

粗粒叠层石研究进展

刘萧萧¹, 刘超^{1*}, 胡霞²

1. 河南理工大学 资源环境学院, 河南 焦作 454000;

2. 河南理工大学 学术出版中心, 河南 焦作 454000

[摘要] 相对于其他种类叠层石,粗粒叠层石在地质历史中首现时间最晚,沉积记录最为稀少,是一类特殊的微生物岩。如何利用有限的沉积记录系统揭示控制其形成的内生和外生因素,对于认识微生物与环境相互作用方式及整个地质历史时期叠层石微观组构演变的驱动机制具有重要意义。基于西澳鲨鱼湾和巴哈马地区仍在生长的粗粒叠层石研究成果,综述了地质历史时期所有典型粗粒叠层石的宏观形态特征、微观纹层组分和沉积环境等信息,并对其形成的古气候、海平面和古海洋物理化学条件背景进行了对比分析。含丰富真核生物(如硅藻和绿藻)的微生物席捕获和黏结粗颗粒的能力比单纯的蓝细菌微生物席更强,粗粒叠层石的突然出现可能与大型真核生物的演化有关。大多数粗粒叠层石形成于受潮汐、波浪或风暴作用影响的浅海或边缘海环境中,反复动荡的海水促使颗粒持续供应至微生物席表面。间歇性高能环境中海水离子浓度较高且离子类型丰富,有助于提高微生物席胞外聚合物的黏性及黏结颗粒的能力。同时,海水中碳酸盐饱和度不足以促使微生物席发生钙化,但能支撑粗粒叠层石后续岩化过程。除此之外,较高的海水温度、缓慢波动上升的海平面、适宜的大气 CO₂ 含量、相对较高的海水碳酸盐饱和度和较少的后生生物也是形成粗粒叠层石的有利条件。虽然海相粗粒叠层石形成的必要条件已逐渐明晰,但这类特殊微生物岩的成因解释仍存在一些不足和不确定性,需要在粗颗粒的来源、粗粒叠层石的发育规模和陆相粗粒叠层石形成机制等方面做进一步研究,以约束内生和外生因素对粗粒叠层石形成的控制作用。

[关键词] 粗粒叠层石; 捕获和黏结; 微生物席; 沉积环境; 胞外聚合物

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Coarse-grained stromatolites: a review of the present state of research

LIU Xiaoxiao¹, LIU Chao^{1*}, HU Xia²

1. Institute of Resources and Environment, Henan Polytechnic University, Jiaozuo 454000, China;

2. Academic Publishing Center, Henan Polytechnic University, Jiaozuo 454000, China

Abstract: Coarse-grained stromatolites are a unique type of microbialite that emerged relatively late in geological history; however, only limited sedimentary records of coarse-grained stromatolites have been found to date. In this review, we utilize these scarce sedimentary records to unravel the intrinsic and extrinsic factors governing their formation. This endeavor holds immense significance in comprehending the intricate interplay between

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第一作者: 刘萧萧(2000—), 女, 硕士研究生, 研究方向: 沉积地质学, E-mail: 16619835329@163.com。

***通信作者:** 刘超(1989—), 男, 教授, 研究方向: 沉积地质学、地层学, E-mail: liuchao661030@126.com。

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microorganisms and their environment, as well as elucidating the driving mechanisms behind the evolution of stromatolite microfabrics throughout geological epochs. Based on the research findings of coarse-grained stromatolites in Shark Bay, Western Australia and the Bahamas, this study provides a comprehensive review of the macromorphology, microstratification, and sedimentary environment of classic coarse-grained stromatolites throughout geological history. Furthermore, a comparative analysis was conducted to examine and compare the different background factors, such as paleoclimate, sea levels, and paleo-ocean physicochemical conditions, which influenced their formation. Microbial mats rich in eukaryotes, such as diatoms and green algae, exhibit a significantly greater capacity for trapping and binding coarse particles compared to simpler cyanobacteria-dominated microbial mats. The abrupt emergence of coarse-grained stromatolites may be linked to the evolutionary development of larger eukaryotic organisms. Most commonly, these structures form in shallow or marginal marine environments under the influence of tides, waves, or storms where turbulent water facilitates continuous particle supply onto the surface of microbial mats. High ion concentration and diversity in seawater within this intermittent high-energy environment contribute to improved adhesion properties of extracellular polymers and enhanced particle binding ability for microbial mats. Meanwhile, calcium carbonate saturation in such settings is insufficient to promote calcification of microbial mats, but it can support subsequent lithification processes involved in forming coarse-grained stromatolites. Additionally, relatively higher sea temperatures, gradual fluctuations in sea levels, suitable atmospheric CO₂ content, elevated seawater calcium carbonate saturation levels, and lower metazoan biodiversity all favor favorable conditions for the development of coarse-grained stromatolites. Although the conditions necessary for the formation of marine coarse-grained stromatolites have been increasingly clarified, there remain certain limitations and uncertainties in the genetic interpretation of these special microbialites. Further research is required to investigate the sources of coarse particles, the development scale of coarse-grained stromatolites, and the formation mechanisms of continental coarse-grained stromatolites, which could provide a better understanding of the influence of both intrinsic and extrinsic factors on their formation.

Key words: coarse-grained stromatolites; trapping and binding; microbial mat; depositional environment; extracellular polymeric substance

微生物岩是指底栖微生物群落在生长和代谢过程中通过矿化作用和(或)捕获、黏结异源碎屑颗粒在原地形成的沉积物(岩),是微生物、矿物与外部环境相互作用的产物(Burne and Moore, 1987; Riding, 2011)。这类有机成因的沉积岩不仅蕴含着丰富的古气候(Shen et al., 2005; Liu et al., 2020)、古水文(Chen and Lee, 2014; 齐永安等, 2019; Martin-Bello et al., 2019; Zhi et al., 2024; 谢树成等, 2024)、古海水化学(Najarro et al., 2011; Li et al., 2021)、古生态(Grotzinger and Knoll, 1999; 曹隽等, 2009; Yao et al., 2016; 杨孝群和李忠, 2018)、区域构造(Chen et al., 2002; Shen and Webb, 2004; Yang et al., 2019)和生命演化信息(Allwood et al., 2006; Nutman et al., 2016; Hohl and Viehmann, 2021; 李柯然等, 2024; Van Kranendonk et al., 2025),也是潜在的油气资源储层(罗平等, 2013; 丁一等, 2024; 宋金民等, 2024),具有重要的科学价值和战略意义。

作为一类最为典型的微生物岩,叠层石最早由 Kalkowsky(1908)提出,指层状的有机成因的沉积岩。但由于前寒武纪地层中的叠层石普遍含有无机成因的亮晶纹层(Grotzinger and Rothman, 1996; Grotzinger and Knoll, 1999; Riding, 2008),叠层石的定义因此得到了补充,现主要指由底栖微生物活动在原地形成的具有纹层状构造的微生物岩,其内部可以包含不同比例的化学沉淀物(Riding, 2008, 2011)。相应地, Riding(2011)将地质历史时期的叠层石按微观组构划分为三大类:亮晶壳叠层石、混合壳叠层石和岩化微生物席叠层石(图 1)。其中,岩化微生物席叠层石按粒度又分为细粒叠层石和粗粒叠层石。不同类型叠层石其形成涉及的主要过程不同:亮晶壳叠层石主要涉及非生物矿物沉淀,细粒叠层石主要涉及微生物诱导矿物沉淀,粗粒叠层石则主要形成于微生物的捕获、黏结作用(Awramik and Riding, 1988; Grotzinger, 1990; Frantz et al., 2015)。

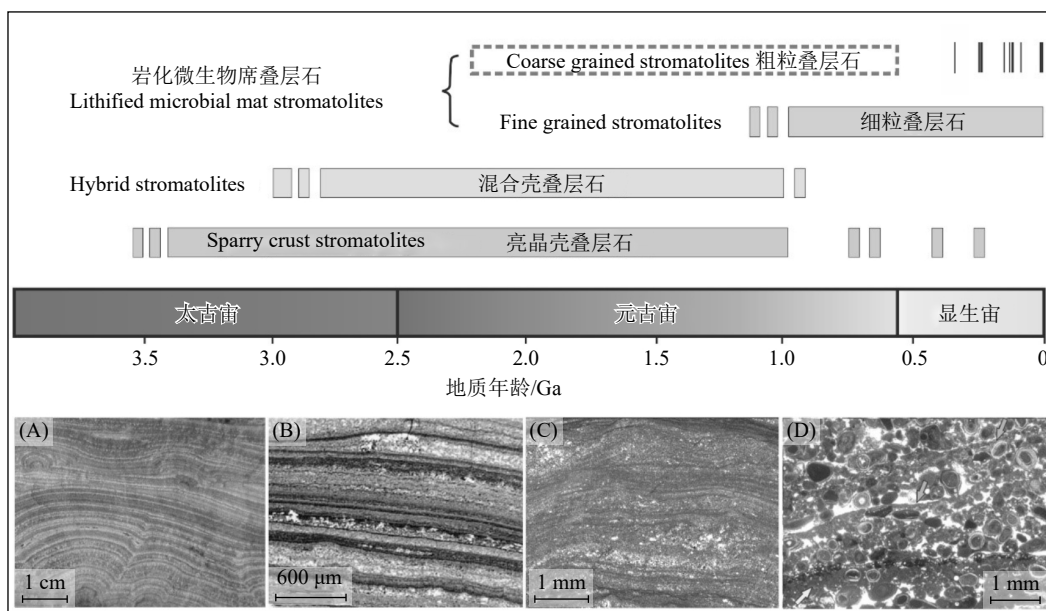


图 1 地质历史时期叠层石微观结构和粒度演化简图(据 Riding, 2011 修改)

Fig. 1 Schematic diagrams illustrating the microfabric and grain size evolution of stromatolites throughout geologic history (A) 亮晶壳叠层石(据 Riding, 2008 修改); (B) 混合壳叠层石(据 Knoll and Semikhatov, 1998 修改); (C) 细粒叠层石(据 Frantz et al., 2015 修改); (D) 粗粒叠层石典型微观特征(据 Suarez-Gonzalez et al., 2014 修改)

叠层石的微观结构和粒度在地质历史时期是阶段性演变的(Grotzinger and Knoll, 1999; Reitner and Thiel, 2011)。太古宙绝大多数时间以亮晶壳叠层石为主, 古元古代和中元古代主要发育混合壳叠层石。中元古代叠层石的丰度开始下降, 并在新元古代基本被岩化微生物席叠层石(细粒叠层石)所取代。前人研究认为, 前寒武纪叠层石微观结构的转变与大气 CO_2 分压、古海洋碳酸盐饱和度的持续下降及蓝细菌 CO_2 浓缩机制的启动有关(Grotzinger, 1990; Grotzinger and Knoll, 1999; Riding, 2006; Reitner and Thiel, 2011)。相比之下, 澳大利亚西部鲨鱼湾和巴哈马地区现代海洋则以发育柱状或穹隆状粗粒叠层石为特征(Logan, 1961; Dravis, 1983; Reid et al., 2000, 2003a), 但这类叠层石在深时海相沉积序列中却极为罕见, 仅记录于某些晚古生代和中—新生代地层中(Suarez-Gonzalez et al., 2019)。粗粒叠层石的出现受微生物群落的组成与演化, 还是特定的气候、海洋物理化学及生态条件控制, 至今仍无定论。本文在综述现代及深时典型粗粒叠层石宏观、微观特征和增生-岩化过程的基础上, 通过对比它们发育的背景条件, 深入探讨内生和外生因素对这类特殊微生物岩形成的控制作用, 为进一步约束其环境指示意义提供新见解。

1 粗粒叠层石的概念、时代分布及特殊性

粗粒叠层石是指主要通过底栖微生物群落的直立丝状体和分泌的胞外聚合物(EPS)捕获、黏结粒度较粗(通常粒径 $\geq 1 \text{ mm}$)的异源碎屑颗粒(鲕粒、似球粒和生物碎屑等)而形成的具有粗糙纹层的波状、穹隆状或柱状微生物岩(Riding et al., 1991a; Riding, 2011)。现代海洋中最典型的粗粒叠层石位于巴哈马(Black, 1933; Dravis, 1983; Dill et al., 1986; Feldmann and McKenzie, 1998; Reid et al., 2000; 张薇, 2020)和澳大利亚西部鲨鱼湾(Logan, 1961; Awramik and Riding, 1988; Reid et al., 2003a)。此外, 美国佛罗里达(Ginsburg et al., 1954)、百慕大群岛(Gebelein, 1969)、波斯湾(Kinsman and Park, 1976)、开曼群岛(Jones and Goodbody, 1985)、波利尼西亚(Sprachta et al., 2001)和古巴科科斯岛(Bouton et al., 2016)等地区也有零星分布。

直到 20 世纪 90 年代, Riding et al. (1991a)才在西班牙南部新近系发现了类似于现代粗粒叠层石的微生物岩。后续大量实例研究表明, 粗粒叠层石还记录于少数中生代和晚古生代海相地层中, 包括白垩系巴雷姆-阿普特阶(Barremian-

Aptian)(Braga et al., 1995; Immenhauser et al., 2005; Suarez-Gonzalez et al., 2014)和土伦阶(Turonian)(Rodríguez-Martínez et al., 2012)、侏罗系牛津阶(Oxfordian)(Matyszkiewicz et al., 2006)、三叠系拉丁阶(Ladinian)(Mercedes-Martín et al., 2013)和奥伦尼克阶(Olenekian)(Woods, 2013)以及泥盆系法门阶(Famennian)(Chow and George, 2004)。最近, Angonese et al. (2024)在巴西 Paraná 盆地晚侏罗世河流相地层中首次发现了硅质粗粒叠层石。

粗粒叠层石在地质历史长河中首现时间最晚, 沉积记录最稀少(图 1)。元古宙和显生宙许多海相混合壳叠层石和细粒叠层石也形成于被粗颗粒(尤其是鲕粒)所包围的沉积环境中(Awramik and Riding, 1988; Rasmussen et al., 1993; Knoll and Semikhatov, 1998; Suarez-Gonzalez et al., 2016), 但其内部细腻的纹层构造和碎屑颗粒的分布位置(被动的充填孔洞)暗示微生物的捕获和黏结作用并不明显(Knoll and Semikhatov, 1998; Frantz et al., 2015)。同样的现象也记录于现代及深时湖泊相叠层石中(Paul and Peryt, 2000; Chidsey Jr et al., 2015)。由此推断, 粗粒叠层石形成条件可能较严苛, 是一类特殊的微生物岩。

2 现代海洋粗粒叠层石

现代海洋粗粒叠层石多形成于盐度正常或咸化的沿海浅水环境(水深小于 10 m), 受潮汐作用影响较大, 典型代表是巴哈马和西澳鲨鱼湾地区的叠层石(图 2)。

巴哈马 Highborne Cay 粗粒叠层石生长于盐度正常的开阔海洋环境, 受移动沙丘和潮汐的影响(Dill et al., 1986; Riding et al., 1991b; Reid et al., 2000; Visscher et al., 2000; Decho et al., 2005; Planavsky and Ginsburg, 2009; Bowlin et al., 2012)。其纹层粗糙, 在顶部未岩化的微生物席中通常含有被蓝细菌捕获的碳酸盐颗粒砂, 岩化纹层中可见钙化的蓝细菌菌丝体(图 2)。粗粒叠层石的增生-岩化过程与微生物席中微生物功能群的交替及其代谢活动密切相关, 主要涉及异源碎屑颗粒的捕获、黏结和碳酸盐矿物沉淀 2 个过程(Reid et al., 2000, 2003b; Jahnert and Collins, 2012)。Reid et al. (2000)在巴哈马 Highborne Cay 浅潮下带粗粒叠层石中首次识别出 3 类微生物席。在沉积速率很高的水体环境中, 后生生物的生存受

到抑制, 第 1 类微生物席(主要含稀疏的丝状裂须藻蓝细菌)通过其分泌的 EPS 和其固有的快速向上生长、包绕能力能高效地捕获和黏结悬浮鲕粒(Frantz et al., 2015), 形成稳固的颗粒层。研究表明, 此颗粒增生过程没有表现出明显的钙化现象(Reid et al., 2000), 并可以由其他微生物独立或共同参与完成(如硅藻、绿藻和席藻属等蓝细菌; Awramik and Riding, 1988; Riding et al., 1991a; Bowlin et al., 2012)。随着沉积速率的下降, 第 2 类微生物席开始发育, 为表生薄层钙化生物膜(泥晶壳), 厚 20~60 μm , 含丰富的异养微生物、无定型 EPS、文石针和少量的裂须藻蓝细菌。无机碳、硫同位素证据表明硫酸盐还原菌降解 EPS 在泥晶壳形成过程中起到了很大作用(Visscher et al., 2000; Andres et al., 2006), 与微环境中碳酸盐饱和度的增加有关(Dupraz et al., 2009)。随着沉积速率持续降低, 第 3 类微生物席发育于钙化生物膜之下, 含大量的穿石球状蓝细菌(endolithic *Solentia* sp.)和无定向排列的裂须藻蓝细菌。前者具有钻孔功能, 在硫酸盐还原菌的协同作用下能快速充填微钻孔(泥晶化), 连通不同的碳酸盐颗粒, 形成厚 200~1 000 μm 的鲕粒焊接层或泥晶化层(Macintyre et al., 2000)。除沉积速率外, 微生物席类型的转变还与埋藏时间、波浪或风暴作用、水温变化和光照强度等环境因素有关(Riding, 2011)。3 类微生物席交替发育, 不断增生、岩化, 最终保存为巴哈马典型的粗粒叠层石。澳大利亚西部鲨鱼湾 Hamelin Pool 潮下带柱状粗粒叠层石发育规模较大(高达 2 m)(图 2; Logan et al., 1974; Awramik and Riding, 1988; Reid et al., 2003a; Cutts et al., 2022), 它以蓝细菌和硅藻组成的微生物群落共同捕获、黏结异源碎屑颗粒为特征。其形成过程与巴哈马地区略有差别(Reid et al., 2003a; Jahnert and Collins, 2012), 表现在除上述 3 个增生-岩化过程外, 还包括 2 个同沉积成岩过程: (1)碎屑颗粒边缘广泛沉淀碳酸盐泥晶套, 其可能与硫酸盐还原菌旺盛的代谢活动有关(Dupraz and Visscher, 2005; Baumgartner et al., 2006; Jahnert and Collins, 2012); (2)文石晶体填充开放孔洞, 主要为无机过程。

西澳鲨鱼湾和巴哈马地区现在仍在生长的粗粒叠层石为沉积学家研究其增生-岩化过程和控制因素提供了天然实验室(Visscher et al., 2000;

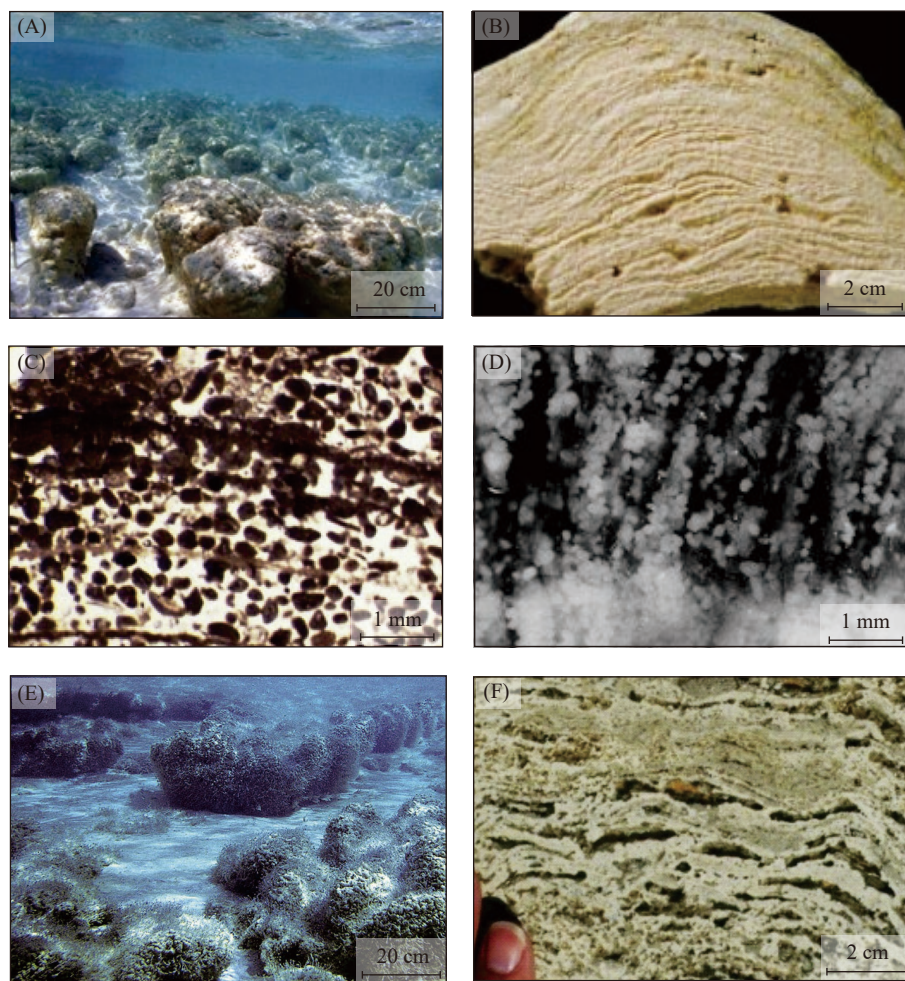


图 2 现代海洋粗粒叠层石

Fig. 2 Modern marine coarse-grained stromatolites

(A)、(B)巴哈马 Highborne Cay 浅潮下带柱状粗粒叠层石, 其中(B)为垂向切面, 展示纹层宏观特征(据 Reid et al., 2000; Browne, 2011 修改); (C)巴哈马 Stocking Island 潮间带粗粒叠层石镜下照片, 显示纹层由颗粒层和薄泥晶层组成(据 Browne, 2011 修改); (D)Lee Stocking 岛潮间带粗粒叠层石顶部微生物席垂向切面, 可见蓝细菌菌丝体(黑色)捕获黏结的碳酸盐颗粒砂(白色)(据 Browne et al., 2000 修改); (E)、(F)西澳大利亚 Hamelin Pool 潮下带发育的柱状粗粒叠层石及其垂向抛光切面(据 Riding, 2000; Playford et al., 2013 修改)

Reid et al., 2003a; Bowlin et al., 2012; Jahner and Collins, 2012)。但仅仅依靠现代的研究实例不能有效地约束气候、海平面和海洋化学(如碳酸盐饱和度)等外生因素对粗粒叠层石形成的影响和控制作用, 因此, 需要与深时粗粒叠层石展开对比研究。

3 深时海相粗粒叠层石

基于早期对巴哈马和西澳大利亚等地区粗粒叠层石的研究, 沉积学家 20 世纪 60 年代曾认为蓝细菌的捕获和黏结作用可能普遍参与了古代微生物岩的形成(Fischer, 1965; Gebelein, 1969), 但古代微生物岩明显缺乏可与现代粗粒叠层石相比

拟的宏、微观特征。直到 20 世纪 90 年代, 零星的深时粗粒叠层石记录才被逐渐发现、报道(表 1; Riding et al., 1991b; Suarez-Gonzalez et al., 2019)。西班牙东南部阿尔梅里亚地区发育的中新世粗粒叠层石是通过“捕获和黏结”作用增生的(Riding et al., 1991a), 其在发育规模、宏观形态、微观结构、颗粒组成(鲕粒、似球粒)和沉积环境(受潮汐流、海浪影响的鲕粒浅滩环境)等方面与巴哈马 Lee Stocking 岛“巨型”潮下带柱状粗粒叠层石(Feldmann and McKenzie, 1998)非常相似。流动的沙丘有效地抑制了后生生物的发展, 为粗粒叠层石的生长提供了有利条件。除蓝细菌外, 绿藻和硅藻等藻类也起到了捕获粗碎屑颗粒的作用。

表 1 现代及深时典型粗粒叠层石沉积记录

Table 1 Sedimentary records of typical coarse-grained stromatolites in modern and ancient times

地层时代与地点	沉积环境	宏观特征	微观特征	参考文献
现代, 巴哈马群岛	潮间带-潮下带上部, 正常海水盐度、受潮汐作用影响	粗粒叠层石呈柱状, 高达 2 m, 上部有未岩化的微生物席	纹层粗糙, 厚 1~5 mm; 在未岩化微生物席中可见蓝细菌捕获黏结的碳酸盐颗粒砂; 岩化纹层中有钙化的蓝细菌丝菌体	Visscher et al., 2000; Reid et al., 2003b; Andres and Reid, 2006; Bowlin et al., 2012
现代, 鲨鱼湾	高盐度海湾, 潮下带上部	粗粒叠层石呈圆柱状、圆顶状, 偶见分枝; 纹层通常向上凸出至波浪形, 在厘米级别范围内连续	颗粒层中可见粒径为 0.5~2.0 mm 的碳酸盐颗粒; 泥晶层主要由微晶文石组成, 呈凝块状	Awramik and Riding, 1988; Reid et al., 2003a
中新世 El Joyazo 组, 西班牙东南部	潮流冲刷的鲕粒浅滩环境, 正常海水盐度	粗粒叠层石和不规则凝块岩交互形成微生物丘, 单个微生物丘高 1.5 m, 宽 4 m	纹层连续性较好, 缺乏大的孔洞, 见由似球粒和鲕粒组成的不规则层状或柱状构造	Riding et al., 1991a; Braga et al., 1995
早白垩世 Leza 组, 西班牙北部	受潮汐影响的沿海湿地环境	粗粒叠层石与鲕粒颗粒灰岩互层, 横向延伸可达 100 m	颗粒层和泥晶层交替出现, 颗粒层由鲕粒、似球粒、内碎屑和生物碎屑组成; 泥晶层局部形成毫米级的穹隆状。在颗粒层中偶见钙化的蓝细菌丝菌体	Suarez-Gonzalez et al., 2014, 2016
晚侏罗世牛津阶底部, 波兰南部	高水动能水下高地, 低沉积速率, 高盐度	凝块岩和粗粒叠层石交互形成微生物礁, 厚约 12 m, 横向延伸稳定	粗粒叠层石纹层呈水平或倾斜状, 厚 1~3 mm, 局部见生物扰动构造。颗粒纹层中鲕粒、似球粒和生物碎屑较常见	Matyszkiewicz et al., 2006, 2012
中三叠世晚期拉丁阶, 西班牙东北部	潮间-潮下带, 颗粒滩前中-高能水动能环境	粗粒叠层石发育于厚约 3 m 的半椭圆形生物礁内	粗粒叠层石由颗粒层和泥晶层交替发育组成, 纹层厚度为毫米至厘米级别; 颗粒层含鲕粒、似球粒、内碎屑和石英颗粒, 深色微晶纹层为平行层状至波浪状	Mercedes-Martín et al., 2013, 2014
早三叠世奥伦尼克阶, 美国内华达州	潮间带和浅潮下带	板状	纹层厚 2~3 mm, 颗粒层由似球粒、鲕粒、内碎屑和骨骼颗粒组成	Woods, 2013
晚泥盆世法门阶, 澳大利亚西部	礁后高能浅潮下带至礁坪的过渡环境	凝块岩和波状粗粒叠层石组成“人”字形微生物礁, 顶部呈穹隆状, 底部平坦	颗粒层含有被捕获和黏结的异源粗颗粒, 包括鲕粒、似球粒、内碎屑、钙质球粒, 顶部为凝块泥晶	Chow and George, 2004

西班牙北部喀麦隆盆地早白垩世 Leza 组粗粒叠层石由等厚的富颗粒层和富泥晶层交替组成(图 3; Suarez-Gonzalez et al., 2014), 明显有别于现代海洋粗粒叠层石纹层特征(图 2-C)。这表明, Leza 组粗粒叠层石既可以通过微生物席捕获黏结碎屑颗粒方式增生, 也可以通过微生物诱导原位钙化方式增生。其特殊的增生过程和纹层样式与其特殊的沉积环境有关。Leza 组粗粒叠层石形成于受潮汐影响的沿海湿地环境, 经历了

盐度和碳酸盐饱和度等水化学波动和潮汐环境中典型的水动力变化, 这些物理、化学环境变化交织在一起, 促使富颗粒层和富泥晶层交替增生, 最终形成 Leza 组粗粒叠层石。波兰南部晚侏罗世牛津阶粗粒叠层石发育于高盐度、高水动能水下高地环境(Matyszkiewicz et al., 2006, 2012)。光养蓝细菌的大量爆发使微生物席捕获、黏结碎屑颗粒更加高效, 并促使叠层石快速胶结成岩。这种快速胶结作用也记录于巴哈马潮下-潮

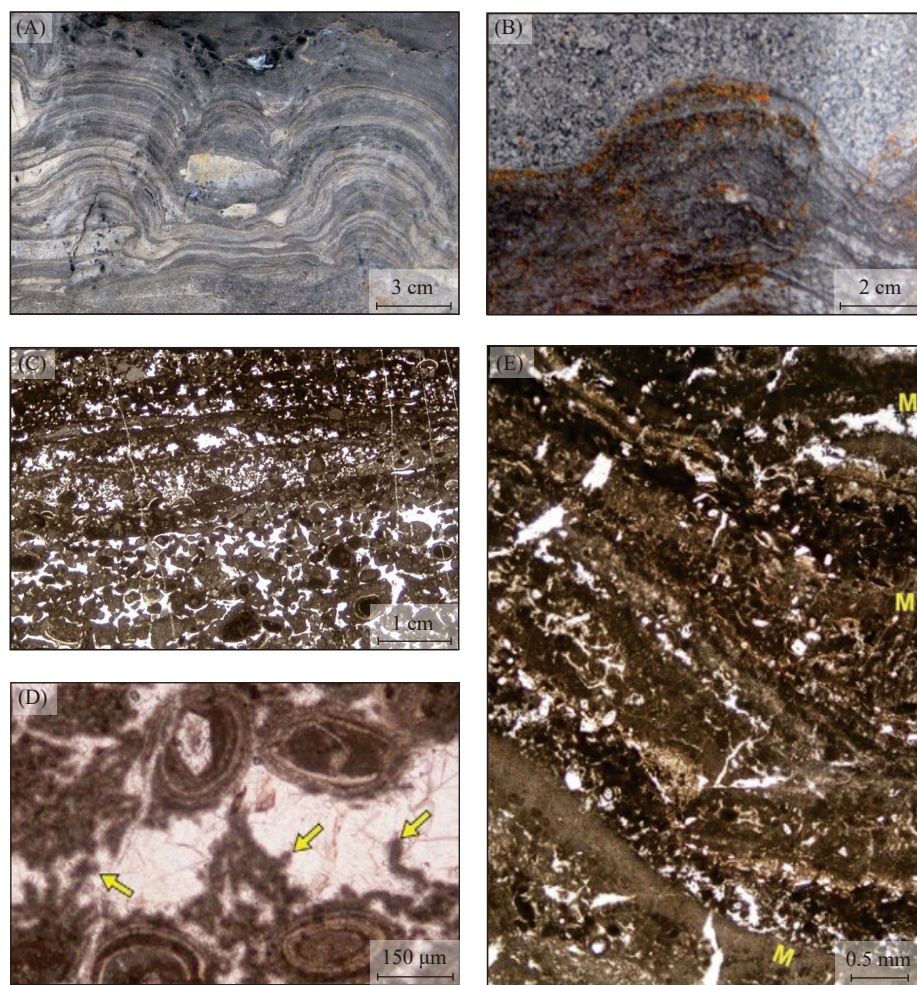


图 3 西班牙北部早白垩世 Leza 组的粗粒叠层石(据 Suarez-Gonzalez et al., 2014 修改)

Fig. 3 Coarse-grained stromatolites of the Early Cretaceous Leza Formation, northern Spain

- (A)早白垩世 Leza 组穹隆状粗粒叠层石宏观特征;(B)粗粒叠层石(下)与鲕粒颗粒灰岩(上)直接接触;
(C)粗粒叠层石微观照片,显示纹层由富颗粒层和富泥晶层组成;(D)富颗粒层中保存的钙化蓝细菌菌丝体
(箭头所指);(E)粗粒叠层石纹层中包含着丰富的颗粒
(即使在高角度纹层中也是如此,体现了蓝细菌对颗粒的捕获和黏结作用,
注意以泥晶为主的纹层 M 比现代及其他深时粗粒叠层石厚)

间带正在生长的粗粒叠层石表面微生物席中 (Reid and Browne, 1991; Golubić and Browne, 1996)。Woods (2013) 和 Mercedes-Martín et al. (2013) 分别研究了美国内华达州早三叠世和西班牙东北部中三叠世的粗粒叠层石, 它们均发育于受潮汐影响的颗粒滩前或滩后浅海环境。

澳大利亚西部坎宁盆地 Lennard 陆架晚泥盆世波状粗粒叠层石发育于“人”字形微生物礁中 (Chow and George, 2004), 其宏观形态类似于现代巴哈马 Lee Stocking 岛 (Dill et al., 1986; Riding et al., 1991a) 和西澳大利亚鲨鱼湾 (Logan, 1961) 潮下带粗粒叠层石。虽然受成岩作用影响, 其内部未见

钙化蓝细菌化石, 但考虑到 Lennard 陆架其他同期的礁滩沉积序列中广泛保存有肾形藻、葛万菌等蓝细菌 (Kerans, 1985), 同时考虑到其内部碎屑颗粒组成与周围沉积物相似, Lennard 陆架粗粒叠层石被认为是由微生物捕获、黏结碎屑颗粒增生、岩化而成 (Chow and George, 2004)。

4 粗粒叠层石形成的影响因素

粗粒叠层石是微生物、矿物与外部环境相互作用的产物, 其形成受一系列内生、外生因素的控制和影响 (Reid et al., 2003b; Riding, 2011)。主要因素包括微生物的组成与演化、水动力和水

化学条件、后生生物扰动及古气候条件。

4.1 微生物的组成与演化

微生物席是粗粒叠层石形成的生物基础,其构造复杂,通常存在于叠层石或其他水下微生物岩表面(Krumbein, 1994; Costerton et al., 1995)。微生物席的生物组成、生物膜及其分泌 EPS 的数量和性质,会直接影响到微生物席的捕获、黏结能力及钙化和原地碳酸盐沉淀过程(Reid et al., 2000; 温志峰等, 2004)。现代海洋粗粒叠层石微生物席中,除蓝细菌外,还包括硅藻、绿藻和许多其他生物(Fischer, 1965; Gebelein, 1969; Monty, 1973; Awramik and Riding, 1988; Falkowski et al., 2004; Bengtson et al., 2009; Riding, 2011),这些富含真核生物的微生物席捕获和黏结粗颗粒的能力比单纯的蓝细菌微生物席更强。例如, Riding et al. (1991b)在对巴哈马 Lee Stocking 岛粗粒叠层石研究中注意到,微生物席中大型绿藻负责捕获粗碎屑颗粒,而硅藻和蓝细菌则负责黏结各种尺寸颗粒。Frantz et al. (2015)通过室内培养实验也观察到了类似现象。而华北中元古代铁岭组柱状细粒叠层石也被解释为由蓝细菌微生物席通过捕获、黏结碳酸盐泥增生岩化形成(Tosti and Riding, 2017),但柱间不稳定碎屑沉积物并没有被微生物席所捕获。这表明,粗粒叠层石的形成不仅需要活性黏结生物(如蓝细菌、硅藻)捕获、黏结碎屑颗粒,还需要大型藻类(如绿藻)共同参与捕获粗粒沉积物(Awramik and Riding, 1988; Frantz et al., 2015)。

微生物席表面的黏附力也影响着粗粒叠层石的形成。不同种类的蓝细菌分泌的 EPS 黏度和含量不同,其形成的黏附力也不同(Hu et al., 2003; Bahulikar and Kroth, 2008)。EPS 由蛋白质、碳水化合物和其他大分子组成,其黏度不仅取决于高分子化合物的初级结构和分子质量,还取决于单体(单糖和氨基酸)的综合三维结构和分子形状。不同种类的蓝细菌产生的 EPS 存在不同的单糖和连接类型, EPS 种类越多,黏性就越强(Hu et al., 2003)。同时黏度也受酸碱度值、无机盐和带电离子成分的影响。此外,微生物席表面的黏附力还与 EPS 的含量呈正相关关系,后者受营养物质浓度、光照强度、温度以及蓝细菌自身特性等因素制约(De Philippis and Vincenzini, 1998)。

4.2 水动力和水化学条件

现代及深时海相沉积记录指示粗粒叠层石通常形成于受潮汐、波浪或风暴影响的间歇性高能沉积环境(表 1)。在这些环境中,持续、反复的海水搅动会周期性地搬运异源碎屑颗粒到叠层石表面,并驱动不同微生物席交替发育(Reid et al., 2000; Eckman et al., 2008; Suarez-Gonzalez et al., 2014)。同时,移动的潮道沙丘和季节性高咸化海水能大大减少后生生物的捕食和破坏作用,有利于粗粒叠层石的增生、岩化与保存(Tomás et al., 2013)。

粗粒叠层石顶部微生物席能黏结碎屑颗粒,主要依靠蓝细菌分泌的大量柔软、富有“黏性”的 EPS(Decho et al., 2005)。这些通过光合作用生产的 EPS 具有大量带负电的官能团(如羧基、羟基、羰基等),它们能有效地吸附碎屑颗粒表面的 Ca^{2+} 和 Mg^{2+} , 并导致微环境中碳酸盐饱和度下降,进而阻碍微生物席(蓝细菌)的钙化或早期岩化(Dupraz and Visscher, 2005; Dupraz et al., 2009)。现代及深时粗粒叠层石大都形成于浅海环境,海水中较高的离子浓度和多样性会增强 EPS 的黏附力。EPS 不仅具有“黏性”表面,它们也是矿物沉淀的主要场所(Burne and Moore, 1987; Dupraz et al., 2009)。研究表明,当 EPS 中 Ca^{2+} 数量达到饱和后,微生物席钙化作用可能会随即发生(Arp et al., 2003),并严重削弱其颗粒捕获和黏结能力(Suarez-Gonzalez et al., 2016)。大陆盐湖环境中含有丰富的电解质,微生物席表面 EPS “黏性”较强,这也是某些盐湖微生物岩中含有少量黏结颗粒的原因(Brasier et al., 2018; Vennin et al., 2019)。但与此同时,盐湖往往具有高碱度、高碳酸钙饱和和状态等特点(Dupraz et al., 2013),这会导致 EPS 内发生早期矿物沉淀,从而阻碍其捕获和黏结过程。在淡水环境中,微生物席表面 EPS 丰度较高,但由于缺乏电解质, EPS 黏结碎屑颗粒的能力较弱,且光合作用会促进蓝细菌发生早期钙化(Spears et al., 2008)。因此,粗粒叠层石可能仅形成于碳酸盐饱和度不高但又能支撑后续岩化过程的浅海环境中。

4.3 后生生物扰动

培养实验及地质记录均表明,后生生物的捕食、挖掘作用会破坏微生物席的发育与保存,在一定程度上解释了显生宙叠层石数量稀少的现

象(Walter and Heys, 1985; Fenchel, 1998; Mata and Bottjer, 2012)。虽然现代及深时粗粒叠层石往往伴随着高盐度或高侵蚀速率沉积环境(Bowlin et al., 2012; Suosaari et al., 2016),不适合后生生物生存,但后生生物扰动的痕迹确实存在。例如,白垩系 Leza 粗粒叠层石颗粒纹层中含有很多介形虫和有孔虫生物化石,它们具有高丰度、低分异度等特点,暗示其可能代表了生物扰动(Suarez-Gonzalez et al., 2014)。侏罗系牛津阶粗粒叠层石中保存有很多粪球粒化石,Matyszkiewicz et al. (2006)认为这些粪球粒是以海胆为食的蟹类所排泄,因此推测叠层石在生长过程中也受到了生物扰动。除了无脊椎动物外,大型绿藻(如囊臼藻)在微生物席表面定殖也能对叠层石构成扰动,表现为绿藻死亡后在叠层石内部留下等体积的空腔(Riding, 2011)。巴哈马群岛现代粗粒叠层石中可以观察到很多由大型藻类和双壳、腹足类等钻孔生物留下的孔洞,这些生物产生的扰动会阻碍、破坏纹层发育,在中尺度上影响叠层石的形态(Andres and Reid, 2006)。

4.4 古气候条件

海洋微生物通过吸收海水中溶解的 CO_2 和 HCO_3^- 进行光合作用,形成初级生产力,这种固碳行为主导了长期碳循环,并对地球气候产生了关键影响(Walker et al., 1981; Berner et al., 1983; Kasting and Catling, 2003)。当大气 CO_2 含量过高时,海水中溶解无机碳(DIC)含量升高,海洋发生酸化,从而严重影响海洋生物的生存环境,不利于碳酸盐岩的形成。而大气 CO_2 含量过低,会导致叠层石形成所必需的生物与非生物作用交替的节律性受到干扰,阻碍叠层石的发育(张静和张宝民, 2021)。海水碳酸盐体系(如 CO_3^{2-} 浓度、碳酸钙饱和度)通过调控溶解态 CO_2 浓度和酸碱度,直接影响微生物的生理活性和固碳效率(朱华玺等, 2025)。海水中 DIC 含量适宜且钙含量较高是最利于微生物进行光合作用、促进碳酸钙沉淀的环境(Arp et al., 2001)。

对地质历史时期所有经典粗粒叠层石形成的古气候、海平面和古海洋物理化学生态条件背景进行分析(图4),发现粗粒叠层石多发育于温室气候期,最适宜其形成的 $p\text{CO}_2$ 值在 2×10^{-3} 左右(图4-B)。同时,较高的海洋表面温度(图4-A)和缓慢波动上升的海平面(图4-C)也是

粗粒叠层石形成的有利条件。自早古生代以来,海洋微生物岩丰度总体呈长期波动下降趋势(图4-E; Riding and Liang, 2005a),与海水碳酸钙饱和度和状态(图4-F; Riding and Liang, 2005b)呈正相关关系,但与海洋后生物多样性演化趋势相反(图4-D; Sepkoski, 1997)。粗粒叠层石总体形成于微生物岩丰度较高时期(图4-E),其可能与同期较高的海水碳酸钙饱和度及后生生物的减少有关。但值得注意的是,新近纪粗粒叠层石发育于大气 CO_2 浓度和海水碳酸钙饱和度极低、后生物多样性较高的冰室气候期,其形成环境需进一步研究。

5 结论与展望

粗粒叠层石是微生物、矿物与外部环境相互作用的产物,其形成受一系列内生、外生因素的控制和影响。微生物席中不同种类的蓝细菌产生的 EPS 具有不同的黏附力,含有丰富真核生物(如硅藻和绿藻)的微生物席捕获和黏结粗颗粒的能力比单纯的蓝细菌微生物席更强,粗粒叠层石的突然出现可能与微生物群落的组成及大型真核生物的演化有关。大多数粗粒叠层石形成于受潮汐、波浪或风暴影响的浅海或边缘海环境,反复动荡的海水促使颗粒持续供应至微生物席表面。此外,海水中较高的离子浓度和丰富的离子类型有助于提高微生物席 EPS 的黏性,海水中碳酸钙饱和度不足以促使微生物席发生钙化,但能支撑粗粒叠层石后续岩化过程。相对较高海水温度、缓慢波动上升的海平面、适宜的大气 CO_2 含量以及较低的后生物多样性也是粗粒叠层石形成的有利条件。

虽然海相粗粒叠层石形成的必要条件已逐渐明晰,但这类特殊微生物岩的成因解释仍存在一些不足和不确定性。首先,粗粒叠层石中的颗粒(尤其是鲕粒)是否必须异源? Suarez-Gonzalez and Reitner (2021)描述了一种在高盐度静态湖中通过原位沉淀形成的鲕粒,这些近球形鲕粒排列在一起形成厘米级别的不规则聚集体,类似于粗粒叠层石中的颗粒层;而聚集体上下层充满 EPS 基质,似粗粒叠层石中由微生物群落生长和代谢活动形成的暗色泥晶纹层。通过重复的微生物活动、矿物沉淀及漫长的成岩作用改造,极有可能形成像早白垩世 Leza 组中粗粒叠层石一

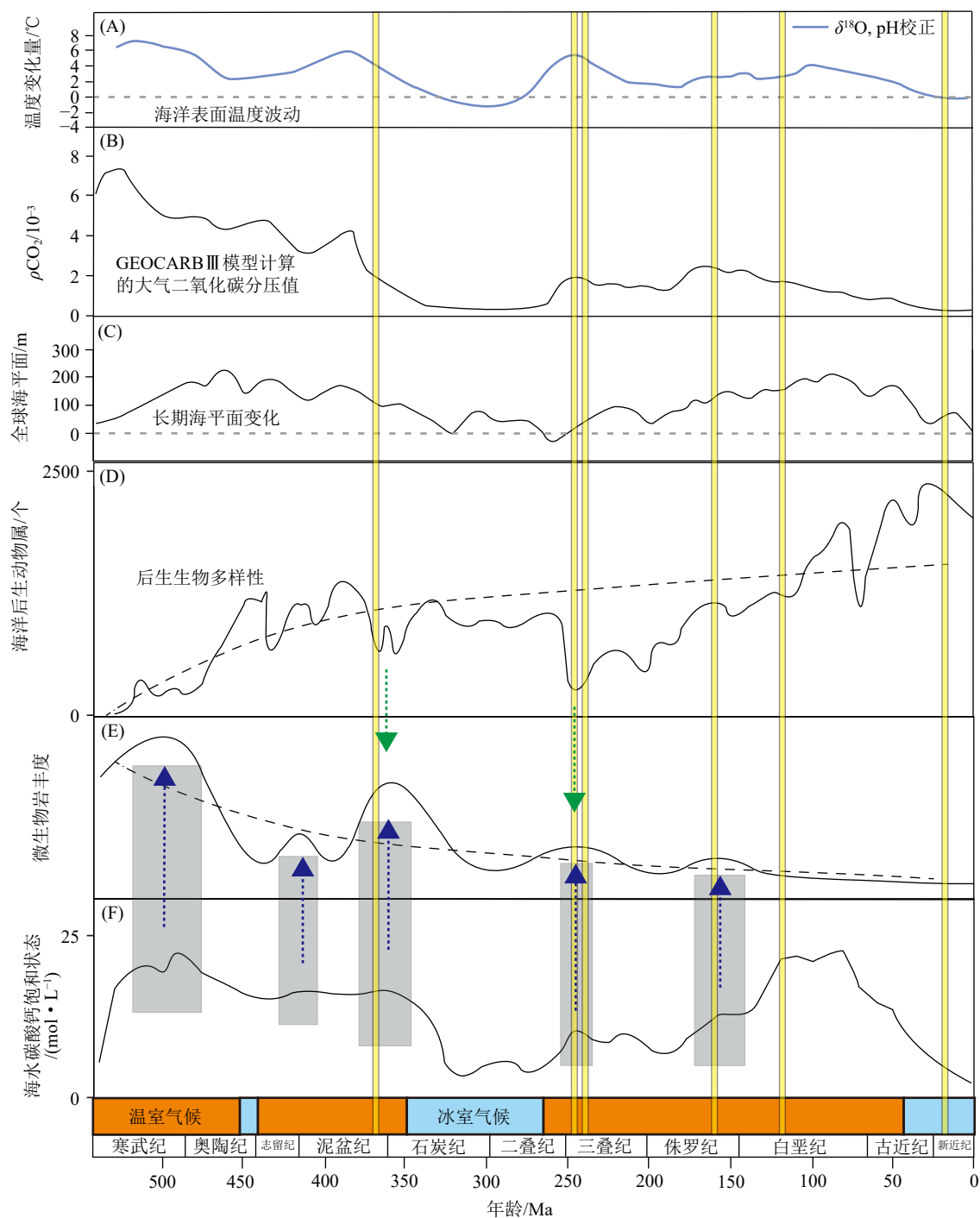


图 4 显生宙粗粒叠层石记录(黄色方框)与古气候、海平面和古海洋物理化学生态环境演化关系

Fig. 4 Correlation between the coarse-grained stromatolite records of the Phanerozoic era (yellow box) and the evolutionary patterns of paleo-climate, sea level fluctuations, as well as physicochemical and ecological conditions of ancient oceans

(A) 古海洋表面温度波动曲线(Royer et al., 2004); (B) 根据 GEOCARB III 模型计算的大气 $p\text{CO}_2$ 平均值(Royer et al., 2004); (C) 长期海平面变化曲线(Haq and Al-Qahtani, 2005; Haq and Schutter, 2008); (D) 海洋后生动物属级多样性(Sepkoski, 1997), 似乎与微生物岩丰度呈负相关关系(绿色箭头); (E) 微生物岩丰度曲线(Arp et al., 2001); (F) 海水碳酸钙饱和状态变化曲线(Riding and Liang, 2005a), 似乎与微生物岩丰度呈正相关关系(灰色方框与蓝色箭头)

样的沉积组构。其次, 通过对地质历史时期所有经典海相粗粒叠层石的宏观形态进行对比, 发现不同时期发育的粗粒叠层石规模也不尽相同。

是何外部环境因素控制着粗粒叠层石的发育规模? 第三, Angonese et al. (2024) 最近在巴西 Paraná 盆地晚侏罗世河流相沉积地层中首次发现了硅

质粗粒叠层石,其是通过微生物捕获黏结碎屑砂和原位二氧化硅沉淀形成,受到水化学和陆源沉积物供应(风成沉积控制)等特定环境的影响。陆相粗粒叠层石的普适形成机制是什么?海相和陆相粗粒叠层石的发育是否存在耦合?沉积学家需要在今后的研究工作中聚焦这些问题,进一步约束内生和外生因素对粗粒叠层石形成的控制作用。

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