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专论与综述

石油污染生态系统中细菌群落结构及其代谢机制研究进展

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摘　要：石油化工产品的不合理处置与泄漏导致石油及其衍生物大量释放到环境中，由此造成的环境污染问题日益严重，石油污染已成为全球性公害之一。微生物修复技术凭借其成本低、环境友好等优势，广泛应用于石油污染的治理。大量研究表明功能微生物群落在石油污染生态系统的修复体系中发挥了重要的作用。其中，细菌是最主要、最活跃的石油降解微生物。然而，在原位/异位生物修复过程中，存在功能菌群在污染体系中难维持、易失调及石油烃降解途径不明晰等问题。因此，本文总结了石油污染自然生态系统和微宇宙实验体系中的细菌群落结构、石油烃代谢机制及相关功能基因，并对微生物法处理石油污染的未来研究方向提出展望，为石油污染场地生物修复方案的制定提供理论参考。

关键词：石油污染；细菌群落；降解机制；功能基因；微宇宙

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Bacterial community structure and metabolic mechanism in petroleum-contaminated ecosystem: a review

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Abstract: Unreasonable treatment and leakage of petrochemical products lead to massive release of petroleum hydrocarbons into the environment. Petroleum pollution has been a global concern. Being cost-efficient and environmentally friendly, bioremediation has been widely used for the removal and degradation of products in petroleum industry. Accumulation evidence has shown that functional microbial communities play an important role in the bioremediation of petroleum-contaminated environment, particularly bacteria. However, the *ex-situ* and *in-situ* bioremediation faces the following challenges: ease of functional microflora imbalance and unclear degradation pathway of petroleum hydrocarbons. Thus, this review summarizes the structures, metabolic pathways of petroleum hydrocarbons, and functional genes of bacterial communities in different types of petroleum-contaminated environments and microcosmic bioremediation experimental systems. Moreover, the trends of research on microbial treatment of petroleum pollution are summarized. Thereby, this study is expected to serve as a reference for the formulation and implementation of microbial remediation schemes for petroleum-contaminated sites.

Keywords: petroleum pollution; bacterial community; degradation mechanism; functional genes; microcosm

石油是多组分复杂混合物，包含脂肪烃、单环芳烃、多环芳烃、胶质和沥青质等物质。地下储罐、轮船、油井及废弃炼油厂产生的泄漏导致石油及其衍生物大量排放到环境中，造成表层土壤、地下水及海洋污染。石油烃具有毒性且难以降解，对生物和人类健康存在潜在危害，所以石油污染已成为当前亟须解决的环境问题[1]。淋洗、热力修复、化学氧化和生物修复技术已广泛应用于石油污染的处理。其中，微生物修复技术凭借其成本低及无二次污染的优势，成为众多石油污染场地修复治理的关键技术[2]。然而，石油烃生物降解途径尚不清晰，且单一微生物无法有效降解复杂的石油组分。同时，在原位/异位生物修复过程中，微生物种群间互作关系尚不明确，功能菌群难以在复杂的石油污染体系中维持。

基于自然石油污染体系和微宇宙修复体系生态结构解析，将石油降解微生物资源有效整合，对于功能菌群在污染体系中适应度的提升及不同条件下石油烃生物处理效果的提升至关重要。研究表明，细菌是最主要、最活跃的石油污染物降解微生物[3]。在好氧条件下，细菌利用单加氧酶或双加氧酶对石油烃进行选择性催化转化[4]。与好氧降解相比，石油烃厌氧降解途径研究不足，主要集中于代谢的第一步途径[5]。此外，细菌也可利用趋化作用、寄生于

菌丝、生物乳化剂和表面活性剂等降解石油烃[6-7]。深入挖掘石油烃降解途径和功能基因，有助于微生物定向修复石油污染潜力的开发。因此，本文总结自然/微宇宙模拟石油污染生态系统中的细菌群落结构，阐述石油烃的多种细菌代谢机制，以期为石油污染场地微生物修复方案的制定和实施提供理论参考。

1 石油污染生态系统中的细菌群落结构

为了解污染环境中细菌群落特征和它们对污染物的代谢情况，研究者们采用分子生物学和组学技术对炼油厂和化工厂周边土壤、红树林、海洋沉积物、海水等不同受石油污染环境的细菌群落结构进行了考察，并对参与石油原位和异位生物降解的细菌群落及其代谢特征展开了探究。

1.1 石油污染自然生态系统中的细菌群落结构

由于土壤中的绝大多数微生物无法进行分离培养，传统的纯培养技术难以反映不可培养微生物在污染物生物降解中发挥的作用，所以研究者们提出使用分子生物学技术更加全面地分析污染环境中微生物群落的结构和代谢功能。随着高通量测序技术的快速发展和普及，宏基因组、宏转录组和扩增子测序等技术被广泛应用于监测石油污染环境中微生物群落结构的动态变化研究。基于各种组学技术解析的各类石油污染环境的细菌群落特征如表 1 所示。

在炼油厂周边的农田和工业场地的污染土壤中存在多种优势细菌属，包括 *Megamonas*、*Paenibacillus*、*Bacillus*、*Aquicella*、*Alicyclobacillus*、*Anaeromyxobacter*、*Bdellovibrio*、*Nitrospiria*、*Oscillospiria*、*Mycobacterium*、*Pseudomonas*、*Burkholderia*、*Chromobacterium*、*Xanthomonas* 和 *Acinetobacter*[8-9]。中国北部不同油田土壤中的优势细菌属包括 *Microvirga*、*Mycobacterium*、*Defluviicoccus*、*Halomonas*、*Alcanivora* 和 *Marinobacter*[11]。在被多环芳烃(polycyclic aromatic hydrocarbons, PAHs)污染的农田中，Zhou 等[9]发现 *Mycobacterium* 和 *Pseudomonas* 是石油污染土壤中的优势细菌属。此外，Roy 等[22]考察了来自 3 个炼油厂的污泥样本，发现存在可能降解石油的优势菌属 *Mycobacterium*、*Pseudomonas*、*Longilinea* 和 *Geobacter*。结合表 1 中已报道的数据，*Mycobacterium* 和 *Pseudomonas* 最可能成为石油污染环境中细菌群落的优势菌属。

沿海地区常受到石油污染的影响，许多研究考察了海洋沉积物中的细菌群落结构特征。在沉积物中检测到的芳香烃浓度范围为 0.157−99.400 mg/kg，远高于海水中的浓度[25-33]。对世界各地沿海污染区域沉积物中细菌群落的调查发现，*Desulfbacteraceae*、*Desulobbaceae*、*Desulfromonadaceae*、*Gebacteraceae* 和 *Syntrobacteraceae* 等细菌科，以及 *Alcanivorax*、*Alteromonas*、*Marinbacter*、*Winogradsky*、*Zeaxanthinibacter*、*Thalassospira* 和 *Acinetbacter* 等细菌属的相对丰度较高[31]。Cabral 等[21]在巴西沿海红树林的高浓度石油污染沉积物中观察到了 *Desulfococcus* 和 *Desulfatibacillum*。此外，在受污染的红树林土壤中还发现了一些与解毒途径相关的菌属，包括 *Aromatoleum*、*Desulfitobacterium*、*Vibrio*、*Rhodopseudomonas*、*Bradyrhizobium*、*Ruegeria*、*Mycobacterium*、*Burkholderia*、*Maritimibacter*、*Frankia*、*Pseudomonas*、*Novosphingobium* 和 *Roseobacter*[21]。海洋沉积物中细菌群落的结构分析表明，*Proteobacteria* 和 *Firmicutes* 门的相对丰度较高[30-31]。*Proteobacteria*、*Cyanobacteria* 和 *Actinobacteria* 是污染海水中的优势细菌门[25]。

表 1　石油污染自然生态系统的细菌群落特征

Table 1　Characteristics of bacterial community in petroleum-contaminated ecosystem

样品类型 Sample type	污染物种类 Pollutant type	优势细菌 Dominant bacterial species	参考文献 References
土壤 Soil	Aliphatic hydrocarbons	*Megamonas*, *Paenibacillus*, *Bacillus*, *Alicyclobacillus*, *Oscillospiria*, *Aquicella*, *Anaeromyxobacter*	[8]
	Aromatic	*Mycobacterium*, *Pseudomonas*	[9]
	Aromatic	*Achromobacter*, *Acinetobacter*, *Halomonas*, *Marinobacter*, *Roseovarius*	[10]
	Petroleum hydrocarbon	*Microvirga*, *Mycobacterium*, *Defluviicoccus*, *Halomonas*, *Alcanivora*, *Marinobacter*	[11]
	Petroleum hydrocarbon	*Rhodanobacter*, *Sphingomonas*	[12]
	Petroleum hydrocarbon	*Bacillus*, *Virgibacillus*, *Pseudomonas*	[13]
	Petroleum hydrocarbon	*Algiphilus*, *Pseudomonas*	[14]
	Petroleum hydrocarbon	*Halorhodospiraceae*, *Lactobacilliceae*	[15]
	Petroleum hydrocarbon	*Proteobacteria*, *Bacteroidetes*, *Actinobacteria*, *Acidobacteria*, *Gemmatimonadetes*, *Nitrospirae*, *Firmicutes*, *Verrucomicrobia*, *Elusimicrobia*	[16]
	Petroleum hydrocarbon	*Proteobacteria*, *Alphaprotobacteria*, *Chloroflexi*, *Chlorobi*, *Acidobacteria*	[17]
	Petroleum hydrocarbon	Actinobacteria, Proteobacteria, Saccaribacteria	[18]
	Petroleum hydrocarbon	*Alcanivorax*, *Rhodanobacter ginsengisoli*, *Acidobacterium capsulatum*, *Acidocella*	[19]
	Petroleum hydrocarbon	*Streptococcus*, *Bacillus*, *Sphingomonas*, *Arthrobacter*, *Rhodobacteraceae*, *Porticoccus*	[20]
红树林 Mangrove	Aromatic	*Aromatoleum*, *Desulfococcus*, *Desulfatibacillum*, *Desulfitobacterium*, *Vibrio*	[21]
炼油残渣 Refinery residue	Aliphatic hydrocarbons	*Mycobacterium*, *Pseudomonas*, *Geobacter*, *Longilinea*	[22]
	Petroleum hydrocarbon	*Bacillus*, *Geobacillus*	[23]
	Petroleum hydrocarbon	*Methylobacillus*, *Methylococcus*, *Comamonas*, *Hydrogenophaga*, *Rhodobacter*, *Flavobacterium*	[24]
海水 Sea water	Aromatic	*Proteobacteria*, *Cyanobacteria*, *Actinobacteria*	[25]
	Aromatic	*Oceanospirillaceae*, *Pseudomonas*, *Colwellia*, *Cycloclasticus*, *Pseudoalteromonas*	[26]
	Aromatic	*Proteobacteria*	[27]
	Aliphatic hydrocarbons	*Oceanobacter*, *Oleispira*	[28]
	Petroleum hydrocarbon	*Alcanivorax*, *Cycloclasticus*, *Oleispira*, *Oleiphilus*, *Thalassolituus*	[29]
海洋沉积物 Marine sediment	Aromatic	*Proteobacteria*, *Chloroflexi*, *Verrucomicrobia*, *Planctomycetes*, *Nitrospirae*, *Ignavibacteriae*, *Gemmatimonadetes*, *Latescibacteria*, *Firmicutes*, *Parcubacteria*	[30]
	Aromatic	*Proteobacteria*, *Bacteroidetes*, *Firmicutes*, *Acidobacteria*	[31]
	Aromatic	*Acinetobacter*	[32]
	Aromatic	*Alcanivorax*, *Alteromonas*, *Marinobacter*, *Winogradskyella*, *Zeaxanthinibacter*	[33]

2010年发生的墨西哥湾原油泄漏事件被称为历史上最大的环境灾难之一，研究者们对受污染的海洋区域展开了长期的调查评估。结果显示，石油泄漏后海洋污油中微生物群落的优势菌属为 *Cycloclasticus*、*Methylobacter*、*Methylococcus*、*Oceanospirillales*、*Pseudomonas* 和 *Colwellia*[26]；随着污油被不断降解，群落的优势菌属转变为 *Colwellia*、*Cycloclasticus*、*Pseudoalteromonas* 和 *Thalassomona*[26]；在事故发生一年后，残余污油中的优势菌属包括 *Stappia*、*Erythrobacter*、*Rhodovulum* 和 *Thalassospira*，它们可能参与了石油的降解[34]。

细菌的群落组成在不同的污染环境(土壤、海洋沉积物、海水和红树林等)间存在差异。然而，在上述污染环境中同时发现了一些细菌类群，它们是石油污染环境的优势菌群，并且具有降解石油的功能。例如，在石油污染的土壤、炼油污泥和红树林沉积物中发现了大量的 *Mycobacterium*、*Pseudomonas* 和 *Bacillus*；石油污染海水中的优势菌属主要为 *Pseudomonas*、*Oleispira* 和 *Alcanivorax*。此外，*Colwelllia* 和 *Cycloclasticus* 仅在墨西哥湾漏油事故中被发现。这些在污染环境中与石油降解功能密切相关的优势菌，是未来生物修复研究中筛选分离的目标功能菌株。

1.2 微宇宙生物修复系统中的细菌群落结构

微宇宙系统是一种包含自然生态系统中主要组分和生态学过程的模拟生态系统，能够提供自然生态系统的群落结构和功能。在已报道的自然衰减、生物强化和生物刺激等石油污染的微宇宙生物修复研究中，通常以脂肪烃或多环芳烃作为污染物进行试验。表 2 总结了部分已完成的微宇宙生物修复试验所使用的样品类型、污染物种类、修复方式及优势细菌。

大多数微宇宙生物强化实验中所添加的细菌属于 *Proteobacteria* 和 *Firmicutes*。*Proteobacteria* 和 *Firmicutes* 的代表性细菌(如 *Pseudomonas* sp.和 *Bacillus* sp.)已被应用于研究多环芳烃的胞外降解[51-52]。在多环芳烃降解的微宇宙实验中，多种细菌作为外源生物被投加入试验系统中，具体菌属包括 *Bacillus*、*Pseudomnas*、*Stenotrophomonas*、*Sphingomonas*、*Methylobacterium*、*Rhodococcus*、*Bradyrhizobium*、*Aquamicrobium* 和 *Chryseobacterium*[39-41]。Muthukumar 等[36]研究了 *Pseudomonas aeruginosa* PP3 和 *Pseudomonas aeruginosa* PP4 的石油污染土壤修复效果，结果发现与未接种相比降解率均提高了 50%。Liu 等[35]在含有多种脂肪烃的微宇宙土壤中接种 *Pseudomonas aeruginosa* 和 *Bacillus licheniformis* 进行 60 d 的生物强化修复，并探究了它们与本土微生物群落的竞争关系，结果发现，微宇宙系统运行结束后，二者在菌群中相对丰度分别为 0.78%和 4.10%，即 *Bacillus licheniformis* 在降解方面发挥的作用更大，而 *Pseudomonas aeruginosa* 在与本土微生物群落竞争中处于劣势。利用红树林土壤进行的微宇宙研究发现，在石油污染侵入后，菌群中的优势菌属为 *Marinobacterium*、*Vibrio*、*Marinobacter*、*Cycloclasticus*、*Roseobacter* 和 *Ferrimonas*[42-43]。Liu 等[44]在地中海深海污染的微宇宙试验中发现，在石油污染后形成了以 *Oceanospirillaceae*、*Alteromonodaceae* 和 *Alcanivoraceae* 为优势菌群的微生物群落，并推测它们可能是具有石油降解功能的细菌。*Proteobacteria* 细菌已被广泛应用于石油污染修复的水体微宇宙试验中，属于该菌门的物种可能在生物修复中具有较高的应用潜力[44-45]。Chuah 等[46]在石油污染的海水微宇宙中投加 *Pseudomonas* 的石油降解菌，该微宇宙系统运行后的石油烃降解率达到 84.1%。在受污染的海岸带样品中，dos Santos 等[42]和

表 2 生物修复石油污染的微宇宙实验

Table 2 Microcosm experiment on bioremediation of petroleum pollution

样品种类 Sample type	修复方法 Treatment	污染物种类 Pollutant type	优势细菌 Dominant bacteria species	参考文献 References
土壤微宇宙 Microcosm soil	Bioaugmentation	Petroleum hydrocarbon	*Pseudomonas aeruginosa*, *Bacillus licheniformis*	[35]
	Bioaugmentation, biostimulation	Petroleum hydrocarbon	*Acinetobacter*	[36]
	Bioaugmentation	Petroleum hydrocarbon	*Pseudomonas aeruginosa*	[37]
	Bioaugmentation, biostimulation	Petroleum hydrocarbon	*Alcanivorax*	[38]
	Bioaugmentation	Aromatic	*Bacillus firmus*	[39]
	Bioaugmentation, biostimulation	Aromatic	*Pseudomnas aeruginosa*, *Stenotrophomonas maltophilia*	[40]
	Bioaugmentation, biostimulation	Aromatic	*Sphingomonas melonis*, *Methylobacterium radiotolerans*, *Rhodococcus sovatensis*, *Bradyrhizobium elkanii*, *Aquamicrobium lusatiense*, *Chryseobacterium culicis*	[41]
沉积物微宇宙 Microcosm sediment	Natural attenuation	Aliphatic hydrocarbons	*Marinbacterium*, *Marinobacter*, *Cycloclasticus*	[42]
	Biostimulation	Aromatic	*Vibrio*, *Roseobacter*, *Ferrimonas*	[43]
水体微宇宙 Microcosm water	Biostimulation	Aliphatic hydrocarbons	*Proteobacteria*	[44]
	Biostimulation	Aliphatic hydrocarbons	*Proteobacteria*	[45]
	Biostimulation	Petroleum hydrocarbon	*Pseudomonas*, *Erythrobacter*	[46]
	Bioaugmentation, biostimulation	Petroleum hydrocarbon	*Acinetobacter*, *Bacillus*	[47]
摇瓶培养 Shake-flask culture	Bioaugmentation	Petroleum hydrocarbon	*Enterobacter*	[48]
	Bioaugmentation	Petroleum hydrocarbon	*Pseudomonas aeruginosa*	[49]
	Bioaugmentation	Petroleum hydrocarbon	*Pseudomonas*, *Acinetobacter*, *Enterobacter*	[50]
	Bioaugmentation, biostimulation	Aromatic	*Pseudomonas lini*, *Pseudarthrobacter polychromogenes*	[51]
	Bioaugmentation, biostimulation	Aromatic	*Bacillus subtilis*	[52]

Zhou 等[43]使用第二代测序技术检测出了 *Marinobacter*、*Cycloclasticus*、*Vibrio* 和 *Roseobacter* 的优势细菌。

上述这些细菌可能稳定存在于石油污染环境中，因此可以把它们认定为生物修复试验中需要优先考虑的功能细菌。现有的生物强化微宇宙试验中，*Pseudomonas* 是最常见的外源投加菌属，未来应加强在石油污染环境中具有高丰度的其他菌属细菌的分离和降解特性研究，并将这些细菌作为生物强化投加的外源菌群，或将其作为生物刺激进行调控的本土菌群，从而增强对石油污染物的降解效果。

2 石油及其衍生物的代谢降解机理

细菌可以通过多种酶催化的复杂代谢反应完成对石油及其衍生物的降解，这些酶包括脱氢酶、细胞色素 P450 酶、过氧化物酶、漆酶

和加氧酶等[53]。微生物可以在好氧/厌氧条件下通过不同途径降解石油组分，其涉及的酶和功能基因不尽相同。表 3 总结了利用分子生物学和组学技术解析的石油组分降解功能基因。此外，细菌在好氧/厌氧条件下降解石油烃的途径汇总结果如图 1 所示。

2.1 好氧降解涉及的酶和功能基因

在烷烃的好氧降解过程中，细菌首先产生烷烃羟化酶或单加氧酶。单加氧酶根据其电子传递系统和分子结构分为依赖性红素氧还蛋白还原酶和细胞色素 P450 单加氧酶。依赖性红素氧还蛋白还原酶是由烷烃羟化酶、红素氧化蛋白酶和红素氧化蛋白还原酶组成的多酶复合体。此外，还有 2 种单加氧酶也被报道参与了长链烷烃的降解，分别是长链烷烃降解单加氧酶和黄素单加氧酶[54,70]。烷烃的好氧降解途径可以分为 2 条：途径I为末端氧化途径，其又分为单末端氧化和双末端氧化途径，在单末端氧化途径中，首先通过氧化末端甲基从而生成伯醇，生成的伯醇然后被氧化成醛和脂肪酸，之后再发生 β-氧化，最终进入三羧酸循环[83]。然而在某些情况下，产生的脂肪酸可能在末端甲基的 ω 位发生 ω-羟基化，生成 ω-羟基脂肪酸，再转化为二羧酸，最后进入 β-氧化途径，这就是双末端氧化途径。途径II为次末端氧化途径，烷烃在该途径的降解中首先产生仲醇，然后再氧化成相应的酮和酯，最后被酯酶水解，产生乙酸和伯醇[83]。

烷烃降解基因主要包括 *alkB* 和 *almA*。*alkB* 基因已经作为生物标志物被用于分析环境样本中微生物的石油降解能力[27]。Nie 等[84]在 *Mycobacterium* 、 *Gordonia* 、 *Rhodococcus* 、 *Burkholderia* 、 *Rhodobacter* 、 *Acinetobacter* 和 *Marinobacter* 的基因组序列中均发现了 *alkB* 基因的存在，同时，上述菌属都已被报道为不同石油污染环境中的优势菌属或在生物修复试验中所投加的强化菌属。*almA* 是一种编码黄素结合单加氧酶的基因，能够参与长链烷烃的代谢，并且存在于 *Acinetobacter*、*Alcanivorax* 和 *Pseudomonas* 等石油污染环境中常见的细菌[54-55,70]。

细胞色素 P450 酶是一种常见的芳香烃降解功能单加氧酶。P450 酶主导的反应类型包括羟基化、脱烷基化、环氧化、脱氨、脱硫、脱卤和过氧化等。Maier 等[85]发现在石油污染环境中大量存在的 *Acinetobacter* 可以利用细胞色素 P450 酶降解 C5−C10 的石油烃化合物。此外，在能够降解石油及其衍生物的 *Mycobacterium*、*Rhodococcus* 、 *Novosphingobium* 、 *Dietzia* 和 *Alcanivorax* 等细菌属中也检测到了该酶[84,86]。

双加氧酶在芳香烃的好氧代谢中起着至关重要的作用。芳环裂解双加氧酶能够催化芳香环裂解[87]，根据裂解方式的不同，其又可分为外二醇双加氧酶(通过邻位裂解催化)和雌二醇双加氧酶(通过间位裂解催化)[88]。芳环双加氧酶则可以在芳香族底物上引入 32 个羟基，形成顺式二醇[63]。环羟基化双加氧酶是一种可以催化芳香环反应的关键酶，其包括黄素蛋白单加氧酶、Rieske 型非血红素铁加氧酶和可溶性双铁多组分加氧酶。多环芳烃环羟基化双加氧酶(PAH-ring hydroxylating dioxygenase, PAH-RHDα)基因在芳香族化合物(如苯酚、萘、菲、芘和苯并芘等)的生物降解中起着关键作用，是稠环芳烃代谢的重要功能基因[89]。Liang 等[90]利用宏基因组学探究了红树林沉积物和油田土壤中细菌 *PAH-RHDα* 基因的分布规律，结果发现 *Burkholderia* 、 *Pseudomonas* 、 *Mycobacterium* 、 *Ralstonia* 、 *Sciscionella* 、 *Polymorphum* 和 *Rhodococcus* 等油田区的优势菌中均含有 *PAH-RHDα*。研究表明，在多种分子生物学技术的检测下，多环芳烃污染环境中的多种细菌均

表 3 与石油组分生物降解相关的功能基因

Table 3 Functional genes related to biodegradation of petroleum components

样品类型 Sample type	降解条件 Degradation condition	污染物 Contaminant	技术手段 Techniques	功能基因 Functional genes	参考文献 References
土壤 Soil	Aerobic	Crude oil	RT-qPCR	*alkB1*, *alkB2*, *almA1*, *almA2*	[54-55]
	Aerobic	Phenanthrene, benzo[a]pyrene	qPCR, extender sequencing	*PAH-RHDa*	[56]
	Aerobic	Crude oil	Macrogenome, phylogenetic analyses	*EDO*	[57]
	Aerobic	Crude oil	Genomic fingerprints, phylogenetic analyses	*catA*	[58]
	Anaerobic	Toluene	qPCR	*bssA*, *bamA*	[59]
	Anaerobic	Benzene	Metatranscriptomic	*bam*	[60]
沉积物 Sediment	Aerobic	Crude oil	Macrogenome, metatranscriptomic	*catA*	[61]
	Anaerobic	Petroleum hydrocarbon	Cloning, phylogenetic analyses	*assA*	[62]
	Anaerobic	Naphthalene, 2-methylnaphthalene	Phylogenetic analyses	*bnsABCDEFGH*	[63]
	Anaerobic	Petroleum hydrocarbon	Cloning, extender sequencing	*masD*, *assA*	[64]
	Anaerobic	Alkanes	Cloning, extender sequencing	*masD*, *assA*	[65]
	Anaerobic	Aliphatic hydrocarbon	Metatranscriptomic, phylogenetic analyses	*mcrA*	[66]
炼油残渣 Refinery residue	Anaerobic	Petroleum hydrocarbon	Macrogenome, RT-qPCR	*mcrA*, *dsrB*	[22]
海水 Sea water	Aerobic	Crude oil	GeoChip	*alkB*, *nagG*, *pchCF*	[67]
	Aerobic	Polycyclic aromatic hydrocarbons	Metatranscriptomic, extender sequencing	*catA*	[68]
	Aerobic	Fluorene, phenanthrene, pyrene	DGGE, extender sequencing, cloning	*PAH-RHDa*	[69]
摇瓶培养 Shake-flask culture	Aerobic	Long chain alkanes	Extender sequencing, RT-qPCR	*almA*, *almR*	[70]
	Aerobic	n-hexadecane, phenanthrene	cloning, RT-qPCR	*CYP52*, *CYP53*	[71]
	Aerobic	Polycyclic aromatic hydrocarbons	qPCR, metagenomic	*pahE*, *pahAc*	[72]
	Aerobic	Phenol, benzoic acid	Cloning, RT-PCR	*catRBCA*	[73]
	Aerobic	Catechol, phenol, benzoic acid	Metagenomic	*catA*	[74]
	Anaerobic	Crude oil	T-RFLP, extender sequencing	*bssA*, *nmsA*	[75]
	Anaerobic	Alkanes	Extender sequencing	*assA*	[76]
	Anaerobic	Toluene	Cloning	*bss*, *bbs*	[77]
	Anaerobic	Aromatic hydrocarbons	Alignment of the protein sequences	*badDEFGAB*	[78]
	Anaerobic	Aromatic hydrocarbons	Extender sequencing	*bamBCDEFGHI*	[79]
	Anaerobic	Aromatic hydrocarbons	Heterologous gene expression	*bcrABCD*	[80]
	Anaerobic	Crude oil	Cloning, qPCR	*assA*	[81]
油藏 Oil reservoirs	Anaerobic	Crude oil	qPCR, macrogenome	*dsrAB*	[82]

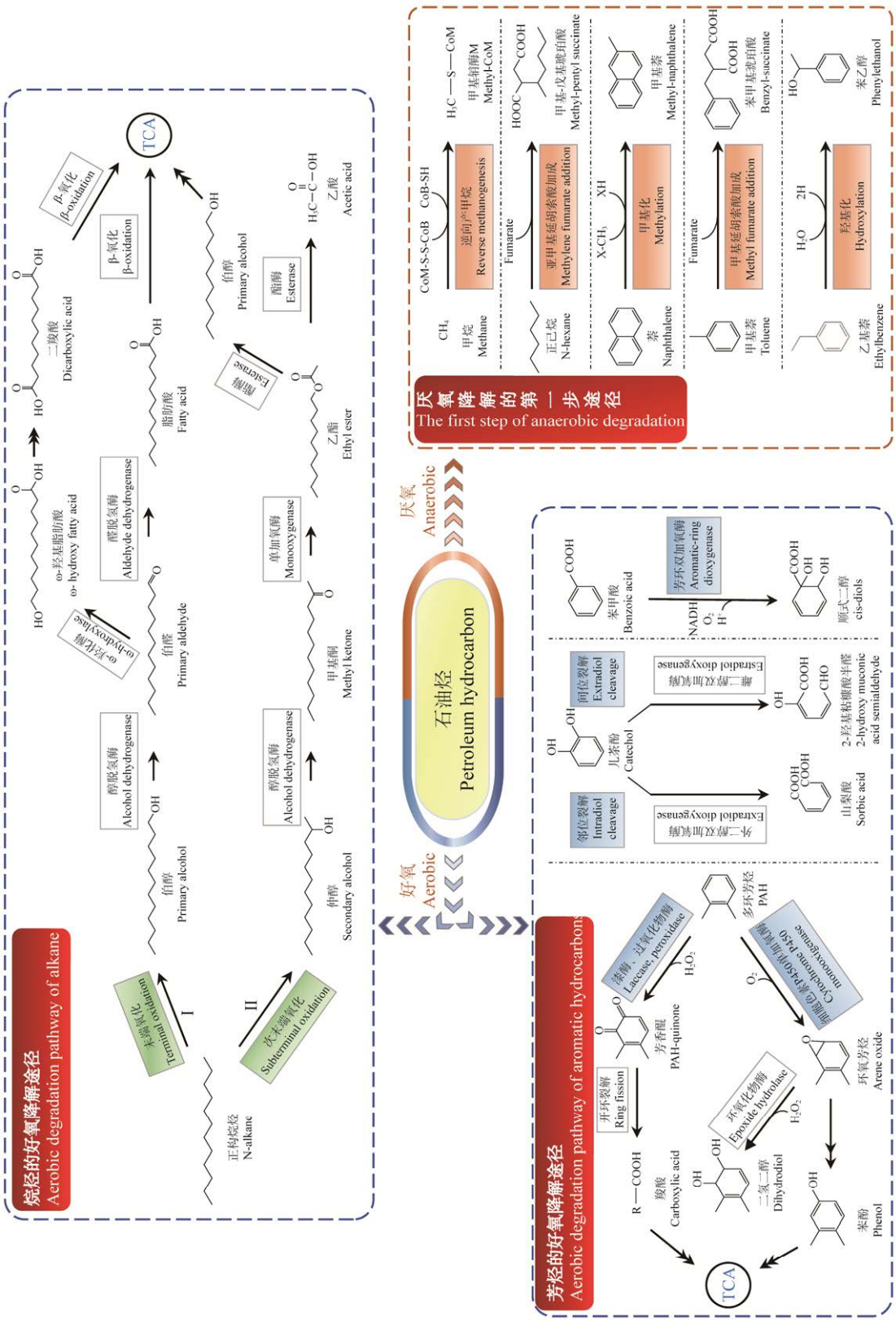

图 1 细菌好氧/厌氧降解石油烃的途径汇总

Figure 1 Summary pathways of aerobic/anaerobic degradation of petroleum hydrocarbons by bacteria.

表现出了较高的 *PAH-RHDα* 基因丰度[56,69]。芳香环羟化双加氧酶的基因根据降解底物的不同对应不同的基因名称，如 *aph* (苯酚)、*bph* (联苯或多氯联苯)、*bnzA* (苯)、*nah* (萘)、*cbaA* (氯苯甲酸)、*xylX* (甲苯/苯甲酸)、*todC1* (甲苯)、*cumA1* (己烯)、*ipbA1* (异丙苯)、*edoA* (乙苯)和 *ebdA* (烷基苯)等。编码 PAH-RHDs (α 亚基)的基因 *pahAc* 由于其保守序列和对底物的特异性，而广泛应用于细菌的标记[72]。研究者们设计不同环境微生物中 *pahAc* 的特异或简并引物，并将其用于评估多环芳烃降解功能基因的丰度和多样性。Cebron 等[91]以 *pahAc* 基因靶向控制污染土壤和沉积物中多环芳烃的生物降解。Shahi 等[92]发现，在受污染土壤中，随着多环芳烃被不断降解，*nah* 和 *phnAc* 基因的丰度显著上调。

在好氧条件下，多环芳烃分子首先氧化成二氢二醇，随后被代谢成儿茶酚和原儿茶酸等中间产物，这些中间产物在邻位或间位裂解，最后进入三羧酸循环。*EDO* 基因是一种编码外二醇双加氧酶的基因，其作用是引起儿茶酚类化合物芳香环的裂解，目前已经在 *Pseudomonas*、*Cupriavidus*、*Rhodococcus*、*Sphingomonas* 和 *Burkholderia* 等菌属中检测到[57]。*catA* 和 *catB* 基因在中间产物儿茶酚的好氧降解途径中发挥着重要的作用。*catA* 将儿茶酚降解为顺式-己二烯二酸，之后 *catB* 再将其进一步降解为粘康酸内酯，这 2 种基因可以作为标记基因应用于监测好氧条件下的石油污染物生物降解情况[60]。Cabral 等[61]考察了石油污染红树林沉积物的宏转录组，发现在 *Desulfatibacillum alkenivorans* AK-01 的基因组中存在 *catA*。此外，与降解儿茶酚相关的基因簇 *catRBCA* 已经在 *Halomonas organivorans*、*Pseudomonas*、*Colwellia*、*Corynebacterium glutamicum* 和 *Pseudomonas chlororaphis* 等细菌中检测到[58,68,73-74]。上述的 *Desulfatibacillum*、*Pseudomonas* 和 *Colwellia* 均是在石油污染环境中常见的优势细菌属。

2.2 厌氧降解涉及的酶和功能基因

与好氧生物降解相比，目前针对厌氧生物降解途径涉及酶和基因的研究相对较少。石油烃的厌氧降解方式与好氧降解不同，还原反应中的主要电子受体包括 Mn^{4+}、NO_3^-、SO_4^{2-}、Fe^{3+}和 CO_2 等。石油烃的厌氧降解途径包括延胡索酸加成、羧化、羟基化、甲基化和逆向产甲烷，生成的代谢物最终被生物体吸收或完全氧化。

延胡索酸加成是多种脂肪烃和芳香族化合物厌氧生物降解的主要途径。*assA*/*masD* 和 *bssA* 作为编码延胡索酸加成酶系的关键基因，已作为生物标志物被用来检测厌氧条件下细菌对石油烃的降解能力[64,75,93]。Bian 等[93]研究发现烷烃的厌氧降解从烷基琥珀酸合成酶(*assA*/*masD* 基因)介导的延胡索酸加成反应开始。*masD*/*assA* 基因已经在 *Desulfothermus naphthae*、*Desulfatibacillum alkenivorans* AK-01、*Desulfosarcina* sp. BuS5 和 *Smithella* sp.等多种石油烃厌氧降解菌中检测到[76,81]，其中 *Desulfatibacillum* 属是石油污染红树林沉积物中的优势菌属。*bssA* 基因与甲苯、乙苯、间二甲苯和对甲酚等芳烃化合物的厌氧降解密切相关[77]。Toth 等[94]在原油的生物降解研究中发现，*Desulfotomaculum* 属和 *Peptococcaceae* 科的部分细菌中存在 *bssA* 基因。Blázquez 等[77]也在 *Azoarcus* sp. CIB 对甲苯和间二甲苯的厌氧生物降解中检测到了该基因的表达。

一些厌氧途径通过将石油烃化合物羧化进行降解，包括硫酸盐还原、反硝化、铁还原、产甲烷和光合作用反应等。在厌氧条件下，甲苯可以通过羧化被降解，其中涉及的基因也在 *Aromatelum aromaticum* EbN1 (*bssABCDEFGH*)、*Thauera aromatica* K172 (*bssABCDEFG*)、*Thauera*

aromatica T1 (*bssABCDE*)和 *Desulfotignum* sp. YB01 (*bssABCDEF*)等细菌中被检测到[59,63,77]。

硫酸盐还原菌可以在厌氧条件下将 SO_4^{2-} 转化为 S^{2-}，易于代谢反应的进一步进行，对于石油烃化合物的降解有重要作用。此外，硫酸盐还原菌还可以使用不同的化学物质作为电子供体，如乙酸盐、乳酸盐、琥珀酸盐、甲酸盐、丙酸盐、丙酮酸盐、乙醇、苯酚和苯甲酸盐等。*dsrAB* 基因(编码异化亚硫酸盐还原酶)常被用于确定不同环境中硫酸盐还原菌的多样性，利用 *dsrAB* 基因可以追踪石油污染区产甲烷菌群的亚硫酸盐/硫酸盐还原活动，该基因已被证实存在于油藏中的细菌 *Desulfotomaculum*、*Pelobacter*、*Desulfotignum*、*Desulfovibrio* 和 *Thermodesulforhabdus* 中[82]。

一些细菌可以在厌氧条件下通过脱氢反应降解烷烃并生成醇[95]。芳香烃也可以通过反硝化细菌的脱氢反应被降解。以乙苯为例，乙苯脱氢酶首先使侧链发生羟基化，之后发生氧化和羧化反应并转化为苯甲酰乙酰辅酶 A，最后裂解产生苯甲酰辅酶 A 和乙酰辅酶 A[89]。*bamBC* 属于编码苯甲酰辅酶 A 还原酶的 *bam* 基因簇，在厌氧条件下能作用于苯甲酰辅酶 A 的降解[79]。Carmona 等[79]研究发现，*Geobacter metallireducens* 的苯甲酰辅酶 A 降解功能与 *bamBCDEFGHI* 基因的存在有关。Crosby 等[78]探究了 *Rhodopseudomonas palustris* 对苯甲酸盐的降解机理，结果表明其降解能力是由 *badDEFGAB* 基因簇的表达调控的。Tiedt 等[80]在反硝化细菌 *Thauera chlorobenzoica* 中检测到由 *bcrABCD* 基因编码的苯甲酰辅酶 A 还原酶。研究表明，细菌对萘的降解是从甲基化反应开始的，之后发生延胡索酸加成或羧基化反应，并且 2-甲基萘、间二甲苯、间甲酚和对甲酚的厌氧降解也有类似的途径[96]。

逆向产甲烷途径是一种在油藏、土壤、沉积物等厌氧系统中常见的石油烃生物降解途径。产甲烷的微生物群落可以产生和释放 CH_4 及 CO_2，甲烷排放到大气的过程可以由甲烷氧化菌实现，其有助于在沉积物和土壤等厌氧/好氧区边界的氧化。在该途径的代谢中，互营细菌和产甲烷菌的作用紧密相关，互营细菌可以将石油烃转化为产甲烷菌的底物(如甲酸盐、乙酸盐和丙酸盐等)，后者再将这些化合物降解为 CH_4[97]。

尽管研究者们对石油烃厌氧代谢途径的研究取得了很多进展，但对微生物群落在复杂环境中对石油烃的厌氧生物降解研究依旧不足。为了更好地了解微生物在复杂环境中的降解能力，现有研究普遍使用功能基因标记法探究特定的代谢过程。*mcrA* (编码甲基辅酶 M 还原酶 A)是评估微生物多样性和功能的关键基因之一[75-76,81]。Roy 等[22]使用分子生态学技术分析了石油烃污染样品的细菌群落结构和功能基因，系统发育分析结果表明，在 *Methanobacterium beijingense* 中存在 *mcrA*。Boyd 等[98]研究发现，在深海海底的自然条件下，*mcrA* 与短链烷烃(甲烷、丙烷、丁烷)的氧化有关。

根据现有报道，研究者们对石油烃的好氧降解机制研究较为深入，在自然污染环境和实验室模拟微宇宙环境中发现了大量可能具有石油降解功能的菌种及相关的功能基因，但由于厌氧微生物的培养条件较为苛刻，石油烃厌氧降解途径的信息揭示不足。此外，复杂多环芳烃的微生物代谢途径鲜有报道，这也限制了石油复杂组分的微生物降解研究和环境修复进程。因此，未来应更多地使用分子生物学技术和组学技术(如基因克隆、系统发育分析、宏基因组和宏转录组)揭示环境样品中非培养微生物的多样性，这些技术可以帮助分析微生物对污染物的降解代谢能力，并为功能基因、酶和

代谢途径的预测提供相关信息。综合利用多种组学技术，挖掘核心功能基因、解析代谢途径，对于未来探究污染环境自然衰减潜力、组配高效生物修复菌剂及构建基因工程菌等工作的开展具有重要意义。

2.3 其他代谢机制

细菌群落可以利用不同的机制来促进石油烃降解，包括趋化作用、表面形成生物膜、寄生于菌丝以及生成生物乳化剂或生物表面活性剂等[6]。趋化性是一种微生物特性，细菌能够自发地跟随化学和环境刺激而移动。甲苯和萘等石油烃组分已被证实对一些细菌有化学趋化作用，其作用效果可以通过全细胞记录和拉曼光谱法进行检测分析[54-55]。细菌表面的鞭毛、外膜脂质和蛋白质等物质可以促使石油烃和微生物在接触后进行生物降解[86]。细菌还可以通过在油-水界面形成生物膜来增强对石油烃的吸附，该途径是影响轻非水相液体中石油烃降解的主要因素。生物乳化剂和生物表面活性剂是由微生物产生的表面活性物质，其能够降低不同相位(如水和油)之间的表面张力，有利于不相溶相的混合。Qiao 等[99]证明了细菌表面活性剂对烷烃具有乳化作用。

温度、pH 和盐度等环境因子也会对功能微生物和相关降解机制产生影响。研究表明，污染土壤中石油烃污染物的生物降解程度主要取决于激发生物降解活性的最佳环境条件、污染物的组分类型和生物可利用性[100-102]。Anthony[100]的研究表明，升高温度可以提高烃类污染物的溶解度，降低其黏度，并将长链正构烷烃从固相转移到液相。Thamer 等[101]研究发现，盐度和温度都会影响石油烃降解细菌的生长活性。Leahy 等[102]认为，尽管石油烃可以为细菌生长提供丰富的碳源，但它们并不能提供细菌生长所需的其他营养物质(如氮和磷)，可以通过添加尿素、肥料、钾盐、铵盐和磷酸盐等来调节碳、氮、磷、钾的比例，提高石油烃污染物的生物降解速率。上述的环境因子也是在使用生物刺激法修复石油污染环境时需要重点关注的因素。

细菌可以寄生在真菌菌丝上延伸入土壤深处，增大与土壤中石油烃污染物的接触面积，提高对它们的降解效率。Fernández-Luqueño 等[103]发现，当细菌和真菌协作代谢多环芳烃时，降解速率会提高一倍。因此，将细菌与真菌组合构建混合菌群，是未来开发石油降解菌剂的新研究方向。

通常而言，环境中的细菌不能独自完全代谢石油的全部组分，甚至对于单一组分也不能完全代谢为 CO_2 和 H_2O，因此降解过程往往需要多种细菌的协同作用[104]。例如，Vega 等[105]研究发现，*Arthrobacter* sp.可将石油烃降解的常见下游产物邻苯二甲酸二甲酯降解为邻苯二甲酸单甲酯，但不能进一步继续降解，*Sphingomonas paucimobilis* 则可以降解邻苯二甲酸单甲酯，在两种细菌的协同代谢作用下邻苯二甲酸二甲酯被完全代谢。然而目前对于复杂石油组分的协同代谢机制尚显不足，未来还需要持续深入探究这种协同代谢模式，为高效石油降解复合菌群的构建提供理论依据。

3 结论与展望

细菌群落在石油污染环境的生物修复过程中起着至关重要的作用。在未受污染环境中，石油烃降解细菌占细菌总量的比例低于 0.1%，而在石油烃污染环境中，这一比例可能增加到 1%−10%。因此，污染场地特征(特别是原位细菌群落的检测)的调查和评估极为重要。原位是否存在能够进行石油烃降解行为的细菌，是修复方案制定的重要参考依据之一。通过深入研究污染物类型、细菌群落和环境因素的特征及

相互作用关系，有利于制定更全面的石油污染场地微生物修复方案。分子生物学新技术的应用极大地丰富了研究人员对微生物种类、多样性及其在污染环境中功能的认识，该类技术已成为研究者们分析石油污染环境微生物群落特征的重要手段。

鉴于当前石油污染场地修复的需求，未来应从多方面持续展开探究：(1) 持续丰富和完善功能基因数据库。尽管已发现一些与石油烃降解相关的酶和功能基因，但由于石油组分的多样性与复杂性，现有研究基础仍然不足以满足科学研究与实际应用的需要。以石油组分中的复杂高分子量多环芳烃为例，其生物代谢途径及所涉及的功能基因尚不清楚，一定程度上限制了此类污染物的环境修复研究进程。因此，未来应注重此类关键酶和功能基因的鉴定与新代谢途径的发掘。(2) 开发用于石油污染场地微生物检测的功能基因芯片。基因芯片检测技术是一种前沿生物微量分析技术，近年来已广泛应用于生物学和环境生态学领域。其可以对环境样品进行快速、敏感的高通量检测，提供污染环境中微生物菌群和功能基因变化的重要信息。开发及改进石油降解功能基因芯片，有助于深入研究石油污染环境中的微生态细节过程，预测微生物群落对石油污染压力的响应变化。(3) 基于场地的污染特征及微生物群落分布特征定向筛选功能菌株，并利用合成微生物学技术开发高效复合菌剂。由于石油组分的复杂性，石油污染场地中污染物非单独存在，且单种微生物所具有的底物降解广谱性有限。因此，需要针对石油污染场地中污染物的类型，定向筛选具有石油烃底物广谱性的降解功能菌，进而配制相应的复合修复菌剂，以达到同步或分步代谢各组分污染物的目的，从而实现对污染物复杂组分的全面降解，增强污染场地修复效果。

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