



# 古生代-中生代之交海洋生物泵演变与浮游革命

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**摘要** 探究深时海洋生物泵的演变, 对理解现代海洋碳循环的过程和机制有重要启示意义. 显生宙海洋生物泵主要包括两种类型: 古生代型(古生代-中三叠世)和现代型(晚三叠世-现代). 古生代型生物泵以浅海底栖藻类和浮游疑源类为主导, 现代型由远洋超微浮游生物主导. 此外, 在二叠纪-三叠纪之交大灭绝这一特殊地质历史时期, 由于古生代型的海洋生物泵遭到摧毁, 海洋的碳循环被扰乱, 海洋中短暂出现了由蓝细菌和其他自养细菌为主导的特殊生物泵. 化石记录表明, 浮游藻类(颗石藻和沟鞭藻)在晚三叠世起源并在侏罗纪快速辐射, 促进了现代型远洋浮游生态系统的建立, 即“中生代海洋浮游革命”. 这被认为是中生代海洋化学革命的关键驱动因素, 同时也驱动了海洋底栖生态系统的重组(中生代海洋动物革命). 浮游藻类的繁盛增强了远洋生物泵和碳酸盐泵的固碳能力, 提升了海洋生态系统对碳循环扰动的缓冲能力. 因此, 关键海洋生产者的起源、演化及控制因素是深时碳循环领域未来需要重点研究的科学问题.

**关键词** 初级生产者, 生产力, 碳循环, 海洋浮游革命, 生物演化

## 1 现代海洋生物泵的形成

海洋碳库是地球表层最活跃的一个碳储库, 储量高达 $38.4 \times 10^{12}$  t<sup>[1,2]</sup>, 约为大气的53倍<sup>[3]</sup>, 其碳收支在很大程度上决定了全球气候变化的走向<sup>[4,5]</sup>. 然而, 由于各类物理、化学过程和海洋生态系统复杂的相互作用, 对海洋碳循环的途径和各类过程中碳交换的定量估算仍是一个颇具挑战性的课题, 尤其是海洋储碳机制, 更是研究全球变化及应对措施的核心内容之一<sup>[5]</sup>.

海洋生物泵、微型生物碳泵和碳酸盐泵共同驱动了海洋中的碳循环过程. 生物泵(biological pump)是海

洋主要的储碳途径之一. 其碳存储的主要过程为: 大气中的无机碳被海洋透光层中的生产者通过光合作用固定后, 再经过生物间相互作用和物理沉降, 最终进入深海和沉积物<sup>[6,7]</sup>. 硅藻、沟鞭藻和颗石藻等浮游藻类是现代海洋中的主要生产者, 它们的净初级生产力总量约占海洋生产力的80%, 是生物泵的重要组成部分<sup>[8,9]</sup>. 与这些浮游藻类相关的生源沉降颗粒物通量及其调控机制也是相关领域的研究热点<sup>[5,10]</sup>. 占海洋总有机碳库约90%的惰性有机碳库的形成与微型生物的作用密切相关<sup>[11]</sup>. 微生物(如细菌、古菌等)可以利用活性的溶解有机碳(dissolved organic carbon, DOC)生产生物难以利

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用的惰性溶解有机碳(recalcitrant dissolved organic carbon, RDOC),使得部分碳在水体长期积累,构成海洋水柱储碳.此外,细菌的裂解也是溶解有机碳库碳循环的重要途径.海洋中的病毒贡献了细菌死亡率的40%~60%,海洋初级生产力的约20%经由病毒裂解回到海洋溶解有机碳库再循环.细菌、古菌、病毒是微型生物碳泵(microbial carbon pump)<sup>[12,13]</sup>的主要成员.除了生成有机物外,海洋中的一些生产者还可以合成碳酸钙,比如底栖藻类中的珊瑚藻、浮游藻类中的颗石藻<sup>[14,15]</sup>.这些藻类在生长发育过程中产生的钙质外壳,是海洋碳酸盐岩沉积的主要来源,属于碳酸盐泵(carbonate pump)的主要组成部分<sup>[16~18]</sup>.在3个碳泵的共同作用下,碳酸盐补偿深度、溶跃面随海水和大气化学成分变化而升降,维持了碳循环在地球表层系统的稳定.

以古示今是地球科学领域思考和解决问题的重要方法.通过了解深时海洋生产者和生物泵的演变,可以更深入地理解当前碳循环的过程和机制.深时地质记录表明,现代型海洋生物泵的形成始于晚三叠世-早侏罗世,它的出现有效地缓解了由于海平面升降、大陆风化速率变化而导致的海洋碳循环和海水化学扰动.具有这种调节机制的大洋被称为“白垩大洋(Cretan ocean)”,在此之前的海洋被称为“贝壳大洋(Neritan ocean)”<sup>[19]</sup>.沟鞭藻、颗石藻等现代海洋生产者的起源和辐射在贝壳大洋向白垩大洋的演变中起到了关键作用<sup>[20]</sup>.因此,针对早侏罗世及其后沟鞭藻、颗石藻及二者对碳循环影响的研究成为热点<sup>[21]</sup>.然而,由于海洋生产者是一个庞大的类群,同时其作为生态系统的一部分容易受到环境变化的影响,所以尽管海洋生物泵的转折出现在晚三叠世-早侏罗世,这一转折节点前的生物环境事件中各类海洋生产者演化的研究仍是不可或缺的内容.例如,二叠纪-三叠纪之交的生物大灭绝事件导致了古生代海洋生产者的大规模灭绝和碳循环模式的突变<sup>[22]</sup>.早中生代构造演化带来的海洋营养水平上升和海水含氧量增加使得大个体浮游藻类更为繁盛<sup>[23,24]</sup>.综合来看,晚古生代-早中生代是现代碳循环途径形成的“预备期”,而这段地质历史时期中海洋初级生产者的类群组成、多样性变化、古地理分布及其背后的驱动因素仍有待于更深入的研究,且对深入理解海洋碳循环过程和储碳机制,以及生态系统对全球变暖的响应具有重要启示作用.

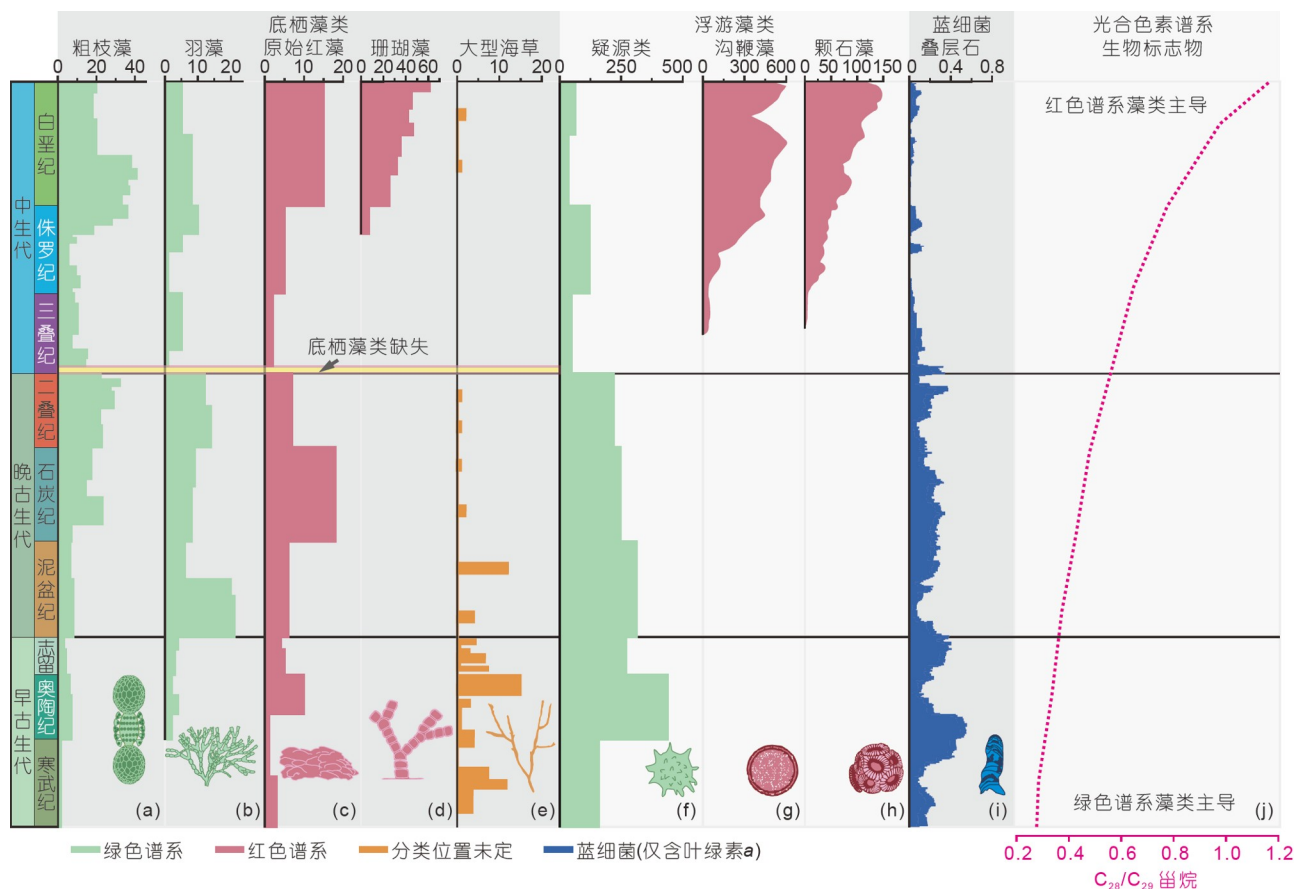
## 2 晚古生代-早中生代海洋初级生产者与生物泵的演化

### 2.1 晚古生代-早中生代主要海洋生产者的演化

在地质历史时期,海洋中的初级生产者主要有两类记录:化石与脂类生物标志化合物.化石主要为矿化或者碳化的藻类和蓝细菌,其形态和结构是主要的分类依据.化石的优点是形态学特征明确,可以开展分类学研究;缺点是非矿化藻类化石难以保存.脂类生物标志化合物则是生产者自身合成的、具有稳定碳骨架的特征有机物,其在理想条件下可以保存十几亿年之久,是研究生产者起源和演化的重要手段,但是生物标志物只能用于指示生产者高级分类单元,不能用于科以下分类单元的研究<sup>[25,26]</sup>.根据现有的地质记录,晚古生代-早中生代的主要生产者类群包括底栖钙藻、非钙化底栖海藻、疑源类、沟鞭藻、颗石藻、蓝细菌、非产氧光合自养细菌(绿硫细菌)和古菌等.

#### 2.1.1 底栖藻类

底栖钙藻是对一切能产生碳酸钙外壳的底栖藻类的统称<sup>[27]</sup>.由于其在系统分类学组成上的复杂性,本文主要选取4个研究程度较高、在化石中也最为常见的类群论述,即绿藻门的粗枝藻目、羽藻目,红藻门的珊瑚藻目和原始红藻类.这4个类群具有较为完备的分类学体系,可作为代表指示底栖钙藻多样性的变化趋势(图1).钙藻在晚古生代进入了一个多样性高峰期,泥盆纪其多样性第一次大幅增加,出现了40多个属,羽藻类的变化最明显(图1).石炭纪-二叠纪是钙藻的第二个高峰期,粗枝藻、羽藻、原始红藻均较为繁盛(图1(a)~(c)).二叠纪的粗枝藻和羽藻共有60多个属被报道,在特提斯洋周围形成了一系列底栖钙藻群落和藻礁(图2(b)).一些地区的钙藻丰度极高,钙藻碎屑占灰岩体积的50%以上,因而这种灰岩被称为裸海松藻灰岩<sup>[39]</sup>.在二叠纪-三叠纪之交,底栖钙藻遭受了严重的灭绝.Flügel<sup>[40]</sup>总结了粗枝藻类的多样性变化,发现全球下三叠统中普遍缺乏钙藻化石,提出了“藻缺失(Algae Gap)”的概念.后续的研究者基于华南高分辨率的化石记录,发现钙藻作为底栖固着的浅海生物,对环境变化敏感,在二叠纪-三叠纪之交大灭绝的第一幕即二叠纪末大灭绝中几乎完全消亡<sup>[41,42]</sup>.直到中三叠世钙藻多样性才逐渐增加,但仍未达到晚二叠世的水平<sup>[29]</sup>.底栖钙藻多样性的转折出现在中-晚侏罗世,以珊瑚藻的起源和快速辐射为标志,其他钙藻的多样性也迅速增加



**图 1** 古生代-中生代主要初级生产者类群变化。(a) 粗枝藻属级多样性<sup>[28]</sup>；(b) 羽藻属级多样性<sup>[29]</sup>；(c) 管孔藻及其他原始红藻属级多样性<sup>[30]</sup>；(d) 珊瑚红藻种级多样性<sup>[31]</sup>；(e) 非钙化大型海草种级多样性<sup>[32]</sup>；(f) 疑源类种级多样性<sup>[33]</sup>；(g) 沟鞭藻种级多样性<sup>[34]</sup>；(h) 颗石藻种级多样性<sup>[35]</sup>；(i) 叠层石的相对丰度，由海相沉积岩单元归一化处理得到<sup>[36]</sup>；(j) 海相碳酸盐岩和硅质碎屑岩原油样品中的平均C<sub>28</sub>/C<sub>29</sub>甾烷比值变化<sup>[37]</sup>。红色谱系：主要光合色素为叶绿素a和c的植物类群；绿色谱系：主要光合色素为叶绿素a和b的植物类群

**Figure 1** Changes in major primary producer groups during the Paleozoic-Mesozoic. (a) Genus-level diversity of Dasycladales<sup>[28]</sup>; (b) genus-level diversity of Bryopsidales<sup>[29]</sup>; (c) genus-level diversity of Solenoporaceae and other ancient red algae<sup>[30]</sup>; (d) species-level diversity of Corallinales<sup>[31]</sup>; (e) species-level diversity of non-calcified marine macroalgae<sup>[32]</sup>; (f) species-level diversity of acritarchs<sup>[33]</sup>; (g) species-level diversity of dinoflagellates<sup>[34]</sup>; (h) species-level diversity of coccolithophores<sup>[35]</sup>; (i) relative abundance of stromatolites, normalized by total number of sedimentary rock units<sup>[36]</sup>; (j) mean C<sub>28</sub>/C<sub>29</sub> sterane ratio of crude oils from marine carbonate and siliciclastic source rocks<sup>[37]</sup>. Red lineage: Chlorophyll a + c containing plants; green lineage: Chlorophyll a + b containing plants

(图1)。在白垩纪，珊瑚藻逐渐在底栖群落中取得优势地位，并延续至今。

非钙化海草的化石记录较少，因为该类化石以碳质压模保存为主，多在特异埋藏中发现<sup>[43]</sup>。碳质压模化石的分类也存在一定的难度，因为细微结构和色素信息无法保存，分类学研究只能进行到属级。古生代非钙化海草多样性呈现降低的趋势(图1(e))，原因可能有两方面：(1) 化石保存困难，自寒武纪以来底栖动物丰度增加，其频繁的活动不利于碳质压膜化石保存<sup>[44]</sup>；(2) 大型藻类群落在寒武纪-奥陶纪发生更替，底栖藻类取代了非钙化藻类在浅海的生态位<sup>[45]</sup>。在泥盆纪，非钙化海草还有较多记录，个别化石的形态和结构较为完

好<sup>[46]</sup>。二叠纪-侏罗纪非钙化海草的化石记录极为缺乏<sup>[47]</sup>，直到早白垩世才有大型褐藻的祖先*Padina*属的报道<sup>[48]</sup>。*Padina*被认为是现代海洋生态系统工程师和浅海最重要的初级生产者褐藻的祖先。

### 2.1.2 浮游藻类

疑源类起源于前寒武纪，其生物多样性在古生代达到顶峰，特别是奥陶纪、志留纪和泥盆纪<sup>[49]</sup>。古生代疑源类与现代浮游藻类的亲缘关系不明，一些可能是沟鞭藻的祖先，更多地被认为是绿藻门单细胞浮游藻类<sup>[50]</sup>。疑源类是早古生代海洋中的主要初级生产者，其多样性及生物量的变化对后生动物的演化产生了重要影响，比如，奥陶纪疑源类的繁盛被认为促进了奥陶纪



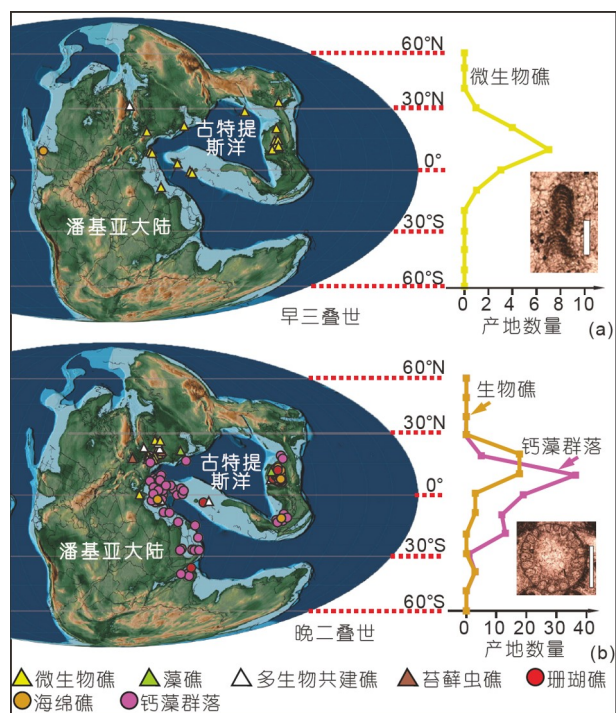


图2 晚二叠世-早三叠世钙藻群落和生物礁的全球分布变化。古地理图修改自文献[38]，主要数据来源为已发表的文献(见附件1)。(a) 早三叠世微生物礁的空间分布和蓝细菌化石照片，比例尺为0.2 mm；(b) 晚二叠世钙藻群落和生物礁的空间分布和羽藻目 *Permodaculus* 属化石，比例尺为1 mm

Figure 2 Changes in the distribution of calcareous algal communities and coral reefs from the Late Permian to Early Triassic. The paleogeographic map was modified from Ref. [38], and the database was compiled from published literatures (in Appendix 1). (a) Spatial distribution of Early Triassic microbial reefs, and the photo of fossil cyanobacteria, scale bar=0.2 mm; (b) Spatial distribution of Late Permian calcareous algae communities and reefs, and the photo of genus *Permodaculus* (Bryopsidales), scale bar=1 mm

生物大辐射事件<sup>[49,51,52]</sup>。在石炭纪疑源类多样性突然下降，被称为“浮游植物断电”现象(phytoplankton blackout)<sup>[53]</sup>。然而，后续的研究表明，在石炭纪、二叠纪和三叠纪，已报道的疑源类均超过200种，远高于以往的统计结果<sup>[54,55]</sup>。从石炭纪开始，疑源类个体大小和形态出现显著变化，主要以个体直径为20~30 μm的球形和具刺疑源类为主(图3(a))。这些化石在之前的研究中被忽略，导致研究者认为疑源类出现缺失。疑源类主要分布在大陆架区域(图3(b))，海平面的高低变化会对其多样性产生较大影响，因而晚古生代海平面的降低可能导致了疑源类多样性的逐步下降。在华南二叠纪-三叠纪之交，疑源类发生了两幕式灭绝，多样性从28种降低到仅1种。疑源类化石丰度整体呈下降的趋势，但是在两幕灭绝期间，小型具刺疑源类的丰度出现小幅回升。

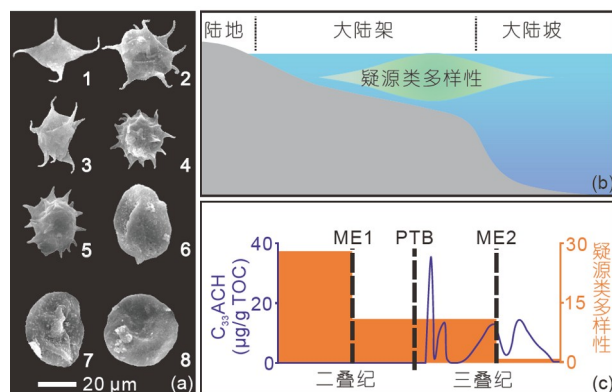


图3 晚二叠世-早三叠世疑源类空间分布及多样性变化。(a) 二叠纪末期海洋疑源类。1, *Veryhachium hyalodermum*; 2, 3, *Micrhystridium pentagonale*; 4, 5, *Micrhystridium breve*; 6, 7, *Leiosphaeridia microgranifera*; 8, *Leiosphaeridia minutissima*。(b) 二叠纪末疑源类的空间分布，修改自文献[56]。(c) 二叠纪-三叠纪之交华南疑源类种级多样性<sup>[55]</sup>与丰度变化<sup>[57]</sup>。ME1, 大灭绝第一幕; ME2, 大灭绝第二幕; PTB, 二叠系-三叠系界线;  $C_{33}ACH$ , 33碳正烷基环己烷

Figure 3 Spatial distribution and changes in diversity of acritarchs from the Late Permian to Early Triassic. (a) Late Permian marine acritarchs. 1, *Veryhachium hyalodermum*; 2, 3, *Micrhystridium pentagonale*; 4, 5, *Micrhystridium breve*; 6, 7, *Leiosphaeridia microgranifera*; 8, *Leiosphaeridia minutissima*. (b) Spatial distribution of acritarchs at the end of Permian, modified from Ref. [56]. (c) Variations in species-level diversity<sup>[55]</sup> and abundance<sup>[57]</sup> of acritarchs from South China during the Permian-Triassic interval. ME1, the first episode of mass extinction; ME2, the second episode of mass extinction; PTB, Permian-Triassic boundary;  $C_{33}ACH$ ,  $C_{33}$  *n*-alkylcyclohexane

此外，生物标志化合物数据也显示具刺疑源类的丰度在该时期出现了显著增加(图3(c), 4(b))，表明该时期的具刺疑源类可能是灾难种。到了中生代，特别是晚三叠世之后，疑源类多样性维持着较低的水平，沟鞭藻和颗石藻成为中生代海洋的主要浮游植物类型。

远洋浮游藻类在中生代开始兴起，主要代表是颗石藻和沟鞭藻。沟鞭藻的化石主要来源于其休眠孢囊，这些孢囊是有性生殖的沟鞭藻生产的。现代沟鞭藻中大约有260个种有此种能力，其中有25种的孢囊是钙化的(即“钙质沟鞭藻”)<sup>[58]</sup>。颗石藻是可以产生钙质鳞片的定鞭金藻，与颗石藻相关的化石主要有两大类：一类是颗石藻的钙化鳞片形成的颗石(coccolith)，第二类是与颗石在结构上具有一定相似性的超微石(nannolith)<sup>[35]</sup>。分子钟证据指示，颗石藻和沟鞭藻可能起源于寒武纪，但目前缺乏化石证据<sup>[26]</sup>。一些研究者在泥盆纪和早三叠世的地层中发现了疑似钙质超微浮游化石的结构<sup>[59,60]</sup>，但是前者与颗石藻的亲缘关系缺乏分类学上证据，后者的时代可能存在疑问。总体而言，当前关于晚三叠世之前的“钙质超微浮游藻类”的报道与中生代

颗石藻和沟鞭藻的演化关系还难以确定<sup>[35]</sup>。晚三叠世是现代海洋浮游藻类起源的关键时期<sup>[61,62]</sup>。卡尼期大量出现的钙球(例如*Orthoithonella*),可能是早期沟鞭藻的钙化孢囊<sup>[61,63]</sup>;超微石的最早记录在卡尼期,颗石则首现于诺利期<sup>[63,64]</sup>。远洋浮游藻类于早侏罗世开始第一次辐射,大多数科级分类单元在这一阶段出现,侏罗纪-白垩纪其多样性持续增加(图1(g), (h))。

三芳甲藻甾烷是沟鞭藻的生物标志化合物,在晚三叠世之前丰度一直较低,在之后的中生代呈现出逐渐增加的趋势,这与Stover等人<sup>[34]</sup>总结的沟鞭藻孢囊化石的多样性变化基本一致(图1(g))。不过,三芳甲藻甾烷的丰度在志留纪和泥盆纪存在两个异常值<sup>[26]</sup>,而沟鞭藻类的另一种生物标志物4-甲基甾烷(4-methylsteranes)甚至在寒武纪早期就已经出现,表明沟鞭藻的起源应该早于晚三叠世<sup>[65-67]</sup>。与沟鞭藻相比,颗石藻类产生的脂质不稳定,以长碳链(C<sub>37</sub>~C<sub>39</sub>)的不饱和酮类物质为主<sup>[68,69]</sup>,因其容易受到还原作用的影响,在新生代之前的地层中很难保存,只有白垩纪的沉积物中有零星报道<sup>[70,71]</sup>。

### 2.1.3 自养细菌与古菌

海洋中的蓝细菌既可以通过钙化保存为化石,也可以保存为各类沉积结构,如叠层石、微生物岩等。叠层石丰度在显生宙呈现逐渐下降的趋势(图1(i)),一定程度上指示了蓝细菌在海洋生态系统中的重要性下降。在石炭纪,蓝细菌化石的丰度和多样性都较为稳定,以*Ortonella*、*Bevocastria*和*Garwoodia*为代表的蓝细菌在核形石与叠层石中较为常见,而*Girvanella*则是生物礁内部壳状结构的重要组成部分<sup>[14]</sup>。在二叠纪,蓝细菌的丰度出现了较大的波动,蓝细菌的丰度原本在晚二叠世处于较低的水平。由于海洋环境的剧烈变化,二叠纪-三叠纪之交的浅海中又广泛出现了蓝细菌爆发事件(图1(i))。古特提斯洋周边的浅海环境中发育了具有独特斑点状、树枝状、纹层状和网状组构的微生物岩(图2(a))<sup>[72,73]</sup>,这些微生物岩可能与蓝细菌爆发形成的水华有关<sup>[74]</sup>。2-甲基藿烷类化合物可以指示蓝细菌和 $\alpha$ -变形菌的丰度,在二叠纪-三叠纪之交不同水深的海洋环境中均发现了2-甲基藿烷类化合物(2-MeHI)的峰值<sup>[57,75]</sup>,结合氮同位素记录分析,蓝细菌可能是当时海洋的主要生产者<sup>[76,77]</sup>。不过,总体上蓝细菌的丰度在显生宙历史上相对较低,在正常的海洋环境中其对初级生产力的贡献可能并不处于主要地位<sup>[26]</sup>。

与蓝细菌类似,其他自养细菌的丰度和空间分布

主要依靠生物标志化合物。如,虽然C<sub>29</sub>降藿烷有多种形成途径,但当其来源于C<sub>29</sub>藿醇时(第29碳位有一个羟基),主要指示变形菌,如甲基营养菌<sup>[78]</sup>。油气数据库中的C<sub>29</sub>/C<sub>30</sub>藿烷比值表明,该数值的大小与时间相关性不大,古生代该值在0.5~1.6之间波动,中生代在0.7~1.8之间波动<sup>[26]</sup>。相反,C<sub>29</sub>/C<sub>30</sub>藿烷比值与纬度位置和沉积环境相关性较高,在中低纬度碳酸盐岩中最高,高纬的远洋页岩中最低<sup>[79]</sup>,表明甲基营养菌多数分布于低纬度的碳酸盐岩台地环境中。海洋浮游古菌占现代海洋水体中原核生物的三分之一以上,在碳氮循环中起着重要的作用<sup>[80]</sup>。该类群中的部分成员是自养或混合营养的类型,可以还原无机化合物(如CO<sub>2</sub>和HCO<sub>3</sub><sup>-</sup>),并将其中的碳固定下来<sup>[81]</sup>。深时地层中古菌常见生物标志物有不规则的无环类异戊二烯和具类异戊二烯链的甘油二烷基甘油四醚(i-GDGT)<sup>[82]</sup>。生物标志物记录显示,白垩纪中期的缺氧事件层中80%的有机碳来源于海洋非嗜热古菌<sup>[83]</sup>,表明该时期浮游古菌固碳作用增强。土耳其和伊朗早三叠世的微生物岩中也发现了古菌,不过其对海洋储碳的贡献还有待进一步研究<sup>[82]</sup>。在二叠纪-三叠纪之交海洋缺氧、硫化事件中,固氮细菌<sup>[84]</sup>、绿硫细菌<sup>[85,86]</sup>等自养细菌也存在爆发现象,且其爆发与大灭绝的幕式存在耦合(图4(c), (d))<sup>[57]</sup>。综上所述,在海洋环境剧烈变化期间,自养细菌和古菌也对海洋初级生产有较大贡献。

晚古生代到早中生代,海洋生产者类群中主要出现了两个重大变化:(1)远洋浮游藻类的崛起;(2)红色谱系藻类(所含光合色素以叶绿素a和c为主)对绿色谱系藻类(所含光合色素以叶绿素a和b为主)的取代(图1)。第一个变化对地球表层系统的碳循环产生了重要影响<sup>[23,24]</sup>,也是后文主要论述的内容。第二个变化受到的关注较少,但也同样重要。不同光合色素谱系藻类的生物学差异能为未来古、中生代海洋环境的对比研究提供新思路。不过,该变化当前主要依据只有生物标志物比值的变化,即绿色谱系藻类主要合成C<sub>29</sub>甾醇类化合物。红色谱系藻类更倾向合成C<sub>28</sub>甾醇类化合物<sup>[87]</sup>,因而二者比值可以指示藻类类群光合色素谱系的演变。高丰度的C<sub>29</sub>甾烷在新元古代就已经出现,一直持续到晚古生代,表明绿色谱系藻类在古生代海洋中可能发挥了更大的作用<sup>[26,88]</sup>。实体化石记录的海洋生产者的多样性曲线也支持该观点:绿色谱系的粗枝藻和羽藻在古生代较为繁盛,而到了中生代红色谱系的珊瑚藻和其他原始红藻类多样性与

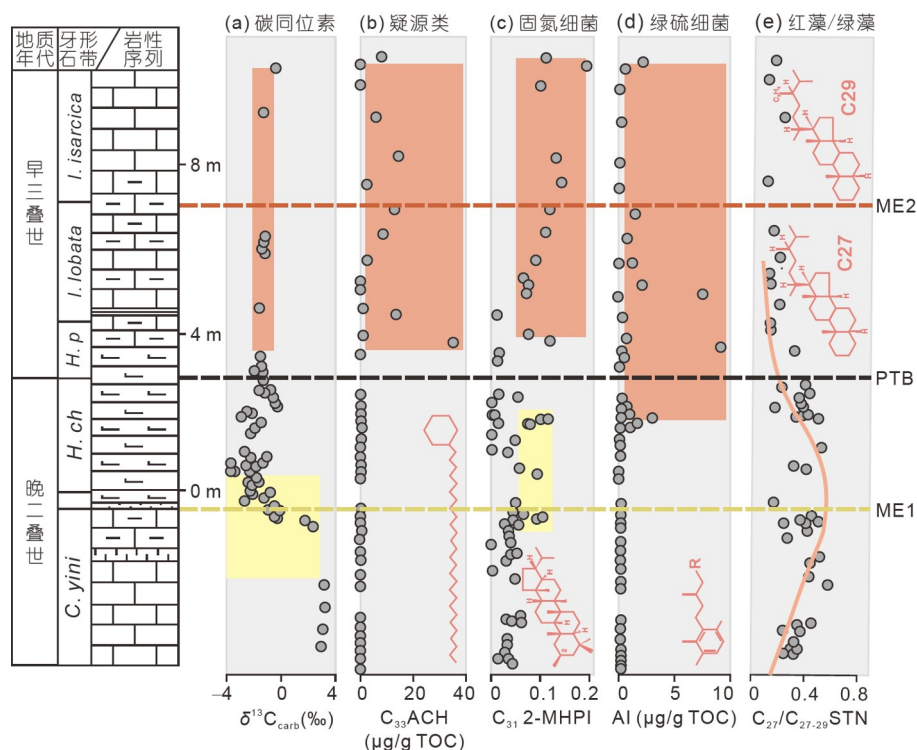


图4 (网络版彩色)二叠纪-三叠纪之交碳同位素与生物标志物指标的变化<sup>[57]</sup>。牙形石带: *C. yini*=*Clarkina yini*带; *H. ch*=*Hindeodus changxingensis*带; *H. p*=*Hindeodus parvus*带; *I. lobata*=*Isarcicella lobata*带; *I. isarcica*=*Isarcicella isarcica*带。(a) 碳酸盐全岩的碳同位素曲线; (b)  $C_{33}$ 正烷基环己烷( $C_{33}$ ACH)总有机碳归一化丰度变化; (c) 31碳2-甲基藿烷指数( $C_{31}$  2-MHPI)变化; (d) 芳基类异戊二烯(Al)总有机碳归一化丰度变化; (e)  $C_{27}/C_{27-29}$ 甾烷比值。PTB: 二叠系-三叠系界线; ME1: 大灭绝主幕; ME2: 大灭绝第二幕

Figure 4 (Color online) Changes in carbon isotopes and biomarker proxies at the Permian-Triassic interval<sup>[57]</sup>. Conodont zone: *C. yini*=*Clarkina yini* zone; *H. ch*=*Hindeodus changxingensis* zone; *H. p*=*Hindeodus parvus* zone; *I. lobata*=*Isarcicella lobata* zone; *I. isarcica*=*Isarcicella isarcica* zone. (a) Carbon isotope curves of composition of bulk carbonate; (b) variations in the TOC-normalized concentrations of  $C_{33}$  *n*-alkyl cyclohexane ( $C_{33}$ ACH); (c) changes in the  $C_{31}$  2-methylhopane index ( $C_{31}$  2-MHPI); (d) variations in TOC-normalized concentrations of aryl isoprene (Al); (e) ratio of  $C_{27}/C_{27-29}$  steranes. PTB: Permian-Triassic boundary; ME1: the first episode of mass extinction; ME2: the second episode of mass extinction

绿色谱系藻类相当。在浮游群落中, 尽管部分古生代的疑源类可能是属于红色谱系沟鞭藻的祖先, 但是生物标志物证据表明, 绝大部分疑源类更有可能是一些小型的单细胞浮游绿藻<sup>[26]</sup>。中生代浮游群落被沟鞭藻和颗石藻主导, 这二者都是红色谱系。这一问题的深入研究还需要高精度的地层格架和更多的化石证据。此外, 大灭绝事件对藻类光合色素谱系的演化影响很大, 比如, 二叠纪-三叠纪之交生物大灭绝中的主幕中即出现了红色谱系藻类取代绿色谱系藻类的现象(图4(e))。

## 2.2 晚古生代-早中生代的生物泵、碳酸盐岩泵与微型生物泵

根据生产者类型、多样性高低、地史分布及古地理分布, 生物泵的演化分为两种类型, 即古生代型和现

代型。古生代型生物泵主要分布于古生代到中三叠世, 其生产者绿色谱系的光合自养生物, 包括底栖藻类和浮游的疑源类, 这二者与自养细菌和古菌是古生代型生物泵的重要组成部分(图5(a))。在古地理分布上, 古生代的生产者主要分布在环特提斯的浅海大陆架区域(图2(b), 3(b))。晚二叠世的底栖钙藻具有明显的纬度多样性梯度, 也就是从赤道向两极多样性递减, 与该时期动物的纬度多样性梯度一致<sup>[89]</sup>。这些钙质生产者与浅海繁盛的底栖动物(如海绵、珊瑚、腕足、海胆、海百合等)一起生产了大量的生源碳酸盐, 是古生代主要的碳酸盐泵。

二叠纪-三叠纪之交海洋环境急剧恶化, 浅海环境中的底栖藻类和钙质动物(如海绵、珊瑚、腕足动物、苔藓虫)大规模灭绝<sup>[41]</sup>, 疑源类多样性也遭受重大打击<sup>[55]</sup>。该时期海洋碳同位素出现负偏(图4(a)), 原有



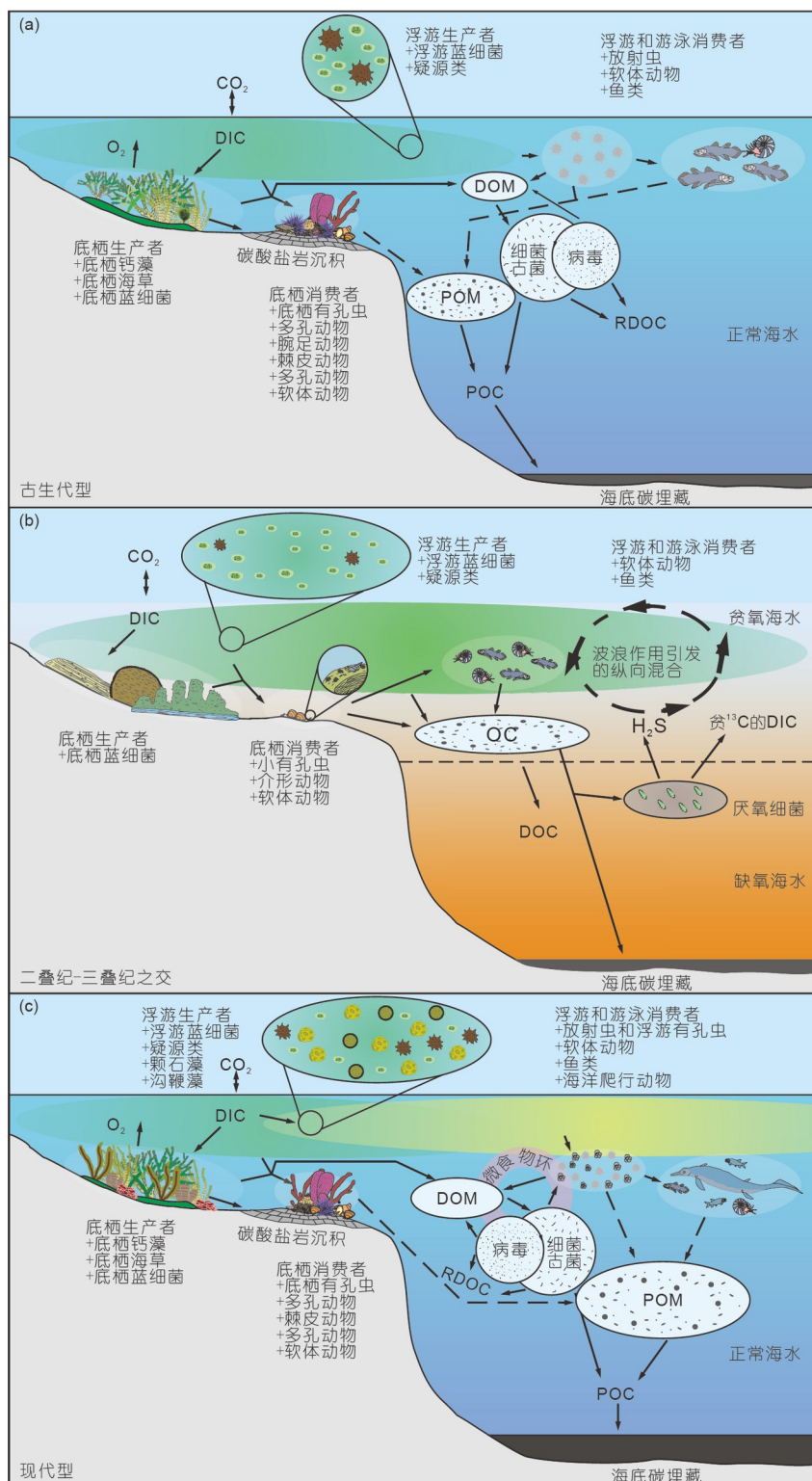


图5 古生代和现代型的海洋生物泵示意图。参考现代海洋生物泵过程，根据文献[11]修改。(a) 古生代型海洋生物泵；(b) 二叠纪-三叠纪之交大灭绝中出现的特殊生物泵；(c) 现代型海洋生物泵

Figure 5 Schematic diagram of the Paleozoic and modern evolutionary stages of the marine biological pump. Modified from Ref. [11] with reference to modern marine biological pump processes. (a) Paleozoic-type marine biological pump; (b) a special biological pump that occurred at Permian-Triassic Mass Extinction; (c) modern-type marine biological pump

的海洋生物泵和碳酸盐泵都受到摧毁<sup>[90,91]</sup>。由于陆源输入增加导致的海水富营养化,促进了蓝细菌在浅海爆发,并成为最主要的初级生产者<sup>[75]</sup>,这一过程加剧了水体缺氧和海水分层<sup>[92,93]</sup>。随着环境恶化,在第二幕灭绝中,固氮细菌和绿硫细菌也出现增多<sup>[57]</sup>。这种由蓝细菌主导,多种微生物(细菌、古菌等)共同组成,主要分布在浅海的生物泵,是二叠纪-三叠纪之交大灭绝期间短暂出现的一种特殊型的生物泵(图5(b))。碳酸盐中的碳同位素深度梯度的出现反映了这种生物泵的主要模式(图5(b)):蓝细菌通过光合作用将大气中的CO<sub>2</sub>转化为有机碳,富含<sup>12</sup>C的溶解无机碳优先进入到有机物中,导致海洋表层 $\delta^{13}\text{C}$ 增大;而在水柱的深层,厌氧细菌对有机物的呼吸释放大量轻碳,导致深层水 $\delta^{13}\text{C}$ 下降<sup>[92]</sup>。这种特殊类型的生物泵一度分布非常广泛,在早三叠世,大多数中低纬度区域的浅海台地均有微生物岩的出现(图2(a))。大灭绝期间低纬度与中、高纬度的碳酸盐泵的构成不完全一致。在低纬度地区,由于后生动物的大规模灭绝导致了生物礁的消失,在牧食压力降低和海水富营养化的共同作用下<sup>[94,95]</sup>,蓝细菌主导的微生物岩大量出现<sup>[57,96]</sup>。而位于中纬度的藏南地区明显缺乏微生物岩沉积,以白云岩、白云质灰岩泥岩为主。这些碳酸盐的来源是以硫酸盐还原菌为代表的异养细菌的代谢活动,即硫酸盐还原导致海水碱度升高,促进了白云石的沉淀<sup>[95,97]</sup>。

尽管前人研究表明,二叠纪-三叠纪之交大灭绝对生产者、生物泵和碳酸盐泵产生了重大的影响,并驱动了海洋生态系统的转型<sup>[22]</sup>,但现代型生物泵和碳酸盐泵并未随着大灭绝后的复苏一同出现<sup>[26]</sup>,海洋依然处于“贝壳大洋”的演化阶段<sup>[20]</sup>。早三叠世、中三叠世生产者的代表主要为疑源类、蓝细菌和底栖钙藻。其中,蓝细菌形成的微生物岩直到中三叠世早期仍有记录<sup>[98]</sup>。底栖钙藻虽然在奥伦尼克期才再次出现<sup>[99]</sup>,但其中三叠世浅海的碳酸盐泵中发挥了重要作用<sup>[100]</sup>。在颗石藻和沟鞭藻起源之前,生源碳酸盐的生产者主要分布在浅海,深海的碳酸盐埋藏很可能是无机类型<sup>[101,102]</sup>。此外,由于古生代海洋初级生产者的丰度变化缺乏可靠的数据,生物泵和碳酸盐泵的碳通量尚难以定量评估。

现代型海洋生物泵形成于晚三叠世,并延续至现代。该类型以远洋分布的浮游生物为主导,初级生产者为超微浮游藻类(图5(c))。在现代型海洋生物泵形成的早期,颗石藻和沟鞭藻等浮游藻类是生产者的主导类

群,它们除了对于有机碳的埋藏产生了重大贡献外,还使生源碳酸盐沉积逐步转向深海<sup>[20]</sup>。

超大型的惰性溶解有机碳库在前寒武纪已经出现,被认为是微型生物碳泵储碳的重要证据之一<sup>[103,104]</sup>。然而,当前缺乏对晚古生代-早中生代RDOC的相关研究,因此对当时微型生物碳泵情况还不清楚。古菌和病毒是地质历史时期微型生物碳泵研究的重要对象,已有研究开始探讨缺氧事件中非嗜热古菌的固碳能力<sup>[83]</sup>,这为进一步探究古菌在微型生物碳泵中的作用奠定了基础。近期,一些对二叠纪-三叠纪之交微生物岩中古菌的报道,也为未来开展晚古生代-早中生代微型生物碳泵的研究提供了方向。根据现代生物分子钟推测,病毒至少在15亿年前就已经出现<sup>[105]</sup>,因此其在晚古生代-早中生代的海洋中应该是存在的。然而,当前大部分病毒感染破坏生物细胞的记录主要来自于白垩纪的陆相昆虫化石中<sup>[106]</sup>,地质历史时期海洋中的病毒记录及其对于海洋碳循环的影响还有待进一步研究。

### 3 中生代海洋三大革命与现代海洋生物泵的形成

早中生代海洋生产者组成、生物泵类型、海洋储碳能力发生了重大变化。中生代海洋浮游生物革命是促成这一转变的核心因素,促进了现代型生物泵的形成,新增了远洋碳库,大大增强了海洋的储碳能力和对碳循环波动的缓冲能力。与此同时,生物圈中还发生了海洋动物革命,以及水圈中发生了中生代中期海洋化学革命。在三大革命相互影响、共同作用下,现代类型的海洋生物面貌、水化学条件、碳循环途径最终形成。因此,中生代海洋三大革命的具体过程、相互关系和驱动因素,是揭示现代型海洋生物泵的形成及其在碳循环中作用的关键。

#### 3.1 中生代海洋革命

中生代海洋革命(Mesozoic marine revolution)最早由Vermeij<sup>[107]</sup>提出。他在对比古生代和中生代晚期的海洋腹足动物化石形态过程中发现,由于硬食性捕食者的演化和其带来的捕食作用加剧,海洋无脊椎生物群落结构在晚中生代出现显著变化,比如底栖生物的移动能力提高、地域化趋势增强等。包括内栖动物增加、贝壳坚固性增强、生态空间利用能力强等。后续研究表明,中生代海洋革命促进了底栖生物群落大规模重组<sup>[108]</sup>和现代演化动物群崛起<sup>[109]</sup>。在这个时期,底



栖动物(包括软体动物<sup>[110]</sup>、腕足、海百合)发生了显著的变化,包括内栖动物增加<sup>[111]</sup>、生态空间利用能力增强<sup>[109]</sup>、捕食强度增加<sup>[112]</sup>等。同时,掠食性的硬骨鱼类、海洋爬行类等脊椎动物也大量出现,这一过程被称为“生物军备竞赛”<sup>[112,113]</sup>。总体上,海洋生物完成了由移动力弱的表栖滤食生物主导到移动力强的高代谢内栖滤食生物、食碎屑生物和捕食生物主导的转变<sup>[114]</sup>,现代类型的海洋底栖-浮游耦合模式生态系统得以建立<sup>[109]</sup>。

对于中生代动物革命的过程及时间节点,当前也有不同认识。前人研究对于这一过程的划分多以动物群落的演变为主要依据。最早认为这一进程开始于侏罗纪,并在白垩纪加速<sup>[107]</sup>。进一步的研究表明,海洋革命存在3个阶段:第1阶段在中、晚三叠世,具有压碎贝壳能力的鱼和龙虾的出现;第2阶段为白垩纪,多种捕食方式的腹足动物的辐射发展;第3阶段在新生代早期,硬骨鱼和蟹类发生辐射<sup>[112]</sup>。也有学者提出了不同观点,主要集中在对三叠纪捕食压力增加的质疑上:比如三叠纪期间硬食性食肉动物丰度低,分布有限,它们的演化未必增加了底栖动物的生存压力<sup>[115]</sup>,且钻孔在三叠纪的捕食中可能也相对无效<sup>[116]</sup>。Vermeij<sup>[117,118]</sup>的新观点则认为,底栖动物的进化创新主要发生在两个时期:晚三叠世-早侏罗世和晚白垩世,且中生代海洋动物的演化与构造演化、陆地生物演化、海水化学条件变化和海洋生产力增高等因素存在联系,并非单一的演化事件,而是生态系统整体现代化的过程。底栖海洋软体动物显著的进化可能不晚于卡尼期<sup>[119]</sup>。在后续的研究中,有学者在中三叠世的鱼类粪化石中发现了大量破碎的双壳和海百合的骨片,支持了海洋捕食压力增加的假说。这表明中生代海洋革命在中三叠世安尼期可能已经开始<sup>[120]</sup>。综上,中生代海洋革命开始的时间节点可能在中三叠世,但标志性的动物群落进化创新大部分发生在晚三叠世及之后。这与颗石藻和沟鞭藻的演化过程存在耦合,同时又受到海水化学条件变化的影响。

### 3.2 中生代中期海洋化学革命

在早侏罗世之前,海平面高度、海洋面积、大陆风化率和海洋钙离子浓度的波动会对碳酸盐沉积与海洋碳循环产生较大的扰动,而这些扰动只能被海洋微弱地缓冲<sup>[121]</sup>。这一观点也被白垩大洋和贝壳大洋模型模拟分析所证实:当上述条件发生变化时,白垩大洋碳

酸盐饱和度在 $-0.6\sim+0.3$ 之间波动,而贝壳大洋的碳酸盐饱和度在 $-2.0\sim+1.0$ 之间波动<sup>[20]</sup>。古生代的生物泵和碳酸盐泵主要分布于浅海水域,难以有效缓冲因环境变化引起的海洋碳酸盐饱和度的变化,因此古生代海洋的碳酸盐饱和度往往较高<sup>[4]</sup>。早侏罗世之后,海水化学性质发生了改变,碳酸盐饱和度逐步下降并趋于稳定。这是生源碳酸盐沉积从浅海向深海转移的结果,也就是“中生代中期海洋化学革命”<sup>[4,20]</sup>。海水化学变化还体现在海水含氧量的增加,侏罗纪大陆架海水含氧量更为充足<sup>[122]</sup>。这可能是远洋浮游藻类繁盛导致的,而海水氧含量上升与浮游藻类个体增大导致的有机碳沉降速度变快共同作用下进一步改变了海洋有机碳的埋藏能力,海平面变化对有机碳埋藏的影响减小,碳循环更为稳定<sup>[123]</sup>。

中生代中期海洋化学革命的启动时间当前尚未有明确结论。Ridgwell<sup>[20]</sup>根据在晚三叠世-早侏罗世生源碳酸盐沉积环境的明显转变,将其时间估计在距今200 Ma左右。然而,生源碳酸盐沉积从浅海向深海的转移是一个渐进的过程,因其受到了海洋颗石藻和沟鞭藻的起源与辐射的重大影响,其启动时间的估计应结合浮游化石起源的研究进行,海洋磷酸盐含量变化、海水硫酸盐含量变化、海水Mg/Ca比值的变化等对海洋浮游生物的出现产生重要影响的因素也应综合考虑<sup>[24,124]</sup>。

### 3.3 中生代海洋浮游生物革命

相对中生代海洋革命和海洋化学革命,中生代海洋浮游生物革命的概念较为模糊。本文将沟鞭藻、颗石藻、浮游有孔虫等远洋浮游生物的崛起(图6(a)-(c))总结为中生代海洋浮游生物革命(简称浮游革命)。当前对中生代浮游生物演化过程的研究主要集中在早侏罗世之后。Suchéras-Marx等人<sup>[131]</sup>根据侏罗纪、白垩纪和新生代的远洋碳酸盐积累速率、钙质超微化石积累速率、颗石化石大小的变化,将浮游生物的演化分为3个阶段:第一阶段开始于早侏罗世,为浮游生物的扩散阶段,大部分化石记录来自大陆边缘海环境;第二阶段开始于早白垩世超微化石积累速率达到顶峰,颗石藻发生显著大型化,并占据了热带远洋;第三阶段为始新世-渐新世,在白垩纪末灭绝后颗石藻和沟鞭藻相对衰落,硅藻和浮游有孔虫发生辐射。

当前对早侏罗世之前的远洋浮游藻类演化的相关研究较少,主要集中在沟鞭藻和颗石藻的起源时间<sup>[61,62]</sup>与驱动因素<sup>[61,64]</sup>。有学者认为,颗石藻和沟鞭藻

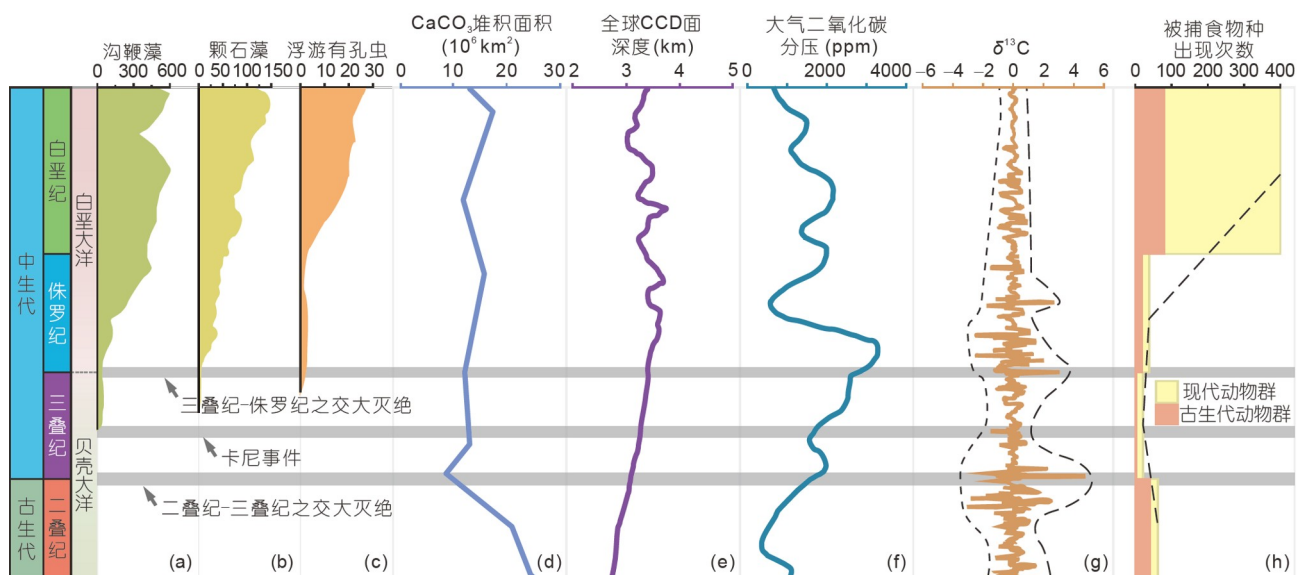


图6 (网络版彩色)中生代海洋革命及其影响。(a) 沟鞭藻种级多样性<sup>[34]</sup>; (b) 颗石藻种级多样性<sup>[35]</sup>; (c) 浮游有孔虫种级多样性<sup>[125]</sup>; (d) 浅水台地碳酸盐岩总面积<sup>[126]</sup>; (e) 全球大洋碳酸盐补偿深度(CCD)<sup>[127]</sup>; (f) 大气二氧化碳分压<sup>[128]</sup>; (g)  $\delta^{13}\text{C}$ 曲线的周期变化<sup>[129]</sup>; (h) 海洋无脊椎动物中被捕食物种的出现次数<sup>[130]</sup>. 1 ppm=10<sup>-6</sup> L/L

Figure 6 (Color online) The Mesozoic marine revolution and its impact. (a) Species-level diversity of dinoflagellates<sup>[34]</sup>; (b) species-level diversity of coccolithophores<sup>[35]</sup>; (c) species-level diversity of planktonic foraminifera<sup>[125]</sup>; (d) total area of platform (shallow water) carbonates<sup>[126]</sup>; (e) global ocean carbonate compensation depth (CCD)<sup>[127]</sup>; (f) partial pressure of atmospheric carbon dioxide<sup>[128]</sup>; (g) periodic variations in the curve of  $\delta^{13}\text{C}$ <sup>[129]</sup>; (h) number of prey species occurrences in marine invertebrates<sup>[130]</sup>. 1 ppm=10<sup>-6</sup> L/L

的起源受到生物圈可利用营养盐与能量水平上升的影响<sup>[124]</sup>, 其过程与奥陶纪疑源类爆发和新近纪硅藻爆发相似。在构造旋回的影响下, 化学计量不平衡(C:P比值高)的群落向平衡(C:P比值低)的群落演化, 海洋中硅和磷的增加与浮游植物群落多样性上升存在耦合关系。输入海洋的营养盐增高, 更有利于大细胞的浮游藻类, 而小细胞的蓝细菌或绿藻则失去优势<sup>[24]</sup>。中生代起源的浮游藻类中, 沟鞭藻起源最早, 可能因为混合营养的习性和较大的细胞, 使沟鞭藻能够适应富营养的环境, 并存储更多的能量<sup>[23]</sup>。

### 3.4 中生代海洋浮游生物革命的意义

传统认识上的中生代海洋革命为海洋生态系统组成、结构和生物生态特征迅速演进的过程, 捕食压力上升引发的“生物军备竞赛”是其主要现象。然而, 前人对该过程的总结主要集中在动物方面, 缺乏对生产者演化的关注。因此, 一系列集中于海洋动物本身组成和其在空间结构、食物链结构上的变化, 更准确地表达应该是“中生代海洋动物革命”。而中生代海洋革命的内涵要更广, 除了动物革命, 中生代中期海洋化学革命和中生代海洋浮游生物革命也是其重要的组成部分。其中, 中生代海洋浮游生物革命是连接“动物革命”和

“化学革命”的关键一环(图7)。

中生代海洋浮游生物革命影响了海洋生态系统, 改变了海洋物质循环和能量流动的模式。沟鞭藻的出现, 加速了初级生产者产生的物质和能量向更大体型的消费者与更高的营养级转移, 海洋生态系统的中等营养水平获得了更多的资源, 为海洋动物革命提供了动力<sup>[23]</sup>。在晚侏罗世, 颗石藻和沟鞭藻多样性与丰度的增加, 对海洋中以碎屑和浮游生物为食的底栖无脊椎动物产生直接影响: 一方面流入底栖生物群落的能量增加; 另一方面浮游生物向远洋扩张促进了底栖生物栖息地向远洋拓展<sup>[110]</sup>。小型底栖无脊椎动物的演化与辐射进一步影响了更为复杂的海洋食碎屑和食腐动物的演化。白垩纪具有不规则外形的海胆和异形菊石也被认为与食物(小型海洋无脊椎底栖动物)的丰富度和多样性增加密切相关<sup>[132]</sup>。近期, 对古囊状蟹在晚侏罗世到早白垩世鳃腔结构演化的研究表明, 其潜穴能力增强与浮游藻类辐射导致的深海生物碎屑增多存在关联<sup>[133]</sup>。值得注意的是, 捕食频率在侏罗纪到白垩纪这一数值呈指数式增长, 捕食次数的峰值与海洋浮游生物多样性的峰值同时出现(图6(h))。

除此之外, 浮游革命的重要意义在于促进了“白垩大洋”的形成。由于海洋浮游生物群落的辐射, 生源碳

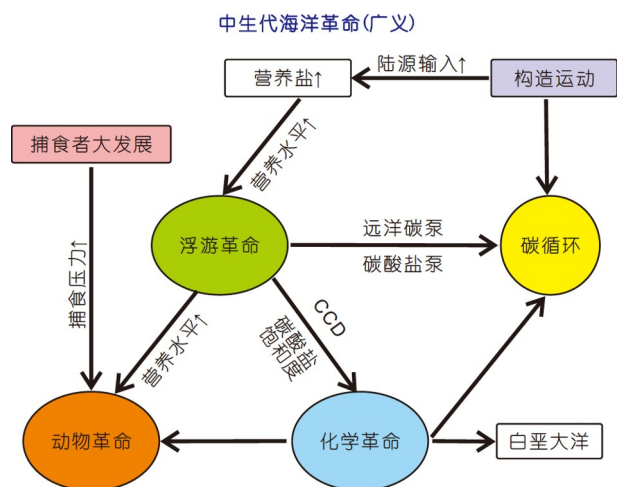


图7 (网络版彩色)中生代海洋革命过程及其对碳循环的影响  
 Figure 7 (Color online) Processes of the Mesozoic ocean revolution and their impact on the carbon cycle

酸盐沉积模式由古生代的浅海底栖型扩张到现代的远洋浮游型(图6(d)). 从侏罗纪开始海洋生物泵的调节作用更为明显, 全球碳同位素波动幅度逐步变小(图6(g)), 深海碳酸盐的堆积和溶解成为调控碳循环的重要环节<sup>[4,129]</sup>, 为现代海洋生态系统提供了稳定的环境. 生物地球化学模拟结果表明, 浮游生物的繁盛是古生代和中生代海洋缺氧/缺氧动力学差异的关键因素<sup>[134]</sup>, 中生代的多次大洋缺氧事件并未直接导致大规模灭绝, 只造成了部分类群多样性较小的波动<sup>[135,136]</sup>.

现代海洋生物泵对碳循环的调节, 主要是通过浮游生物调节海水碳酸盐饱和度和大洋碳酸盐补偿深度(carbonate compensation depth, CCD)实现的. 因此, 远洋浮游生物的崛起被认为是中生代中期海洋化学革命的直接驱动因素<sup>[121]</sup>. 当火山活动而导致大气中CO<sub>2</sub>增多时浮游藻类可以通过生物泵的作用将无机碳埋入深海, 降低大气二氧化碳分压, 海洋表层碳酸盐饱和度上升, 同时大洋碳酸盐补偿深度增加. 因此, 自侏罗纪开始, 在构造控制的环境事件和生物泵的共同作用下, 全球CCD开始出现频繁波动(图6(e)), 大气二氧化碳分压逐步下降(图6(f)).

#### 4 有待解决的科学问题

晚古生代-中生代生产者和生物泵的演变过程还缺乏精细的研究, 涉及碳循环的若干重要过程还不甚清楚, 且缺乏定量评估. 例如, 古生代底栖藻类、疑源类在海洋生产力的比例, 二叠纪-三叠纪之交大灭绝期间海洋生产力的升降问题<sup>[137,138]</sup>, 早、中三叠世藻类的

复苏及其对碳循环的影响<sup>[99,139]</sup>, 晚三叠世卡尼事件与海洋沟鞭藻和颗石藻起源之间是否存在关联<sup>[61,62]</sup>, 三叠纪-侏罗纪之交大灭绝对浮游藻类演化的影响<sup>[140,141]</sup>. 此外, 海洋藻类光合色素谱系的演替与生物泵的效率之间的关系并不明确. 晚古生代和中生代的大气-海洋各个碳库之间发生碳交换的过程和总量缺乏定量研究. 由于沟鞭藻和颗石藻是中生代生源碳酸盐沉积向深海扩张的直接驱动力, 是海洋有机碳储量增加的主要贡献者, 同时也是藻类光合色素谱系演替的典型范例. 因此, 远洋浮游藻类的起源时间和驱动因素等问题的研究对于解决以上科学问题具有重要的参考价值.

#### 4.1 远洋浮游藻类的起源时间

沟鞭藻和颗石藻被认为是红色谱系藻类中浮游类群在中生代的代表, 当前被认为起源于晚三叠世. 沟鞭藻最早出现在晚三叠世卡尼期(233 Ma), 颗石藻最早在诺利期的中后期出现(215 Ma). 然而这种“突然”的起源与生物标志物的证据并不一致, C<sub>28</sub>/C<sub>29</sub>甾烷比值变化曲线表明从古生代到中生代藻类色素谱系的演变是一个渐变过程(图1(j)). 沟鞭藻的生物标志化合物在志留纪和泥盆纪出现了两次异常峰值, 暗示了其在三叠纪之前可能已经存在<sup>[26]</sup>. 颗石藻的早期演化主要来自分子钟的证据, 对现存的定鞭金藻7个目的代表的核糖体小亚基基因序列(SSU-rDNA)测序的结果表明, 定鞭金藻类的钙化可能出现在距今约270~240 Ma之间<sup>[16]</sup>. 因此, 红色谱系的浮游藻类在晚三叠世之前的演化有待进一步研究.

#### 4.2 远洋浮游藻类起源驱动机制

沟鞭藻和颗石藻辐射的驱动因素目前仍在讨论之中, 有多种观点. 例如, 二叠纪末的大灭绝可能促进了红色谱系浮游植物的生态地位的上升<sup>[142]</sup>; 沟鞭藻和颗石藻的铁系数低于绿色藻类与蓝细菌, 使其在中生代较为富氧和高硫酸盐的海洋环境中具有竞争优势<sup>[143,144]</sup>; 钙化的浮游藻类出现可能是对海洋中钙浓度上升的适应性反应<sup>[145]</sup>. 以上观点均能在一定程度上解释浮游植物在中生代的繁盛. 然而, 显生宙出现了多次海洋钙离子浓度上升, 以及以氮和磷元素为代表的营养盐浓度上升事件, 这些事件并未导致具钙化能力的浮游藻类辐射. 因此, 浮游藻类的钙化能力出现的驱动因素仍是未来研究的重点.



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## 补充材料

附件1 晚二叠世-早三叠世钙藻群落和生物礁的全球分布

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Summary for “古生代-中生代之交海洋生物泵演变与浮游革命”

# Paleozoic-Mesozoic turnover of marine biological pump and Mesozoic plankton revolution

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The evolution of deep-time marine biological pumps (BPs) is critical to our understanding of the processes and mechanisms of the present-day carbon cycle. The Late Paleozoic-Early Mesozoic was a key period for the formation of modern marine biological pumps. Two types of Phanerozoic biological pump have been recognized: Paleozoic (Paleozoic-Middle Triassic) and Modern (Late Triassic-Modern). The Paleozoic-type pump comprises benthic algae and acritarch, whereas the Modern-type pump consists mainly of pelagic plankton. Geological records show that the Permian-Triassic extinction event destroyed the Paleozoic BP. Then, a special BP composed of cyanobacteria and other autotrophic bacteria, briefly appeared during the Permian-Triassic extinction interval. The Modern-type BP consists primarily of pelagic nanoplankton that originated in the Late Triassic. Fossil records suggest that the origin and rapid radiation of nanoplankton (coccoliths and dinoflagellates) during the Late Triassic to Early Jurassic promoted the establishment of modern plankton ecosystem. The rise of pelagic plankton such as dinoflagellates, coccolithophores, and planktonic foraminifers in the Mesozoic is summed up as the Mesozoic plankton revolution. The Mesozoic plankton revolution changed the patterns of marine material cycling and energy flow. The proliferation of nanoplankton accelerated the transfer of material and energy from primary producers to larger consumers and higher trophic levels, increasing the resources available to mesotrophic levels of marine ecosystems. The increased availability of energy resulted in rapid changes in composition, spatial structure, and food chain structures of marine fauna. The resulting “biological arms race” is summarized as the Mesozoic marine animal revolution. The Mesozoic plankton revolution was also the key driver of the Mid-Mesozoic revolution in terms of the regulation of ocean chemistry. Before the Early Jurassic, fluctuations in sea level, ocean area, continental weathering rates, and oceanic calcium ion concentrations produced large perturbations in carbonate deposition and the oceanic carbon cycle, which were only weakly buffered by the ocean. After the Early Jurassic, seawater chemistry changed—With the decrease and stabilization of carbonate saturation due to the transfer of biogenic carbonate from the shallow to the deep marine deposits—Mainly as a result of the rise of nanoplankton and tectonic movement. Changes in seawater chemistry are also reflected in the increased oxygen concentration therein. The oxygen concentration was higher on the Jurassic shelf, likely due to pelagic planktonic algal blooms. The occurrence of phytoplankton increased the efficiency of pelagic biological and carbonate pumps, and the accumulation and dissolution of deep-sea carbonates began to emerge as an important link in the carbon cycle; this improved the buffering capacity of ocean against environmental disturbances. It also provided a stable environment for the creation of modern marine ecosystem, and several oceanic anoxic events that occurred in the Mesozoic did not directly lead to mass extinctions of marine animals, causing only small fluctuations in the diversity of some taxa. Therefore, the Mesozoic plankton revolution is a critical link between the animal and chemical revolutions, and these three processes make up the Mesozoic marine revolution. The origin and evolution of key marine producers and their controlling factors are important topics that need to be studied. However, there are few high-precision studies on the evolution of primary producers and biological pumps during the Late Paleozoic-Early Mesozoic. In addition, the timeline and mechanisms driving the origin of pelagic phytoplankton are key questions that need to be addressed. To solve these problems, the evolution of photosynthetic pigment lineages and the paleogeographic distribution of algae, along with the changes in the size of plankton during the early Mesozoic, require further research attention.

**primary producer, productivity, carbon cycle, marine plankton revolution, biological evolution**doi: [10.1360/TB-2021-1220](https://doi.org/10.1360/TB-2021-1220)