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Review 综 述

海洋沉积物微生物介导有机碳转化研究进展

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摘 要：海洋沉积物是地球上最大的有机碳库，其中生存的微生物总量大、分布范围广、类群多样、代谢方式复杂，并共同构成海洋沉积物微生物组。海洋沉积物微生物组介导的有机碳降解与矿化过程不但能为沉积物中的生命活动提供物质和能量，也能参与调控碳循环过程，并在长时间尺度上对地球气候系统产生重大影响。沉积物中的有机碳在复杂多样的微生物代谢活动下被逐步降解，其最终的矿化过程与不同的电子受体消耗相偶合，并形成对应的地球化学分区。研究海洋沉积物微生物及其介导的有机碳转化过程对我们深入认识沉积物中的元素循环过程，并进一步评估其对整个地球系统的影响具有重要科学意义。本文对海洋沉积物微生物组的体量、包含的微生物多样性、代谢活性以及在不同地球化学分区中主要的微生物类群和代谢机制进行综述，最后基于研究现状展望了海洋沉积物微生物组的未来研究方向。

关键词：海洋沉积物；微生物组；有机碳转化；生物地球化学循环

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Research progress on microbiome and organic carbon transformation in marine sediment

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Abstract: Marine sediment is the largest organic carbon reservoir on Earth, and the microorganisms thereof constitute the marine sediment microbiome which are in large quantity, widely distributed, with diversified lineages and versatile metabolic capacities. The organic carbon degradation and mineralization processes mediated by the marine sedimentary microbes not only provide material and energy for life in the sediments, but also participate in carbon cycling processes and have a significant impact on the Earth's climate system for long time scales. Organic carbon in sediments is gradually degraded by complex microbial metabolic activities, and its final mineralization process sequentially couples with the depletion of different electron acceptors which forms the corresponding geochemical zones in marine sediment. The study of marine sedimentary microbiome and the associated organic carbon transformation processes is important for our in-depth understanding of elemental cycling processes in sediments and further assessment of their impact on the Earth system. This review provides an overview of the quantity of the marine sediment microbiome, the diversity of microorganisms, their metabolic capacities as well as the major microbial taxa and metabolic mechanisms that forms geochemical zones. Finally, based on the current research status, the future research directions of marine sedimentary microbiome are prospected.

Keywords: marine sediment; microbiome; organic carbon transformation; biogeochemical cycle

在全球气候变化的背景下，对全球碳循环的宏观收支及微观机制的研究显得尤为重要。据政府间气候变化专门委员会(Intergovernmental Panel on Climate Change, IPCC)报道，减少碳排放是抑制全球变暖的重要途径[1]。海洋碳库与大气碳库以及陆地碳库不断交换，处于动态变化的状态[2]。在海洋系统中，由陆地环境输入或海洋表层的浮游生物光合作用产生的有机碳会随着沉降作用进入海洋深层[3]。沉降过程中，大部分有机碳经过一系列的物理、化学及生物降解作用被彻底矿化为二氧化碳，而剩下的部分有机碳以颗粒有机碳(particulate organic carbon, POC)的形式抵达沉积物表面[4]。在沉积物中，有机碳在微生物水解和发酵代谢过程的作用下逐渐降解为简单的小分子化合物，并最终被矿化为二氧化碳或转化为甲烷。根据反应的能级大小和电子受体的可利用性，有机碳矿化过程主要在微生物活动的介导下依次与氧气、硝酸盐、锰和铁氧化物、硫酸盐等电子受体的还原过程相偶联。而在电子受体耗尽的深部沉积物中，微生物代谢产生的小分子化合物被产甲烷古菌利用产生甲烷，并由扩散作用向沉积物上层迁移，大部分在硫酸盐甲烷转换带(sulfate-methane transition zone, SMTZ)被氧化

为二氧化碳，返回到无机碳库中。

从宏观角度来看，沉积物中的碳循环是整个地球系统碳循环过程中的重要一环，影响着碳库的收支平衡并进一步调节地球系统的气候变化[5]。而在微观角度上，沉积物中由微生物代谢活动所介导的碳循环与其他元素循环过程相偶联，深入研究海洋沉积物中微生物组的规模、分布以及活性，对我们认识和理解海洋沉积物中的元素循环过程及其对整个地球系统的影响有着重要的意义。

1 沉积物微生物组的体量、分布及微生物多样性

大部分海洋沉积物处于黑暗、高压、低能量的环境，却蕴含着由微生物组构成的体量巨大的深部生物圈[6]。1998 年，Whitman 等[7]首次估算出全球海洋沉积物中含有的细胞量约为 3.5×10^{30} 个，对应的生物量约为 300 Gt。随着研究的深入和更多位点数据的加入，沉积物细胞总量的估算值也在不断更新。基于目前研究结果显示，海洋沉积物中细胞总量在 10^{29} 量级[$(2.90-5.39)\times10^{29}$ 之间][8-10]，与全球海水、土壤中的微生物细胞总量处于同一数量级[11]。

微生物在海洋沉积物中分布范围广。Herberling 等[12]以接近微生物存活上限的 120 ℃为温度界限，估测洋底生物圈的体积接近海水的总体积(约 10^{18} m^3)，且在最深至 5 km 的洋壳中仍存在微生物。目前，通过大洋钻探发现在温度达 120 ℃的俯冲带沉积物及洋底 2.5 km 深处的沉积物中均存在微生物活动的证据[13-14]。微生物在海洋沉积物中分布具有一定的规律性。研究显示，沉积物中微生物的分布受沉积速率、距陆架距离及有机碳含量等因素控制[15]。从全球分布来看，富含有机碳的陆架边缘区域沉积物中微生物细胞丰度最高，而寡营养的开放大洋沉积物中细胞丰度最低[8]。垂直方向来看，沉积物中微生物细胞丰度随沉积物深度增加而降低，且两者变化遵从幂律[8-9]。值得注意的是，沉积物中细菌和古菌细胞的分布也具有一定的规律性。Hoshino 等[16]对全球不同海域沉积物样品中细菌和古菌 16S rRNA 基因进行定量并估算其细胞丰度，发现在陆架边缘沉积物中古菌细胞占比(40.0%)高于远洋沉积物(12.8%)。此外，古菌占比也随采样位点水深增加而呈现降低的趋势[16]。

海洋沉积物微生物组由多样的微生物类群构成。Hoshino 等[17]对采集自全球 40 个位点的 299 份沉积物样品进行了 16S rRNA 基因测序和分析，发现沉积物中微生物种群的丰富度(richness)与海水及表层土壤相当。沉积物中微生物类群多样性的变化具有一定的规律性。通过对上述沉积物样品中的微生物群落进行聚类分析，Hoshino 等[17]发现沉积物中微生物群落可分为两大类，即在近岸有机碳含量丰富区域的厌氧微生物群落和在开放大洋沉积物中的有氧微生物群落。总体来看，沉积物中细菌种群丰富度高于古菌。在厌氧沉积物中，细菌和古菌种群丰富度均随沉积物深度增加而逐渐降低；在有氧沉积物中，细菌种群丰富度随沉积物深度增加而逐渐降低，古菌种群丰富度则呈现为较稳定的状态[17]。厌氧沉积物中细菌类群由暗黑菌门(*Atribacteria*)，绿弯菌门(*Chloroflexi*)和浮霉菌门(*Planctomycetes*)所主导；古菌类群主要由泉古菌门(*Crenarchaeota*)特别是其中的深古菌纲(*Bathyarchaeia*)所主导。在有氧沉积物中细菌类群主要由变形菌门(*Proteobacteria*)和厚壁菌门(*Firmicutes*)所主导；古菌类群主要由奇古菌门(*Thaumarchaeota*)所主导。在一些区域沉积物中也存在特定的古菌类群高度富集

的现象。例如，在秘鲁沿岸(Peru Margin)沉积物中的深古菌[18]，孟加拉湾(Bay of Bengal)深部沉积物中的纳古菌门(*Nanoarchaeaeota*)[17]等类群在古菌中占比超过 90%；在波罗的海(Baltic Sea)和下北半岛(Shimokita Peninsula)部分站位沉积物中的广古菌(*Euryarchaeota*)和阿斯加德古菌(*Asgardaeota*)以及日本海(Japan Sea)和秘鲁沿岸沉积物样品中 *Hadesarchaeaeota* 等古菌类群占比超过 70%[17]。

此外，在冷泉、热液、海沟等一些特殊的地质构造环境中也存在特定微生物类群富集的现象[19-24]。例如，冷泉(cold seep)广泛存在于全球陆架边缘区域沉积物中，伴随着由沉积物深部向上渗漏的甲烷或多碳烷烃，形成独特的冷泉生态系统[25-26]。与普通沉积物相比，冷泉沉积物中甲烷厌氧氧化古菌(anaerobic methanotrophic archaea, ANME)、甲基球菌目(*Methylococcales*)的有氧甲烷氧化细菌、脱硫杆菌目(*Desulfobacterales*)的硫酸盐还原细菌以及硫发菌目(*Thiotrichales*)的硫氧化细菌等微生物类群高度富集[27-29]，且这些冷泉微生物的群落组装机制很可能受环境中烷烃的渗漏强度所驱动[30]。

大多数沉积物微生物目前尚未在实验室获得其纯培养菌株。据估计，海洋沉积物中超过 80%的细胞属于未培养种(species)，其中约 20%的细胞属于未培养门(phyla)[31]。

2 沉积物微生物细胞活性

沉积物中有机碳的可利用性随深度增加而逐渐降低[32]，大部分的沉积物微生物生活在能量限制的环境中。沉积物中细胞活性难以直接定量，因此研究多利用地球化学模型等手段，使用沉积物孔隙水中微生物代谢底物(产物)的消耗(产生)速率进行进一步估算。LaRowe 等[33]利用反应-运移模型(reaction-transport model)对全球海洋沉积物中 POC 降解速率进行估算，并进一步推算出第四纪以来(2.59 百万年)的沉积物中异养微生物利用有机碳的活性在 $10^{-11}-10^{-6}$ g C/cm^3 yr 之间。Bradley 等[34]使用沉积物中POC和电子受体的消耗速率作为参数指标，对第四纪以来沉积物中微生物细胞的能量利用值进行估算，发现海洋沉积物中微生物利用的总能量仅占海水真光层光合作用固定能量的 0.08%，且在近岸表层沉积物中能量利用最高，在埋藏了 2.59 百万年的深层沉积物中能量利用最低。此外，通过整合沉积物中细胞含量数据，该研究计算得出第四纪以来沉积物中 84.0%的微生物细胞生活在低于“生命能量极限” (1.9×10^{-19} W/cell，由 LaRowe 等[35]计算)的环境中。然而，这些生活在极端能量限制条件下的微生物大多仍处于活跃代谢的状态[36-37]。因此，上述对于沉积物微生物活性的研究也引发了科学家对于维持细胞生命活动所需的最小能量以及地球上生命存在的范围等科学问题的思考和探索。总体看来，沉积物中微生物代谢速率缓慢[9,38-40]。据估计，沉积物中微生物生物质(biomass)周转时间约为数百至数千年[38,41]。

虽然沉积物中微生物代谢缓慢，但由于其体量巨大，仍活跃地介导着沉积物中与其他元素循环偶联的碳循环，并最终对地球的气候系统产生影响。据估计，第四纪以来约有 1.46×10^{20} g C 沉降至沉积物中[33]，大部分有机碳在沉积物微生物组活跃的代谢活动作用下被逐渐降解、矿化或由产甲烷古菌转化为甲烷。剩余的一小部分有机碳得以长期保存在沉积物中，在长时间尺度上(超过百万年)参与地球的碳循环，并影响地球的气候系统[42]。

3　沉积物微生物的代谢及其介导的有机碳转化过程

海洋沉积物中的有机碳主要来源于上层水体或陆地环境输入的由光合作用产生的有机物。这些有机碳在沉积物微生物组水解和发酵等多样代谢活动的共同作用下，不断被降解为挥发性脂肪酸(volatile fatty acid, VFA)、甲基化合物、氢气等简单的小分子化合物，最终伴随着电子受体的依次消耗而被矿化为二氧化碳或转化为甲烷，并在沉积物中形成地球化学分区：最上层为有氧区，其次为硝酸盐还原区、锰/铁还原区、硫酸盐还原区，底层为产甲烷区[43] (图 1)。下面将围绕沉积物中与碳循环偶

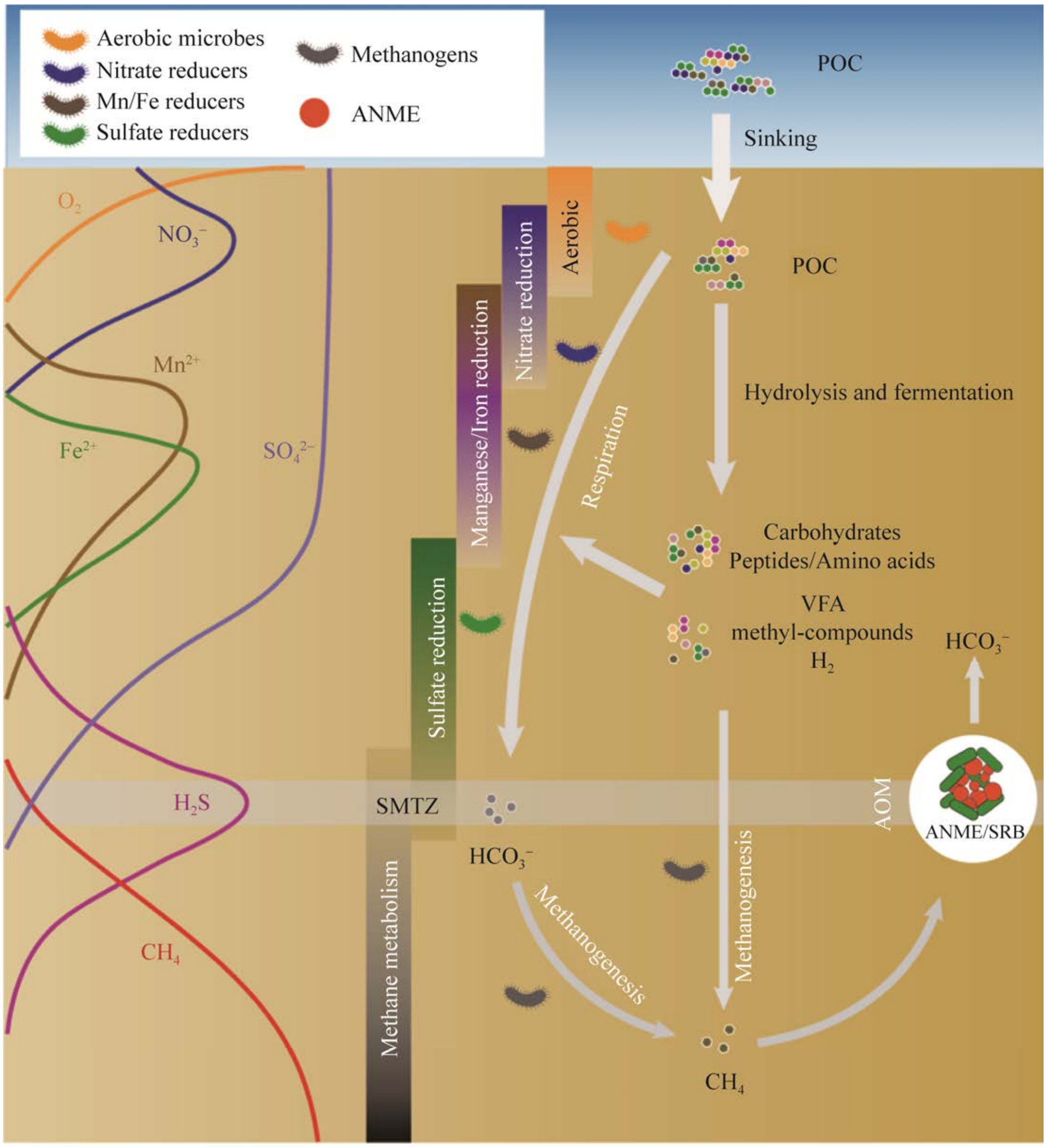

图 1　海洋沉积物微生物介导的有机碳转化过程

Figure 1　Microbial organic matter transformation in marine sediment. ANME: Aerobic methanotrophic archaea; POC: Particulate organic carbon; VFA: Volatile fatty acid; SMTZ: Sulfate-methane transition zone; AOM: Anaerobic oxidation of methane; SRB: Sulfate-reducing bacteria.

联的电子受体层级利用过程，分别介绍沉积物微生物在不同地球化学分区和环境条件下典型的代谢特征及代表类群。

3.1 水解和发酵

通常情况下，有氧沉积物中的复杂有机碳会在胞外水解酶的作用下水解产生糖和氨基酸等小分子化合物[44]。研究显示，在沉积物的不同层位中均存在多样的胞外水解酶[45-46]。此外，Orsi 等[47]发现秘鲁沿岸沉积物中 90%–99%的胞外肽酶和碳水化合物活性酶(CAZymes)由细菌编码，剩余部分可能由古菌和真菌编码。通过基因组分析和富集培养等实验发现，发酵代谢可能是沉积物微生物普遍具有的生存策略[15]。例如，沉积物中包括阿斯加德古菌[48]，深古菌[46,49]，*Thermoprofundales* (即 MBG-D 古菌)[50]，暗黑菌门[51]，*Ca.* Patescibacteria (即 Candidate Phyla Radiation, CPR 细菌)[52]等常见的沉积物微生物类群，具有利用多肽、糖、木质素等物质进行发酵代谢的潜能。然而，由于发酵过程的底物和产物消耗过程复杂多样[53]，且许多微生物可以在发酵代谢和其他代谢策略间转换，因此目前对于介导该过程的微生物类群及其代谢特征的认识仍十分有限。

3.2 有氧氧化

据估计，海洋沉积物中接近一半的 POC 被微生物有氧代谢过程所消耗[33]。沉积物中氧气渗透深度因所处海域环境条件不同而差异巨大，如在有机碳含量较丰富的近岸沉积物中，氧气渗透深度仅为几毫米至几厘米，而在一些寡营养海区，从沉积物表层至基底洋壳均有氧气渗透[54-55]。据估计，全球 9%–37%的洋底之下沉积物处于完全有氧的环境(从表层至基底洋壳)[56]。有氧沉积物中常见微生物类群主要包括变形菌门，厚壁菌门，绿弯菌门和奇古菌门等[17,57]。其中，具有氨氧化和固碳活性的奇古菌在有氧沉积物中广泛分布，被认为在维持表层沉积物生态系统功能中发挥着重要甚至主要作用[58-60]。

3.3 硝酸盐还原

在海洋沉积物孔隙水中氧气耗尽或者几乎耗尽的情况下，有机碳降解过程开始与硝酸盐还原过程偶联。与有机碳降解相关的硝酸盐还原过程包括反硝化作用(denitrification)和硝酸盐异化还原为铵(dissimilatory nitrate reduction to ammonium, DNRA)。反硝化作用中有机碳被氧化，硝酸盐依次被还原为亚硝酸盐、一氧化氮、氧化亚氮和氮气[61]。多种细菌(尤其是变形菌门)和古菌类群可以进行反硝化作用[62]。其中，上述硝酸盐还原为亚硝酸盐步骤通常由膜结合硝酸盐还原酶(respiratory nitrate reductase, NAR)或细胞周质硝酸盐还原酶(periplasmic nitrate reductase, NAP)催化[63]，分别编码上述硝酸盐还原酶亚基的 *narG* 和 *napA* 基因通常被用作检测硝酸盐还原微生物的标志基因[64]。在 DNRA 过程中有机碳被氧化，伴随着硝酸盐依次被还原为亚硝酸盐和铵[61]。在沉积物中发现包括变形菌门中的希瓦氏菌属(*Shewanella*)、弧菌属(*Vibrio*)、辫硫菌属(*Thioploca*)及脱硫杆菌门(*Desulfobacterota*)中的脱硫叶菌属(*Desulfobulbus*)、脱硫杆菌属(*Desulfobacterium*)、脱硫弧菌属(*Desulfovibrio*)等多种微生物类群可以进行 DNRA 过程[65-66]。*nrfA* 基因编码亚硝酸盐还原为铵步骤的关键酶，通常被用作 DNRA 过程的标志基因[65]。据估计，沉积物中硝酸盐还原偶联的有机碳矿化占比为 7%–11%[67-68]。

3.4 锰和铁氧化物还原

在海洋沉积物中硝酸盐耗尽或者几乎耗尽的情况下，有机碳的降解过程继续与锰和铁氧化物还原过程偶联。海洋中的锰和铁氧化物可由陆地(经由河流、风尘等途径)、海底热液、

冰川沉积物及大洋中脊的火山活动等输入[69-73]。在厌氧沉积物中，锰和铁氧化物的理化性质及参与反应过程类似，均可作为有机碳矿化的电子受体被还原为 Mn^{2+}或 Fe^{2+}[74]。包括细菌和古菌在内的多样的微生物类群可以介导与锰和铁氧化物还原偶联的有机碳矿化过程，即异化型锰/铁还原代谢[75-76]。这些微生物在有机碳矿化过程中将有机碳氧化释放的电子传递至锰和铁氧化物上使其被还原，并为自身供能。微生物如何将有机碳氧化产生的电子传递至胞外不溶的氧化物上是目前研究的热点之一[75]。不同的金属氧化物还原菌株可能具有特定的胞外电子传递机制，例如地杆菌属(*Geobacter*)模式菌株使用膜孔蛋白-细胞色素(porin-cytochrome, Pcc)途径传递电子，而希瓦氏菌属模式菌株使用金属还原(metal-reducing, Mtr)途径传递电子[77]。在海洋沉积物环境中，上述反应产生的 Mn^{2+}或 Fe^{2+}可以形成碳酸盐或含硫矿物沉淀埋藏，同时溶解态的 Mn^{2+}或 Fe^{2+}也可以通过扩散作用向沉积物上层有氧区域转移被氧化，并且再次以氧化态形式沉淀[78]。因此，沉积物中的锰和铁氧化物在最终埋藏前，会与有机碳降解相偶联发生多次的氧化还原循环[79]。以铁氧化物为例，其对沉积物中有机碳降解的贡献可取决于环境中水铁矿等较易被利用的无定形铁矿的浓度，据估计，在无定形铁矿浓度高于 15 $\mu mol/cm^3$ 的环境中，与铁氧化物还原偶联的有机碳矿化占比超过 50%[80-81]。

3.5 硫酸盐还原

海洋中含有约 1.3×10^9 Tg 硫酸盐，是地球上最大的硫库之一[82]。按照有机碳矿化反应的能级顺序，硫酸盐还原偶联的有机碳矿化过程产能次于锰和铁氧化物[43]，在该过程中有机碳被矿化为二氧化碳，同时硫酸盐被还原为硫化氢。介导上述异化型硫酸盐还原过程的微生物多样性较高，包含脱硫杆菌门、厚壁菌门、泉古菌门等多种细菌和古菌门类[83]。随着环境样本宏基因组测序数据的积累，具有上述硫酸盐还原代谢潜能的微生物类群仍在不断扩充，其中大部分门类尚未有纯培养菌株[84-85]。此外，在深部海洋沉积物中也发现厚壁菌门，绿弯菌门，暗黑菌门等特定门类硫酸盐还原菌富集的现象[86-87]。在异化型硫酸盐还原过程中，硫酸盐在硫酸腺苷转移酶(sulfate adenylyltransferase, Sat)和腺苷硫酸还原酶(adenylyl-sulfate reductase, Apr)作用下被还原为亚硫酸盐，并接着由异化亚硫酸盐还原酶(dissimilatory sulfite reductase, Dsr)还原为硫化氢[88]。其中，Dsr 催化的亚硫酸盐反应是整个过程的限速步骤[84]，编码其亚基的 *dsrAB* 基因也通常被用作硫酸盐还原代谢的标志基因[83]。据估计，全球范围内与硫酸盐还原过程偶联氧化的有机碳占沉积物有机碳通量的 12%–29%[89]。在海洋厌氧沉积物中，与硫酸盐还原偶联的有机碳氧化是有机碳矿化的主要途径[86]，尤其是在近岸沉积物中，硫酸盐还原偶联的有机碳消耗量可占矿化总量的一半[90]。

3.6 甲烷代谢

在沉积物深部其他电子受体耗尽的情况下，有机碳降解产生的小分子化合物最终被产甲烷菌利用产生甲烷[44]。产甲烷过程是地球上最早演化出的生化代谢通路之一[91]，并在早期地球气候转变过程中发挥重要作用[92]，同时，甲烷也是现代全球气候变化的重要驱动者[93]。目前已获得纯培养菌株的产甲烷菌均为严格厌氧的古菌，且属于广古菌门下的不同类群[94]。随着宏基因组测序技术的发展，在 *Ca.* Verstraetearchaeota、*Ca.* Nezhaarchaeota、奇古菌、*Ca.* Korarchaeota、*Archaeoglobi* 等多个古菌门类的基因组中均发现甲烷代谢关键基因的类似基因[95-101]。由于缺乏纯培养菌株，这些

基因组中甲烷代谢类似基因的确切功能仍待进一步研究确认[102]。根据产甲烷菌所利用产甲烷底物，可以将其主要归为3类：氢营养型(利用氢气/二氧化碳产甲烷)，乙酸营养型(利用乙酸产甲烷)及甲基营养型(利用甲醇、一甲胺、二甲胺、三甲胺等含甲基的化合物产甲烷)[103]。除了以上 3 种主要的产甲烷途径外，在已分离的产甲烷古菌及未培养古菌基因组中也发现了氢气依赖型的甲基型产甲烷代谢途径[94]。通常情况下，在海洋沉积物产甲烷区中主导的产甲烷过程为氢营养型[103-104]，而在一些含有硫酸盐、铁矿等电子受体的产甲烷沉积物中，主导的产甲烷代谢途径可以转变为甲基营养型[105-108]。甲基辅酶 M 还原酶(methyl-coenzyme M reductase, MCR)是以上古菌产甲烷过程中的关键酶[109]，编码其亚基的 *mcrA* 基因通常被用作甲烷代谢微生物的标志基因。

上述产甲烷区沉积物中产生的甲烷会向上层扩散，到达 SMTZ，并在该区域被硫酸盐还原偶联的甲烷厌氧氧化过程(sulfate dependent anaerobic oxidation of methane, S-AOM)消耗。S-AOM 过程通常由硫酸盐还原细菌(sulfate-reducing bacteria, SRB)和 ANME 古菌类群合作完成，两者可以形成紧密结合的细胞团[23,110]，研究推测 ANME 通过潜在的胞外电子传递机制将 AOM 过程中产生的电子传递给硫酸盐还原细菌[111-112]。除了硫酸盐外，AOM 过程也可以和硝酸盐、金属氧化物等电子受体还原过程相偶联[113]。介导 AOM 过程的 ANME 类群多样性较高，且同样属于广古菌门下的不同的分类单位，主要包含在 *Ca*. Methanophagales (ANME-1)和甲烷八叠球菌目(*Methanosarcinale*，包括 ANME-2a/b、ANME-2c、ANME-2d、ANME-3 等主要类群)等目中[114]。其中，ANME-1 和 ANME-2a/b，ANME-2c 等类群在 SMTZ 和冷泉区沉积物中均比较常见[23,30]；ANME-2d 类群多报道于淡水沉积物中[115]；ANME-3 类群主要报道于泥火山环境中[116]。不同的 ANME 类群也占据着不同的生态位，例如，ANME-1 类群常常在沉积物 SMTZ 以下产甲烷区域富集，暗示其具有潜在的产甲烷活性[117-119]。目前，所有的 ANME 类群均未获得纯培养菌株。基因组测序等一系列研究发现，ANME 基因组包含产甲烷古菌产甲烷代谢途径关键酶[119-120]，推测其使用反向的产甲烷代谢途径氧化甲烷[121]。从全球来看，甲烷 CH_4 年排放量约为 500−600 Tg，其中 70%来自于微生物产甲烷过程[103]。在海洋环境中，超过 90%的生物产生的甲烷被 AOM 过程消耗[23]。

4 总结与展望

沉积物微生物组是海洋沉积物中生物地球化学循环过程的重要驱动者。如图 1 所示，沉积物中大分子有机碳首先在水解和发酵过程作用下降解为小分子化合物并最终矿化为二氧化碳或转变为甲烷。根据反应过程中产能大小，有机碳矿化过程会在不同类群微生物代谢活动作用下依次与不同电子受体还原过程相偶联，并在电子受体耗尽的深部沉积物中由产甲烷古菌代谢产生甲烷(表 1)。

一般来讲，沉积物中有机碳的可利用性随深度增加而逐渐降低[32]。然而有机碳可利用性也因所处环境不同而具有差异性。例如，Chen 等[122]通过对沉积物样品的有机碳组分和其消耗速率进行分析，发现在能量匮乏的深海沉积物中，惰性的类腐殖质溶解有机碳可以被消耗利用，且该过程可能与脱卤拟球菌属(*Dehalococcoides*)、厌氧绳菌纲(*Anaerolineae*)、α-变形菌纲(*Alphaproteobacteria*)等微生物类群紧密相关。此外，由于沉积物环境复杂多样，

表 1　海洋沉积物微生物介导有机碳转化的代谢过程和主要功能类群

Table 1　Metabolic processes and major functional taxa involved in organic matter transformation in marine sediment

Metabolism	Functional taxa
Hydrolysis and fermentation	*Asgardaeota*, *Bathyarchaeia*, *Thermoprofundales*, *Atribacteria*, *Ca.* Patescibacteria[47-52], etc.
Aerobic respiration	*Proteobacteria*, *Firmicutes*, *Chloroflexi*, *Thaumarchaeota*[17,57], etc.
Nitrate reduction	*Proteobacteria*, *Desulfobacterota*[62,65-66], etc.
Manganese/Iron reduction	*Proteobacteria*, *Halobacterota*, *Desulfobacterota*[75-76], etc.
Sulfate reduction	*Desulfobacterota*, *Firmicutes*, *Crenarchaeota*[83], etc.
Methane metabolism	*Euryarchaeota*, *Ca.* Verstraetearchaeota, *Ca.* Nezhaarchaeota, *Thaumarchaeota*, *Ca.* Korarchaeota, *Archaeoglobi* [23,95-102], etc.

并不是所有的沉积物中都会表现出上述的有机碳和电子受体分区消耗的现象，在一些沉积物也发现了先前忽视的地球化学分区或隐匿的元素循环。例如，Zhao 等[123]发现在传统经典分区层位外，沉积物中可能广泛存在硝酸盐-铵转换区(nitrate-ammonium transition zone, NATZ)，是厌氧氨氧化活跃代谢的场所；沉积物表层含硫酸盐区域也存在甲基营养型产甲烷古菌和 ANME 共同介导的“隐匿”的甲烷循环[106]；沉积物的产甲烷区存在铁矿驱动的“隐匿”的硫循环[124-125]，并造成产甲烷古菌的类群的转变[105]等。因此，此后需要通过高分辨率采样、更精细的化合物组分分析，综合沉积物地球化学、微生物生态学及实验室模拟培养等手段，对沉积物微生物组在不同环境下介导的元素循环过程及特定活性类群的代谢方式进行评估和研究。

受益于组学技术的发展，我们对沉积物微生物组总体类群分布和多样性组成有了较为宏观的认知。然而由于大部分沉积物微生物缺乏纯培养菌株，我们对其代谢活性和参与的有机碳降解过程认识十分有限。例如，Yu 等[49,126]通过对沉积物进行长期富集培养，发现深古菌、脱卤球菌纲(*Dehalococcoidia*)、*Ca.* Fermentibacterota、纤维杆菌科(*Fibrobacterales*)、拟杆菌目(*Bacteroidales*)、钩端螺旋体属(*Leptospira*)、梭菌目(*Clostridiales*)等微生物类群可以利用木质素、纤维素、酪蛋白和油酸等大分子难降解有机碳进行生长，而其介导的详细降解过程仍需借助菌株分离等手段进一步证实。因此之后仍需发展新型或高通量分离、培养技术对沉积物未培养微生物功能进行验证[127]。此外，微生物的代谢活动也受如温度[13]、压力[128]等多种原位环境因素共同影响，而基于实验室纯菌对其代谢速率、活性等研究与原位环境下估测值有巨大差异[34]。因此后续需要结合原位实验检测、原位环境条件模拟培养、同位素示踪及地球化学模型等手段对沉积物微生物组活性和其介导的碳循环关联的元素循环过程进行综合评估[34,39,129-130]。

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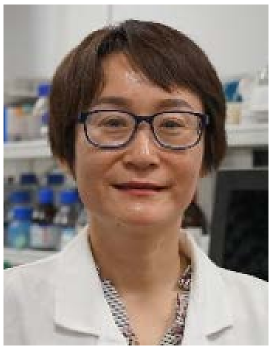

王风平，上海交通大学海洋学院特聘教授、深部生命国际研究中心(ICDLI)执行主任。国家基金委杰出青年科学基金获得者，中国微生物生态学会“周集中突出贡献”奖获得者。长期专注于海洋深部生物圈研究，曾 3 次作为载人深潜科学家深潜海底科考，在国际上引领了海洋深部古菌生态/地球化学功能的研究。发现并命名了一个目前被国际学术界广泛接受的新古菌门——“深古菌”门(*Bathyarchaeota*)，发现其是海洋中新的未知“木质素降解者”，为深入理解海洋碳循环机制作出了贡献。目前担任国际微生物生态学会(ISME)大使(Ambassador)和国际董事(International Board)，欧洲海洋科学钻探(ECORD)科学装置委员会委员，综合大洋钻探计划(IODP)中国科学委员会委员，中国古生物学会地球生物学分会副理事长，中国地质微生物专业委员会副主任，多个国际学术期刊 *Frontiers in Marine Sciences*、*Applied and Environmental Microbiology* 等副主编或编委，为推动中国地质生物学学科发展和提升学科国际影响力贡献了力量。