳酸盐岩钙同位素的组成(Zhao *et al.*, 2020).

4　牙形石形体演化研究

4.1　牙形石"小型化"现象

个体大小是生物形态学重要的指标之一,是生物的生物学、行为学以及生态学等的综合体现(Barbault, 1988; Cotgreave, 1993).Cope在19世纪末就提出:由于大个体对生物的生存更有利,因此生物的个体大小在演化史上是逐渐变大的(Cope, 1885, 1896).为了验证这个观点,Heim *et al.*(2015)统计了542 Ma以来包括17 208个属的海洋生物个体大小,他们发现自寒武纪以来生物个体大小是逐渐增加的.Urbanek(1993)发现,在灭绝时间之后,化石个体的大小明显比灭绝之前的个体大小要小,于是便将该种现象命名为"小型化".同时,除了个体变小之外,Urbanek(1993)还发现大灭绝之后的生物出现了明显的低分异度以及高丰度的现象.显生宙以来,"小型化"事件已经多次在大灭绝事件中被报道,比如志留纪早期的珊瑚(Kaljo, 1996)、泥盆纪晚期的牙形石(Girard and Renaud, 1996; Renaud and Girard, 1999)以及丹麦阶的海胆类(Jeffery, 2001)等.

二叠纪-三叠纪之交生物大灭绝位于显生宙5大灭绝之首(Erwin, 1993, 1994; Stanley, 2016),其后海洋和陆地生态系统长期处于崩溃状态(McGhee *et al.*, 2004; Chen and Benton, 2012),影响了众多门类生物的个体大小演化(Schaal *et al.*, 2016).Newell(1952)首次报道了早三叠世处于"小型化"状态的化石,之后有关此方面的报道则逐渐变多(如:Hayami, 1997, 1998).近来,古-中生代之交生物大灭绝事件中的生物个体大小变化也得到越来越多学者的关注.目前研究最多的是二叠纪-三叠纪之交腕足类个体大小的变化(He *et al.*, 2007b, 2010, 2015, 2016, 2017; Shi *et al.*, 2016; Zhang *et al.*, 2016; Wu *et al.*, 2018; Chen *et al.*, 2019a),除此之外,有孔虫(Song *et al.*, 2011)、腹足类(Payne *et al.*, 2004; Brayard *et al.*, 2015; Nützel *et al.*, 2018)、介形虫(Chu *et al.*, 2015)等的研究也有少量的报道.这些研究表明,温度、氧化还原条件以及食物来源均会对生物个体大小产生明显的影响.值得注意的是,Twitchett早在2007年便提出了生物小型化的4种机理:(1)大型生物个体灭绝;(2)灭绝后小型生物个体变多;(3)大个体暂时性消失;(4)生物个体短期变小(Twitchett, 2007).

早三叠世牙形石个体大小变化研究最早在浙江煤山剖面以及贵州甲戎剖面开展(Luo *et al.*, 2006, 2008b; Chen *et al.*, 2013b).煤山剖面牙形石的研究表明,舟形分子 *Clarkina* 在24e层发生了明显的个体变小现象,而这也与二叠纪–三叠纪之交生物大灭绝的第一幕时间一致(Luo *et al.*, 2006; Song *et al.*, 2013).不仅如此,*Hindeodus*-*Isacicella* 谱系在二叠纪–三叠纪之交也出现了个体大小振荡性变化的现象(Luo *et al.*, 2008b).贵州甲戎剖面牙形石分子的个体大小变化则表明,早三叠世的极热事件使牙形石个体明显变小(Chen *et al.*, 2013b).Leu *et al.* (2019)研究了西藏土隆剖面、巴基斯坦Salt Range剖面、克什米尔Guryul Ravine剖面SS之交的牙形石大小,他们发现不同类型的牙形石在界线附近大小变化不一致.通过对位于南盘江地区的摩天岭剖面进行牙形石个体大小统计后,笔者发现早三叠世的牙形石大小展现出极其快速的变化,与当时的海水条件变化有着明显的关联(Wu *et al.*, 2019).

4.2 牙形石"返祖"现象

在二叠纪–三叠纪之交,作为两个主要类型的牙形石,Gondolelloidea和Anchignathodontidae在此时期经历了不同的演化历史.最显著的变化则发生在二叠纪–三叠纪生物大灭绝事件附近,以 *Clarkina* 为代表的舟形牙形石分子在早三叠世格里斯巴赫亚阶早中期很多地区消失,而以 *Hindeodus* 为代表的梳形分子的分异度以及丰度均有明显的上升(Orchard, 2007).Guex (2016)认为,相对于以 *Hindeodus* 为代表的梳形分子,以 *Clarkina* 为代表的舟形分子代表了牙形石更高级的形态.如图8所示,沿着"*Neospathodus*" *arcucristatus*-*Protoclarkina crofti*-*Clarkina bitteri*-*C. meishanensis*-*C. krystyni* 的演化顺序,牙形石分子出现了明显的齿台向两侧增加变大的现象.由于早三叠世恶劣的环境压力,与"*Neospathodus*" *arcucristatus* 有类似特征的 *Kashmirella timorensis* 出现了齿台消失的现象.实际上,这种现象不仅出现在牙形石个体身上,在菊石、放射虫、有孔虫以及头足类等海洋动物中均有发生.而出现该现象的原因,Guex (2016)也主要归咎于灾难性的环境变化.但是导致这种现象出现的内部机制、基因记忆是如何保存、为何原始形态的生物对环境有更高的耐受力以及这种"返祖"现象快速消失的原因,这些都是需要解决的问题.

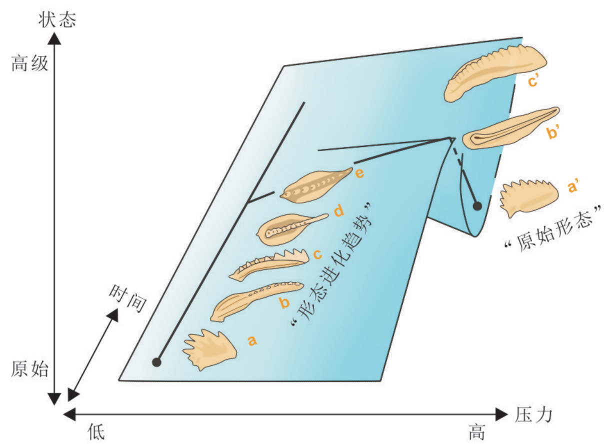

图8 早三叠牙形石演化过程中"返祖现象"(修改自Guex, 2016)

Fig.8 "Retrograde" evolution of the conodont during the Early Triassic (modified from Guex, 2016)

a. "*Neospathodus*" *arcucristatus*; b. *Protoclarkina crofri*; c. *Clarkina bitteri*; d. *C. meishanensis*; e. *C. krystyni*; a'. *Kashmirella timorensis*; b'. *Paragondolella regale*; c'. *P. excels*

5 结论

二叠纪–早三叠世牙形石相关研究包括生物学、地层学、地球化学等众多方面,近些年来均取得了较大进展.由于生物地理分区的影响,目前二叠纪可建立40个全球可对比性牙形石带以及35个区域性牙形石带,而早三叠世的牙形石带则可以进行全球性广泛对比.此时间段内以牙形石作为"金钉子"的有阿瑟尔阶、萨克马尔阶、罗德阶、沃德阶、卡匹敦阶、吴家坪阶、长兴阶和印度阶,另外 *Novispathodus waageni* 和 *Chiosella timorensis* 也有望被选为奥伦尼克阶以及安尼阶底界"金钉子"的标准化石并建立层型剖面.在生物大灭绝过程中,牙形石虽然表现出快速复苏的迹象,但是其仍然受到了环境变化的影响,出现了"小型化"和"返祖"等现象.牙形石地球化学的工作,可帮助研究人员极大程度地理解大灭绝附近以及之后环境演化的复杂历程,包括极端高温与缺氧事件等.

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