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专论与综述

含氟有机废水处理过程活性污泥微生物群落研究进展

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摘　要：随着有机氟化物在各领域的广泛应用，含氟有机废水处理面临巨大挑战。活性污泥作为有机废水处理的核心技术之一，微生物在其中发挥着极其重要的作用。本综述首先聚焦在活性污泥微生物群落多样性、组成、结构和功能及其与含氟废水类型、处理工艺和处理效率之间的关系，进而讨论了功能微生物降解/转化有机氟化物的途径和作用机制，最后展望了结合分离培养降解有机氟化物的关键微生物，以及微生物组学技术解析活性污泥微生物群落构建、互作、代谢等核心问题，以提高对含氟有机废水微生物降解机理的认识，优化含氟有机废水处理工艺。

关键词：含氟有机废水，活性污泥，微生物多样性，微生物降解，微生物组学技术

Research progresses of activated sludge microbial communities in fluorine-containing organic wastewater treatment processes

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Abstract: With wide applications of organic fluorides in various fields, fluoride-containing organic wastewater treatment is facing great challenges. Activated sludge technologies are one of core methods for such a wastewater treatment, in which microorganisms play an essential role. This review is focused on the diversity, composition, structure and function of activated sludge microbial communities in the process of fluorinated organic wastewater treatment and their relationships with wastewater types, activated sludge characteristics, treatment efficiency, degradation pathways and mechanisms of organic fluoride compounds by functional microorganisms in fluoride-containing organic wastewater. We also discuss perspectives for addressing key questions related to the assembly and metabolic interaction of activated sludge microbial communities by isolating key functional microorganisms and/or by microbiome technologies, aiming to

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improve our knowledge about mechanisms for microbial degradation of organic fluoride compounds and optimize fluorinated organic wastewater processes.

Keywords: Fluorine-containing organic wastewater, Activated sludge, Microbial community diversity, Microbial degradation, Microbiome technology

含氟有机物由于表面张力强、耐温性能好，并具有耐燃、绝缘、润滑等特性[1]而被广泛使用，现有上万种工业合成和加工的含氟化学品流通在农药、医药等市场[2]，并与其他氟化物，包括全氟和多氟烷基物质(Per-and polyfluoroalkyl substances，PFASs)和全氟磺酸盐(Perfluorinated sulfonates，PFSAs)构成了持久性有机污染物。这些化合物释放到环境后能残留在废水、地表水、泥沙及土壤中，对生态和人类健康构成威胁[3-7]。如PFASs和PFSAs自20世纪50年代大规模生产和使用以来[8-10]，在环境介质和生物体中已检测到[11-16]，并被证实能引起动物和人类致癌、不孕或其他毒性[17-19]。因此，探索上述有机氟化物的微生物降解特性和机制，提高含氟有机废水的生物处理效果，减少其在环境中的残留至关重要。

利用微生物降解有机和无机污染物具有处理效率高和成本低等特点，是处理难降解有机污染废水的优选方法。活性污泥技术作为最常用的废水生物处理工艺之一，其核心是一个拥有高度复杂微生物群落的污泥生态系统，包括真核生物、细菌、古菌和病毒及相应的环境条件。在该工程系统中，活性污泥通常具有很高的生物多样性[700多个属和数千个操作分类单元(Operational taxonomical units，OTUs)][20]和生物量(一般为2−10 g/L)[21]，其中常见功能菌群有EPS (Extracellular polymeric substances)产生菌[22-23]、除氮功能菌(Ammonia-oxidizing archaea，AOA；Ammonia-oxidizing bacteria，AOB；Nitrite-oxidizing bacteria，NOB)[24]、聚磷菌(PolyP-accumulating organisms，PAO)[25]和复杂有机污染物降解菌(如脱卤菌)[26]。高度多样性的微生物群落在活性污泥絮凝体中有效地聚集在一起，通过吸附、吸收和代谢来实现污染物的去除和降解，以保证废水处理效果[20,27-28]。

研究人员通过分子技术分析含氟有机废水处理过程中活性污泥微生物群落，发现污泥中变形杆菌门、拟杆菌门、绿弯菌门、放线菌门、浮霉菌门、厚壁菌门等为优势类群，且它们所占比例随条件不同而变化[29-33]，这也直接影响有机氟化物的去除效果(表1)。

同时，微生物群落还调控着活性污泥的形成、发育、功能及其稳定性。例如丝状细菌(如*Chloroflexi*、*Sphaerotilus*、*Thiothrix*)过度生长会引起污泥膨胀；某些功能菌(如*Zoogloea*)消失或某些酶(如N-acyl homoserine lactone，AHL)过分表达会使污泥絮凝体解体，影响污泥沉降性能，导致出水中泥水分离不充分，降低处理效果[52-53]。因此，研究和监测微生物群落结构，特别是核心微生物组(Core microbiome)的活性以及菌群的互作机制，对提升活性污泥的降解性能以及整个含氟有机废水处理系统的运行效率和稳定性具有指导意义[54-59]。

明确活性污泥微生物群落功能、代谢机制和降解途径对工艺设计、参数优化、生物强化、促进含氟有机废水去除效率至关重要。要矿化有机氟化物，必须破坏其稳定性较高的碳氟键(CH_3-F，116 kcal/mol)[60]。研究发现活性污泥微生物可通过表达脱卤酶，利用酶促反应直接脱氟，或形成不稳定的代谢中间体，间接降解多种异源化合物。然而，一些含氟产品尤其是某些抗生素药物和全氟物质，由于其本身或其代谢产物的复杂结构和毒性，很难通过生物处理实现矿化。如氟调醇(Fluorotelomer alcohols，FTOHs)在微生物作用下能转化成多氟羧酸和全氟羧酸[61]，而这些全氟烷酸(Perfluoroalkyl acids，PFAAs)却易于与有机组分络合，在微生物酶的催化下钝化形成残基，无法进一步被生物转化[62]。针对此类不能被环境中微生物完全矿化的有机氟化物，

表 1 常规活性污泥(Conventional activated sludge，CAS)或基于 CAS 的含氟有机废水生物处理

Table 1 Biological treatments of fluoride-containing organic wastewater by conventional activated sludge (CAS) or CAS-based processes

	Sample	Treatment process	Dominant microorganisms	Removal efficiency	Alpha-diversity (Shannon)	References
Pharmaceutical wastewater	WWTP	A/A/O	*Thermotogae*, *Synergistetes*	/	Average 5.9	[34]
	WWTP	Aeration tank	*Proteobacteria*, *Bacteroidetes*, *Firmicutes*	/	Average 8.68	[29]
	WWTP	1. Anoxic-oxic (A/O)+biofilter 2. Hydrolysis acidification+A/O 3. Micro-aerobic+UASB+AO	*Proteobacteria*, *Chloroflexi*, *Saccharibacteria* *Proteobacteria*, *Chloroflexi*, *Bacteroidetes* *Proteobacteria*, *Chloroflexi*, *Bacteroidetes*	/ / /	Range 4.22−5.34	[30]
	Synthetic wastewater	Microbial fuel cells MFC	*Proteobacteria*, *Bacteroidetes*, *Actinobacteria*	Ofloxacin 87.31% Enrofloxacin 40.81% Ciprofloxacin 79.60%	Range 2.63−2.54	[31]
	Synthetic wastewater	Biotrickling filters (BTFs) Inoculated with pharmaceutical sludge	*Zoogloea resiniphila* HJ1, *Methylobacterium rhodesianum* H13	80%	/	[35]
	Synthetic wastewater	Sequencing batch reactor (SBR) (Inoculated with aerobic granular sludge)	*Proteobacteria*, *Bacteroidetes*, *Acidobacteria*	Norfloxacin>60%, Naproxen 54.50%	/	[36]
	Synthetic wastewater	Single stage reactor	*Proteobacteria*, *Bacteroidetes*, *Firmicutes*	Ciprofloxacin 63.7%	/	[37]
	Synthetic wastewater	Single stage reactor for removal (Inoculated with activated sludge)	*Beijerinckia*, *Gloeobacter*, *Sphingomonas*, unclassified, *Planctomycetales*, unknown *Cytophagaceae*, unknown *Myxococcales*, and *Sphingomonas*	5-Fluorouracil, >99%	2.969 (0 d), 2.615 (14 d), 2.661 (30 d)	[38]
	Synthetic wastewater	Single stage reactor Inoculated with activated sludge	*Proteobacteria*	/	2.58 (0 mg/L), 2.04−3.04 (50−5 000 mg/L)	[39]
	Synthetic wastewater	Sequencing batch reactor (SBR)	*Bacteroidetes*, *Proteobacteria*	Ofloxacin 70%	/	[40]
	Synthetic wastewater	Medium inoculated with biofilm	*Proteobacteria*, *Bacteroides*	Ciprofloxacin 89.1%	1.73 (0 d), 1.67 (28 d)	[41]
	Synthetic wastewater	Aerobic granular sludge (AGS) bioreactor	*Bacteroidetes*, *Actinobacteria*	/	3.1 (21 d); 3.37 (28 d); 2.46 (42 d) 3.15 (56 d); 3.42 (70 d); 2.89 (86 d)	[23]
	Synthetic wastewater	Aerobic granular sludge (AGS) bioreactor	*Proteobacteria*	Norfluoxetine 87.8%	4.75 (0 d); 5.08 (40 d) 4.39 (80 d); 5.16 (110−140 d)	[42]
Organic fluoride	WWTP	Hydrolysis acidification +Anoxic/Oxic	*Proteobacteria*, *Firmicutes*	26.8%	Average 6.06	[32]
	WWTP	Sequencing batch reactor (SBR)	*Proteobacteria*, *Chloroflexi*, *Bacteroidetes*	>80% (TOC=400 mg/L)	4.05−4.40	[33]

(待续)

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(续表 1)

	Synthetic wastewater	Sequencing batch reactor (SBR) inoculated with granular sludge	*Proteobacteria*, *Bacteroidetes*	/	1.15−1.19 (initial) 1.03−1.05 (end)	[43]
	Synthetic wastewater	Rotating biological contactor (RBC) inoculated with activated sludge	*Proteobacteria*, *Actinobacteria*		0.86−1.26 (first stage) 0.58−1.35 (fifth stage)	[44]
	Synthetic wastewater	Rotating biological contactor (RBC) / inoculated with activated sludge		/	/	[45]
	Synthetic wastewater	Sequencing batch reactors (SBR) inoculated with activated sludge	/	/	/	[46]
	Synthetic wastewater	Sequencing batch reactor (SBR) inoculated with granular sludge	*Serratia*, *Chryseobacterium*, *Xanthomonas*, *Pimelobacter* and *Rhodococcus*	68.9% (2-Fluorophenol)	0.72−1.12	[47]
Aqueous film forming foam	Quaternary Ammonium Polyfluoroalkyl Surfactants	Soil microcosms From a contaminated site	/	70.3%		[48]
	Neat Ansul AFFF	Soil microcosms From a firefighter training area	/	/		[49]
	Synthetic wastewater	Medium Inoculated with activated sludge	*P. oleovorans*, *P. butanovora*	20% (8:2 FTOH) 60% (6:2 FTOH) 70% (4:2 FTOH)		50]
	6:2 Polyfluoroalkyl phosphates	Medium Inoculated with activated sludge	*Nitrospira* sp. and *Prosthecobacter dejongeii*			[51]

注: /: 无数据.

Note: /: No data.

遗传操作方法为其进一步被降解提供了潜在技术。联合微生物组学、微生物组工程和基因工程技术，设计出高表达有机氟化物降解基因或高效功能微生物组是未来生物处理难降解异源污染物的重要手段[63-64]。

海洋、湖泊、河流底泥和土壤等自然环境中微生物群落特征及功能等的深入研究[65-70]，为理解生物工程系统中相关微生物学机制提供了理论基础。最近，研究人员从微生物生态学的角度报道了活性污泥微生物的多样性、功能冗余、群落组装、群落互作、代谢等机制，揭示了不同活性污泥微生物群落结构与环境参数和污染物处理效果的关系[55,71-76]。这些研究为寻找有效措施或策略来解决污水处理问题，如低效的脱氮或除磷[55,77]、污泥膨胀[78]、较差的生物降解(含氟废水)[34]提供了指导。随着对含氟废水处理过程中活性污泥微生物群落多样性、结构功能及降解机理的进一步认知，通过解析活性污泥中功能微生物群落的生态策略，一些能提高微生物在复杂工业废水中适应力的工艺和装置将被开发和应用。

本综述聚焦于含氟有机废水处理过程中活性污泥微生物群落与含氟废水类型、处理工艺和性能之间的关系，讨论了功能微生物降解/转化有机氟化物的路径和作用机制，并展望了结合分离培养关键功能微生物和微生物组学技术解析活性污泥微生物群落构建、互作、代谢等核心科学问题，从而进一步阐明微生物降解含氟有机物的机理，并优化含氟有机废水的处理工艺。

1 制药废水处理过程活性污泥微生物群落结构和功能

1.1 微生物多样性

由于处理高氨氮、高毒性制药废水的活性污泥中微生物群落非常复杂，虽然广受关注，但是其中的微生物群落结构和功能尚无明晰结论。随着分子技术的推广，当前在解析制药废水处理过程活性污泥微生物群落方面取得了一些重要进展。Zhao 等[34]比较了制药废水、市政废水和其他工业废水处理厂活性污泥中的细菌组成和多样性，其平均 Shannon 指数分别为 5.9、8.1 和 6.3。制药废水处理活性污泥中低 α-多样性表明微生物由于受到原料、催化剂和残留抗生素等[79]物质的抑制作用，其生存/适应能力显著降低。在对 8 类制药废水处理污泥的微生物进行全面分析后，*Thauera*、*Kosmotoga*、*Methyloversatilis*、*Hyphomicrobium*、*Petrobacter*、*Chelativorans*、*Desulfovibrio*、*Xanthomonadaceae* 和 *Burkholderiales* 确定为优势菌属。这些菌属通常具有非特异性功能，包括参与电子传递过程，如脱氮脱硫[80-82]、降解有机碳[83]和芳香类[84-85]。此外，由于制药废水对微生物群落存在较高的选择压力，这导致了不同类型制药废水之间的特定/偶发种群(Occasional groups)存在巨大差异，同时也反映出微生物多样性变化和组装过程受到确定性因素(制药废水的类型)的驱动。为了抵抗药物的抑菌作用，处理含氟类抗生素的活性污泥具有更多特异的 OTU[86]，如已被报道的 *Enterococcus*、*Bacteroides*、*Prevotella*、*Parabacteroides* 和 *Sphingopyxis* 是多种抗生素的耐药菌[87-88]。研究发现稀有类群(Rare groups)构成了制药废水污泥中微生物群落的主体，并且这些特异性耐药物种在抗生素胁迫下能从稀有物种转化为优势物种[89-90]。

1.2 微生物群落影响因素

1.2.1 接种源

处理不同类型的制药废水需要特定的功能微生物类群，不同的接种源不仅影响着处理系统中的微生物群落组成，而且直接关系到废水的处理性能。将活性污泥、受污染的沟渠沉积物和渗滤系统的土壤经过 30 d 的废水驯化后，Kim 等[38]发现尽管 3 种泥源之间的群落组成相差很大，但接种了活性污泥和沟渠沉积物的反应器具有较好的制药废水处理效果，这归因于接种源中土著优势菌属 *Sphingomonas*、*Beijerinckia*、*Methylophilus* 和 Unknown *Cytophagaceae* 与氟尿嘧啶(5-Fluorouracil)等药物的转化密切相关；与此同时，不同的群落组成表现出相似的降解性能说明了不同微生物接种系统存在功能冗余；由此推断，环境中可能还分布

着其他有益于处理制药废水的接种源，如来自膜生物反应器的 *Bradyrhizobiaceae* 等菌群。

1.2.2 工艺类型

传统制药废水处理工艺有厌氧/缺氧/好氧(Anaerobic/anoxic/oxic，A^2/O)、序批式反应器(Sequencing batch reactor，SBR/Granular-SBR)、膜生物反应器(Membrane bio-reactor，MBR)或几种方法联合使用(表 1)，不同处理工艺下活性污泥微生物群落差异显著。Ouyang 等[30]研究了接种相同初始污泥的不同处理工艺在处理制药废水过程中的微生物群落组成，发现(UASB+A/O)系统中微生物的α-多样性最高，且 *Proteobacteria*、*Bacteroidetes*、*Chloroflexi* 和 *Acidobacteria* 是其优势菌门；在 UASB 装置中，富集了相对较高的 *Desulfovibrio*、*Desulfobacter*、*Desulfococcus* 和 *Desulfuromonas* 等功能菌，对去除废水中硫酸盐起重要作用；在(A/O+Biofilter)系统中，*Saccharibacteria* 是其优势菌门，其中 *Candidatus* Saccharibacteria bacterium 菌群占据主导地位，这与该系统具有较好的 NH_4^+-N 去除性能密切相关。

1.2.3 负荷冲击

处理系统中底物负荷对微生物群落具有重要影响，探究微生物对底物负荷的响应，能够解析活性污泥中微生物群落组成、多样性和功能与稳定性的关系，进而表征污泥在水质波动下的抵抗或者恢复性能。在处理含环丙沙星(Ciprofloxacin)废水的微生物燃料电池中(Microbial fuel cell，MFC)[39]，运行 1.5 年后虽然活性污泥微生物多样性有所降低，但是 *Proteobacteria*、*Bacteroidetes*、*Actinobacteria* 丰度逐渐增加并成为优势菌，该门类下的一些功能菌属如 *Alcaligenes* (可分泌 HpaM 等酶，催化目标污染物脱羧羟基化)[91-92]、*Chryseobacterium* (可降解恩诺沙星等有机污染物)、*Myroides* (降解芳香烃污染物 3,4-二氯苯胺)、*Stenotrophomonas* (降解环丙沙星和其他新兴污染物)、*Eubacterium*、*Pseudomonas* 和 *Dysgonomonas* 显著富集[31,93]。此外，Davids 等[39]模拟了活性污泥微生物群落对高浓度布洛芬(Ibuprofen)的响应，结果表明布洛芬的选择压力导致了群落结构的显著转变，并刺激产生了对环丙沙星较高抗性且具有生物降解能力的细菌类群(*Proteobacteria* 和 *Enterobacteriales*)。在经过 1 000 mg/L 布洛芬高负荷驯化后，污泥降解环丙沙星的性能明显提高，其原因可能是*γ-Proteobacteria* 种群的剧增及其通过调控高效药物修饰酶的编码基因而加强了微生物对环丙沙星耐药性。

2 氟化工废水处理过程活性污泥微生物群落结构和功能

2.1 常规生物处理工艺中微生物群落

氟化工企业在生产含氟聚合物、含氟精细化学品和含氟药品中间体等产品过程中产生的反应废液和洗涤废水，通常具有高有机物浓度、有毒、成分复杂、强酸强碱等特点，是公认的生化性能较差的废水。虽然微生物在这类废水中的生存能力相对较弱，但对其群落多样性和结构功能研究颇受关注。Xu 等[32]分析了处理氟化工园区内废水的活性污泥微生物群落，发现优势的 *Betaproteobacteria*、*Dechlorosoma* 和 *Thauera* 主要在厌氧和缺氧生物池富集，它们不仅能对苯等复杂有机物进行厌氧降解，还能将高氯酸根转化为氯离子，降低高氯酸盐的浓度。与此同时，含氟废水在流经处理系统后，其氟离子浓度明显提高，这表明上述优势菌可能参与了有机氟的生物降解。此外，氟化工废水污泥中一些低丰度的功能菌群也是维持系统具有良好性能的重要因素，如反硝化菌(*Pseudomonas*、*Roseomonas*)和脱硫菌(*Thiobacillus*)[32]。为进一步探明活性污泥中降解有机氟化物的功能微生物及其群落结构动态变化，王彬浩[33]利用提取自氟化工废水中的含氟有机物，模拟含氟废水用于驯化接种污泥。当反应器在 400 mg/L TOC (Total organic carbon)负荷下，氟化物去除效率稳定在 80%以上时，污泥中微生物群落发生了显著变化，*Rhizobiales*、*Rhodocyclales* 和 *Xanthomonadale* 为主要优势菌群，且检测到了能够降解苯、二氯苯等含卤多环芳烃的

功能微生物(含编码单加氧酶的 *amo* 基因和编码脱氢酶的 *mdh2* 基因)；随后，利用驯化成熟的污泥做进一步实验研究，明确了活性污泥微生物群落受到含氟有机废水中碳氮比、盐度和重金属的显著影响；随着盐度以及重金属种类和浓度的增加微生物多样性明显降低，从而能够降解二苯噻吩(Dibenzothiophene)以及其他杂环芳香烃类(萘和蒽)的 *Xanthobacter* 表现出良好的适应能力，并成为核心菌属。这说明上述菌群在高盐度和重金属等恶劣环境条件中能占据一些特定的生态位，维持其生理和生态功能。这些在处理含氟废水污泥中优势微生物菌群的发现，以及对有机氟化物降解性能的研究有益于提高含氟有机废水的生物处理效率，同时也对利用生物强化技术处理该类废水具有指导意义。

2.2 生物强化工艺中微生物群落

“生物强化”通过添加从自然界中筛选的高效菌株或通过基因工程构建的具有特定功能的高效降解菌，从而提高含氟有机废水处理效率，并促进活性污泥微生物群落的适应性转变。Ramos 等[43]在颗粒污泥-序批式反应器中添加邻氟苯酚(2-Fluorophenol)降解菌后，废水中的邻氟苯酚和 NH_4^+-N 去除效率明显提高；而且当反应器遭遇邻氟苯酚负荷冲击时，添加的生物强化菌群促进了污泥中土著菌 *Acidobacteria* 的生长，能使颗粒污泥中微生物种群丰度快速恢复并维持相对稳定，并促进细菌群落转变到以 *Alphaproteobacteria*、*Betaproteobacteria* 和 *Flavobacteriia* 为优势菌的新群体。尽管强化菌在邻氟苯酚污染物去除方面起关键作用，但是生物强化菌在污泥絮凝体中不能保持优势地位，关于强化菌与土著菌群间的互作机制有待进一步解析。此外，在强化系统中一些与邻氟苯酚降解菌具有相似功能的重要优势种群被识别[43]，如未分类根瘤菌科(Unclassified *Rhizobiales*)、未分类缓生根瘤菌科(Unclassified *Bradyrhizobiaceae*)和未分类酸杆菌 Gp4 (Unclassified *Acidobacteria* Gp4)。Amorim 等[45]在接种活性污泥的旋转生物接触器中添加对氟桂酸降解菌(*Rhodococcus* sp.)，显著提高了反应器对 COD (Chemical oxygen demand)和对氟桂酸的去除率和抗负荷冲击能力；同样地，在实验后期强化菌(*Rhodococcus* sp.)的基因片段在新形成的稳定细菌群体结构中消失了。综上所述，虽然生物强化菌可能并不是新菌群体系中的优势菌，但可以促进污泥中微生物群落对环境压力的适应性；此外，为使强化菌能够提高含氟废水处理效率和有效调控微生物群落，应同时考虑强化菌对有机氟化物的降解能力和微生态系统动态平衡，从而形成降解性能强和抗负荷冲击好的稳定群落。

3 消防泡沫(Aqueous film forming foam，AFFF)废水处理过程活性污泥微生物群落结构和功能

AFFF 废水通常具有大量含氟异构体(前驱体)，由于检测含氟异构体的种类存在差异，当前活性污泥对 PFASs (AFFFs 的主要成分)的去除效率存在一些争议。部分污水处理厂出水 PFASs 浓度高于进水浓度，使得污水处理厂排放污水成为城市河流 PFASs 污染的主要来源[94]。而 Chen 等[95]研究发现活性污泥可以有效地去除废水中的全氟己烷磺酸和全氟己酸且去除效果受到处理工艺类型的影响，如 PFASs 的去除效果：周期循环活性污泥工艺(Cyclic activated sludge system，CASS，32.2%) >氧化沟(Oxidation ditch，OD，17.5%)>厌氧/缺氧/好氧(A^2/O，−1.49%)。Lewis 等[51]考察了 AFFFs 的主要成分 6:2 PAPs (Polyfluoroalkyl phosphates)在活性污泥中的生物转化效能以及微生物群落动态变化，发现在培养系统中接种活性污泥比接种纯菌(FTOH-degrading *Pseudomonas*)具有更高效的生物转化能力。在实验进行 30 d 后，检测到了转化产物 5:2 FTOH、PFHpA [$CF_3(CF_2)_5COOH$]和 PFPeA [$CF_3(CF_2)_3COOH$]。尽管在生物降解结束时活性污泥中微生物多样性和丰度均有所下降，但新出现的 *Nitrospira* sp.和 *Prosthecobacter dejongeii* (降解雌激素等有机物)功能菌[51]显著增强了反应器处理性能。与此同时，烷烃单氧酶参与了 FTOHs

的降解过程[96-97]，因此活性污泥中烷烃降解菌群数量的增加促进了 PAPs 生物转化效率。此外，Zhang 等[98]研究发现 *Dokdonella* spp.、*Thauera* spp.、*Albidovulum* spp. 和 *Caldanaerovirga* spp. 是 6:2 Fluorotelomer alcohol (FTOH)降解菌和耐药菌株；FTOH 负荷增加，反应器群落多样性降低，微生物结构发生明显变化，成为群落结构动态变化的主要驱动力。另外，6:2 FTOH 降解菌、耐药菌群(*Dokdonella*、*Thauera*、*Albidovulum* 和 *Caldanaerovirga*)与多氟烷基酸敏感菌(*Incertaesedis*、*Opitutus* 和 *Bacillariophyta*)同时存在于降解系统中，这表明 6:2 FTOH 降解系统中的微生物群落遵循生态学中“石头-剪刀-布(Rock-scissors-paper)”的共存机制[98]。

4 微生物降解或转化典型有机氟化物的途径和机制

分离和鉴定高效的氟化物降解菌(Organic fluoride-degrading bacteria)，研究其降解途径和脱氟机制、降解酶和功能基因，可为应用基因工程技术拓宽有机氟降解种类、提高微生物降解氟化物能力提供依据。当前，已有文献提供了多种细菌和真菌转化或降解芳香型和脂肪族有机氟化合物的证据。制药废水及氟化工废水污泥、污染土壤、湿地植物根际土和河流沉积物中分离和鉴定了多种高效有机氟降解菌(表 2)，包括慢生根瘤菌(*Bradyrhizobium*)、红球菌属(*Rhodococcus*)、栖热菌属(*Thermus*)、假单胞菌属(*Pseudomonas*)、分枝杆菌属(*Mycobacterium*)、戈登氏菌属(*Gordonia*)等。其中从制药废水活性污泥中分离的高效降解细菌栖热菌属(*Thermus* sp.)，在 pH 为 6.5、温度在 70°C 时，不但可以去除超过 70%的环丙沙星，还能以诺氟沙星、氧氟沙星和恩罗氟沙星等其他喹诺酮类药品作为唯一碳源，去除率分别达到 63%、70%、74%[100]。*Pseudomonas knackmussii* B13 能以对氟苯甲酸(4-Fluorobenzoate)为唯一碳源并对其进行降解[112]；*Ralstonia* sp.能够忍耐高浓度对氟苯胺(1 250 mg/L)，高盐(15 g/L)环境，在 pH 为 6.5、温度为 30°C 时，高效降解对氟苯胺[110]；*Ralstonia* sp.还能以对氟苯胺(Fluoroanilines)作为底物，以共代谢的方式将其去除[111]。*Pseudomonas aeruginosa* HJ4 在 pH 为 3.0−10.0、温度为 35°C 时可保持良好的 Perfluorooctanesulfonate (PFOS)降解能力，转化率超过 67%[116]。这说明活性污泥中含有多种高效的降解菌，且具有较广的有机氟降解能力，对提高含氟有机废水的处理效果起重要作用。

利用基因克隆、酶活性测定和 HPLC-MS/GC-MS-MS 分析代谢物方法，揭示多种降解菌的有机氟降解途径和关键基因。*Microbacterium* sp.和 *Labrys portucalensis* F11 等菌种在好氧环境下降解喹诺酮类抗生素时，一般包括羟基化/去氟化、去甲基化、脱羧和哌嗪环裂解等过程[122]。研究者从受氯苯污染土壤中分离出能够矿化对氟肉桂酸(4-Fluorocinnamic acid)的 *Arthrobacter* sp. strain G1 和 *Ralstonia* sp. strain H1，并明确了该降解过程是通过 β-氧化机制来实现的[109]。6:2 氟调醇(6:2 FTOH，$F(CF_2)_6CH_2CH_2OH$)作为 AFFF 中基础性原料，它的生物降解性能和途径受到高度关注。Kim 等[96]发现 *Pseudomonas oleovorans* 和 *P. butanovora* 能通过两种途径转化 6:2 FTOH (图 1)：途径 I 产生 x:2 酮、x:2 氟调醇(FTOH)和全氟己酸(PFHxA)或全氟辛酸(PFOA)；途径 II 产生 x:3 acid ($C_xF_{2x+1}CH_2CH_2CO_2H$)、x:3 Uacid ($F(CF_2)_xCHCHCOOH$)和全氟丁酸(PFBA)或 PFHxA (x=n−1，n=6 or 8)。由于受到菌株类型、酶诱导剂和还原能力的影响，途径 I 更容易进行。随后的研究发现 *P. fluorescens* DSM 8341 通过表达脱卤酶(Fluoroacetate-dehalogenase)，能在途径 II 中脱去 6:2 FTOH 中一个 C 原子，生成 5:2 Uacid 和 4:3 acid[97]。由于 PFASs 包含烷烃链，通常认为烷烃单加氧酶(Alkane monooxygenase 和 Butane monooxygenase)在生物转化有机氟化物的过程中起重要作用。因此，烷烃单加氧酶成为判断细菌是否具有转化能力的一种检验依据。此外，*Gordonia* sp. NB4-1Y 表达的两种酶(Nitrilotriacetate 和 Monooxygenases)还能将氟调聚物磺酸盐脱硫还原[119]。

表 2　纯菌或混合培养微生物降解有机氟化物

Table 2　Microbial degradation/transformation of organic fluoride compounds by pure strains or mixed cultures

	Contaminant	Microbes	Source	Key enzymes/genes/pathways	References
Pharmaceutical	Ciprofloxacin	*Bradyrhizobium* sp. GLC_01	Activated sludge	Cometabolism (glucose and sodium acetate)	[99]
		Thermus sp.	Activated sludge	As sole carbon source	[100]
	Moxifloxacin	*Labrys portucalensis* sp. strains F11, *Rhodococcus* sp. strains FP1	Industrially contaminated sediment	Cometabolism (acetate)	[101]
	Fluoxetine	*Labrys portucalensis* F11	Industrially contaminated sediment	As sole carbon source, complete removal of both enantiomers; or cometabolism (added acetate)	[102]
	Ciprofloxacin, Floxacin Norfloxacin, Enrofloxacin	*Thermus* sp.	Activated sludge	As sole carbon source Promote (co-substrate sodium acetate)	[100]
	Ciprofloxacin, Norfloxacin	*Phanerochaete chrysosporium*, *Pycnoporus sanguineus*	/	Laccaseand cytochrome P450	[103]
	Enrofloxacin	*Phragmites australis*, *Juncus maritimus*	Rhizospheric sediment	Adsorption or abiotic degradation	[104]
	Flurbiprofen	*Streptomyces* sp.	/	Metabolites: 4′-hydroxyflurbiprofen, 3′,4′-dihydroxyflurbiprofen, 3′-methoxy, 4′-hydroxy-flurbiprofen	[105]
	Norfloxacin	*Microbacterium* sp.	Activated sludge	Metabolites: 8-hydroxynorfloxacin, 6-defluoro-6-hydroxynorfloxacin, desethylene norfloxacin, and N-acetylnorfloxacin	[106]
	Danofloxacin	*Xylaria longipes*	A wood trunk	Products: an oxidation of the terminal nitrogen of the substituted piperazine moiety of the substance	[107]
Organic fluoride	SF_5-substituted aminophenols	*Pseudomonas* spp.	Rhizospheric soil	Convertedto the N-acetylated derivative the N-acetylated; 4-(pentafluorosulfanyl) catechol	[108]
	4-Fluorocinnamic acid	*Arthrobacter* sp. strain G1 *Ralstonia* sp. strain H1	Soil contaminated with halogenated aliphatic compounds	Mineralization Through α-oxidation mechanism; Enzymes i.e., 4-fluorocinnamoyl-CoA hydratase, 4-fluorophenyl-hydroxy propionyl-CoA dehydrogenase, and 4-fluorophenyl-keto propionyl-CoA thiolase	[109]
	4-Fluoroaniline (4-FA)	*Ralstonia* sp.	Activated sludge	Catechol 2,3-dioxygenase catalyzes extradiol cleavage	[110]
	Fluoroanilines	*Ralstonia* sp.	Activated sludge	Cometabolism (4-FA as growth substrate)	[111]
	4-Fluorobenzoate	*Pseudomonas knackmussii* B13	Activated sludge	As the sole carbon source	[112]
	4-Fluorocinnamic acid	*Rhodococcus* strain S2	Biofilm	Assole carbon and energy source Transformation to trans-muconate 3-carboxymuconate and 3-oxoadipate	[113]
	5-Fluorosalicylate	*Pseudaminobacter salicylatoxidans* BN12	Activated sludge	(A) Salicylate 1,2-dioxygenase catalysis; 5-fluorosalicylate, (B) 2-oxo-4-fluorohepta-3,5-dienedioic acid, (C) ‘4-pyruvyl-4-fluorobut-2-en-4-olide’ (D) *cis*- and *trans*-2-oxo-3-(5-oxofuran-2-ylidine) propanoic acid and (E) maleylpyruvate	[114]

(待续)

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(续表 2)

	2-Fluorobenzoate	*Thauera aromatica*	River sediment	As the sole sources of carbon; Enoyl-CoA hydratases/Hydrolases; enoyl-CoA hydratases via α-fluorohydrin formation	[115]
Poly-/Perfluorochemicals	6:2 Fluorotelomer alcohol	*Mycobacterium vaccae* JOB5, *Pseudomonas oleovorans*, *Pseudomonas butanovora*, *Pseudomonas fluorescens* DSM 8341	/	Monooxygenases; Alkane monooxygenase; Soluble butane monooxygenase and fluoroacetate-dehalogenase	[97]
	4:2, 6:2, 8:2 Fluorotelomer alcohol	*Pseudomonas butanovora* *Pseudomonas oleovorans*	/	Pathway I: the production of x:2 ketone (dominant metabolite), and perfluorinated carboxylic acids The pathway II: the formation of x:3 polyfluorinated acid and relatively minor shorter-chain PFCAs	[96]
	Perfluorooctanesulfonate (PFOS)	*Pseudomonas aeruginosa* strain HJ4	Activated sludge	Metabolites: PFBS and PFHxS	[116]
	8:2 Fluorotelomer Alcohol	*Pseudomonas* species OCY4, *Pseudomonas* species OCW4	Soil	Co-substrate (octanol)	[117]
	6:2 Fluorotelomer sulfonamidoalkylbetaine	*Gordonia* sp. strain NB4-1Y	Vermicompost	Metabolites: PFBA, PFPeA, PFHxA, perfluoroheptanoic acid (PFHpA), 4:3 FTCA, 5:3 FTCA, 6:2 FTCA, 6:2 FTUA, 5:2 sFTOH, 5:2 FT ketone, 6:2 FTOH	[118]
	6:2 Fluorotelomer sulfonate	*Gordonia* sp. strain NB4-1Y	Vermicompost	Two nitrilotriacetate monooxygenases	[119]
	6:2 Fluorotelomer alcohol	Fungus: *Gloeophyllum trabeum* *Trametes versicolor*	Soil from U.S. military bases	Metabolites: polyfluoroalkyl substances, such as 5:3 acid ($F(CF_2)5CH_2CH_2COOH$), perfluorocarboxylic acids (PFCAs)	[120]
	6:2 Fluorotelomer alcohol	*Phanerochaete chrysosporium*	Soils	Metabolites: perfluorocarboxylic acids (PFCAs), polyfluorocarboxylic acids	[121]

注：/：无数据.

Note: /: No data.

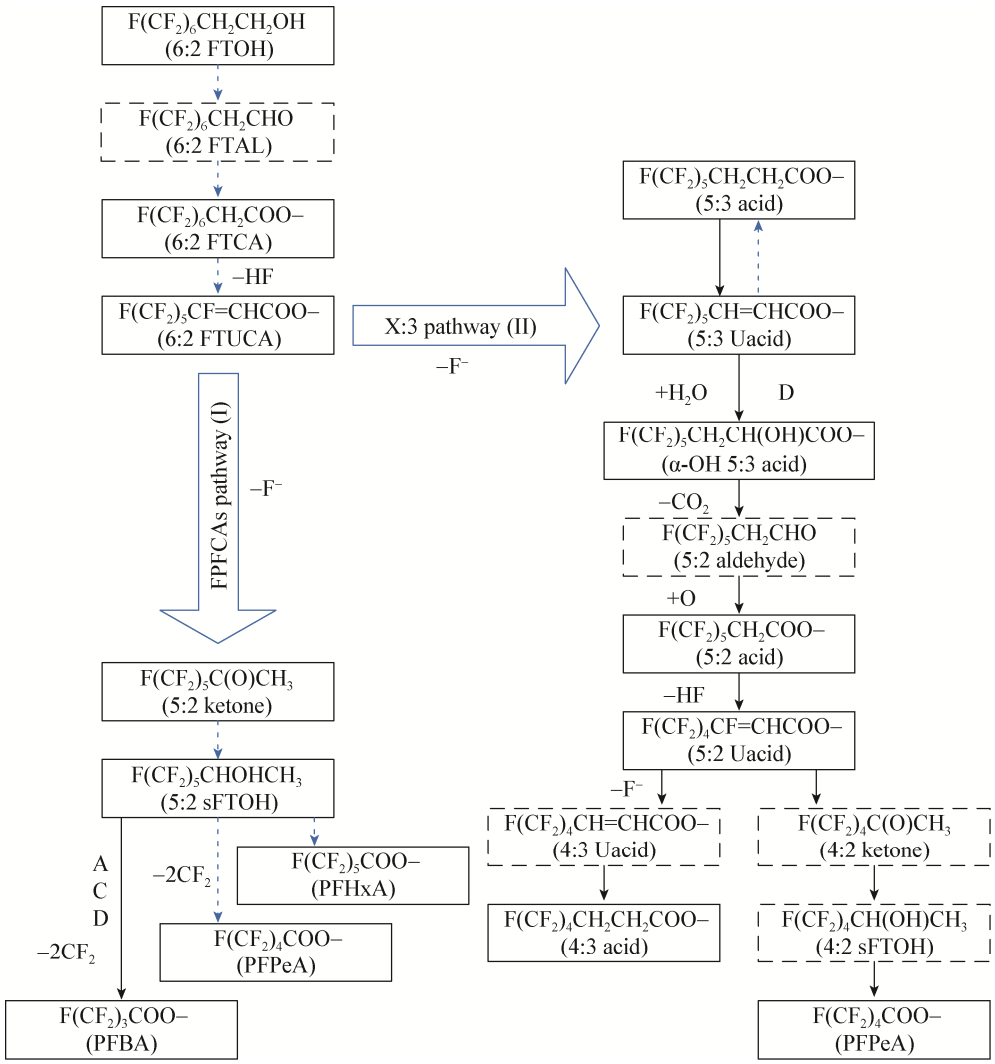

图 1　烷烃降解菌和氟乙酸盐降解菌降解 6:2 FTOH 的途径[97]

Figure 1　6:2 FTOH degradation pathways by alkane-degrading and fluoroacetate-degrading bacteria[97]

注：蓝色箭头表示 A、B、C 和 D 4 种菌均起作用的降解途径(A：*Pseudomonas oleovorans*；B：*Pseudomonas butanovora*；C：*Mycobacterium vaccae* JOB5；D：*Pseudomonas fluorescens* DSM 8341). 不同菌种所起作用的途径用字母(A、B、C 和 D)标注；从 5:3 Uacid 开始的下游转化途径由 *Pseudomonas fluorescens* DSM 8341 调控；虚线框中的化合物是推测的代谢物.

Note: The pathways shared by all four bacteria (A, B, C and D) are presented in blue arrows (A. *Pseudomonas oleovorans*; B. *Pseudomonas butanovora*; C. *Mycobacterium vaccae* JOB5; D. *Pseudomonas fluorescens* DSM 8341). Pathways in different bacteria are marked by their labels (A, B, C and D). The downstream pathways from 5:3 Uacid are largely performed by *P. fluorescens* DSM 8341. Compounds in boxes with dotted line are only predicted.

真菌在降解有机氟污染物方面也有重要贡献。其中喹酮类药的真菌降解途径一般包括：酯化、引入羟基、脱羧、引入甲酰或乙酰基、脱氟、部分降解或由氨基取代哌嗪、在哌嗪环处形成共轭物或取代三号碳原子上羧基[107]。体外酶降解和体内细胞色素 P450 抑制实验表明真菌漆酶和细胞色素 P450 能催化含氟抗生素药物的去除，而且可能的降解途径为：脱氟或脱水→脱羧→哌嗪取代基的氧化[103]；图 2 所示为环丙沙星和诺氟沙星在 *Phanerochaete chrysosporium* 纯培养中的转化过程。此外，*Phanerochaete sanguineus* 还能通过单羟基化和在 N 位脱甲基或脱乙基，使环丙沙星脱氟转化[103]。SF_5 取代的苯胺(SF_5-substituted aminophenols)可以被具有 N-乙酰基转移酶的链霉菌(*Streptomyces griseus*)

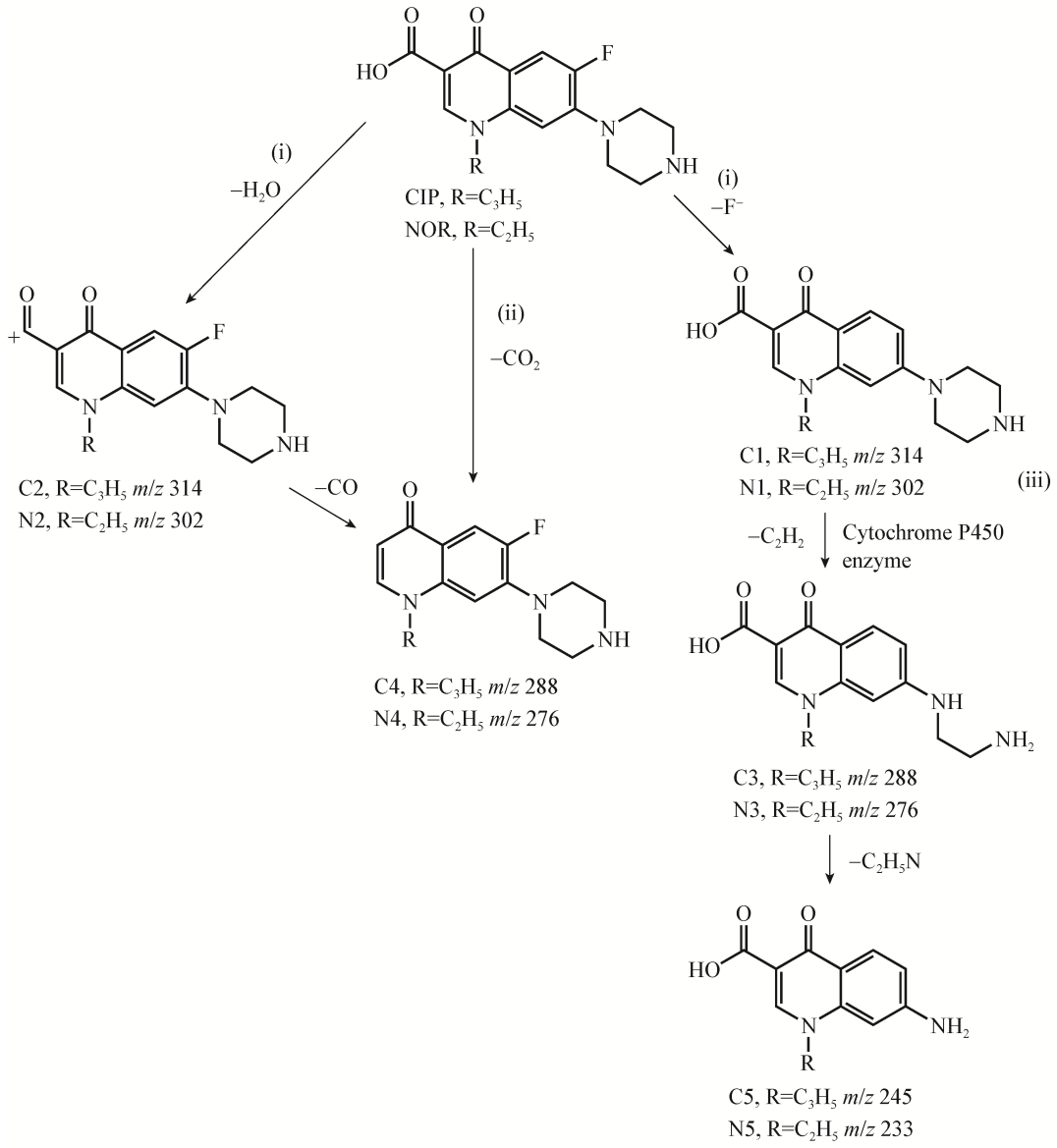

图 2　环丙沙星(CIP)和诺氟沙星(NOR)在 *Phanerochaete chrysosporium* 纯培养中的转化途径[103]

Figure 2　The transformation pathway for ciprofloxacin (CIP) and norfloxacin (NOR) by *Phanerochaete chrysosporium*[103]

转化为 N-乙酰基衍生物[123]。此外，来自 AFFF 污染的军事基地土壤中的 6 种真菌(隶属 *Fusarium* sp.，*Penicillium* sp.和 *Aspergillus* sp.)在纯培养下能够转化 6:2 FTOH[120]。

微生物群落通过把单一底物作为生长碳源或者通过共代谢实现有机氟化物降解。从活性污泥或纯菌属中提取天然酶，并进行酶促实验(Enzymatic reactions)，有助于准确识别特定底物的催化酶以及代谢途径。氧化还原酶和水解酶是难降解污染物污泥中较为常见的酶。Krah 等在酶促降解 20 种微污染药品时，把最主要的生物转化途径归因于酰胺水解[124]。最近的研究发现 *Thaueraaromatica* 以 4-氟甲苯或者 4-氟苯甲酸为底物时，存在一条依赖于 ATP 的 C-F 键断裂途径并最终实现完全矿化，其脱氟机制如图 3 所示[125]。在第 I 类苯甲基辅酶还原酶(BzCoA reductase，BCR)的催化下，4-氟苯甲酰基辅酶 A (4-F-BzCoA)脱氟转化成苯甲酰基辅酶 A (BzCoA)，此过程与伯奇还原反应类似(Birch reduction-like)，

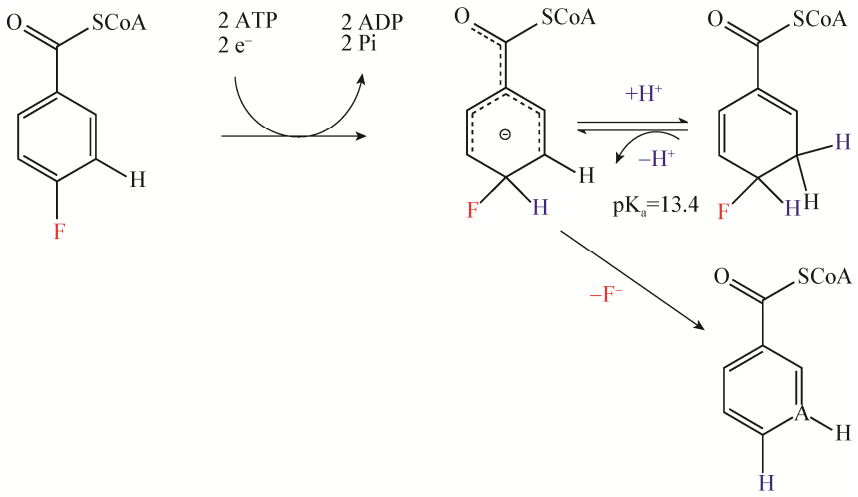

图 3　通过依赖于两个独立 ATP 的 I 类苯甲基辅酶还原酶(BzCoA reductase, BCR)的作用，实现 4-F-BzCoA 潜在转化[125]

Figure 3　Possible mechanism for the conversion of 4-F-BzCoA by ATP-dependent class I BCR (BzCoA reductase)[125]

注：一种类似伯奇反应的机制，包括两个依赖于 ATP 的电子转移步骤和一个产生阴离子状态的质子化步骤，推测 4-F-dienoyl-CoA 中间体(C-3 位)的 pKa (蛋白激酶 A)显著降低，因此在 E1cB 型(共轭碱单分子消除反应)过程中，本质上不可逆的氟释放是由再芳构化驱动的.

Note: It is suggested a Birch-like mechanism involving two single ATP-dependent electron transfer steps and one protonation step, yielding an anionic state. During 4-F-BzCoA conversion, the pKa protein, an assumed 4-F-dienoyl-CoA intermediate (C-3 position) is significantly decreased, resulting in the essentially irreversible fluoride release in an E1cB-type elimination driven by re-aromatization.

并确定 BCR 为 4-氟芳烃类物质降解的特征酶和关键酶[125]。与此同时，在研究 2-氟苯甲酸盐降解机制时，Tiedt 等[115]还发现了 *Thaueraaromatica* 脱氟的另一条途径：2-F 苯甲酸被苯甲酸辅酶 A 连接酶激活后，生成的 2-F 苯甲基辅酶在 BCR 作用下开环，而后续的脱氟过程由烯酰基辅酶 A 水合酶/水解酶催化进行。新发现的烯酰基辅酶 A 水合酶通过形成 α 位-氟醇的脱氟路径，可能是一种具有代表性的酶促脱氟机制。尽管近年来微生物降解含氟有机物的研究取得了重要进展，然而降解机制和降解途径的多样性有待于进一步探讨，应特别关注微生物组或合成微生物群落对有机氟化物的高效降解途径及其机制。

5　展望

活性污泥微生物群落多样性、结构和功能决定了废水处理效率和工艺运行的稳定性。同时，废水特征、氟化物浓度和环境条件及工艺运行是微生物群落组装和动态变化的重要驱动力，从而影响其功能。但是，这些环境因子驱动微生物群落结构变化的生态机制尚不清楚；同时，许多研究涉及了纯培养和混合培养对有机氟化物的降解，而相关的降解途径和微生物代谢酶还需进一步探索[126-127]。微生物组学技术的快速发展将促进对复杂污泥微体系的了解，从而更好地认识含氟有机废水活性污泥处理中的微生物群体结构和功能。当前，含氟有机废水处理过程中活性污泥微生物组的相关研究将聚焦在下列几方面(图 4)：

(1) 解析活性污泥微生物群落多样性及其与生态系统功能和稳定性的关系

活性污泥中不同微生物在降解/转化污染和维持群落稳定方面发挥不同作用。处理不同含氟有机废水的活性污泥其微生物多样性和组成也不同，因而处理系统表现出不同的性能。运用宏基因组、宏转录组、宏蛋白组和宏代谢组多种组学技术，以活性污泥微生物群落为整体，揭示群落多样性与处理效率和稳定性的关系，为构建高效降解有机氟化物的微生物群落提供理论指导。

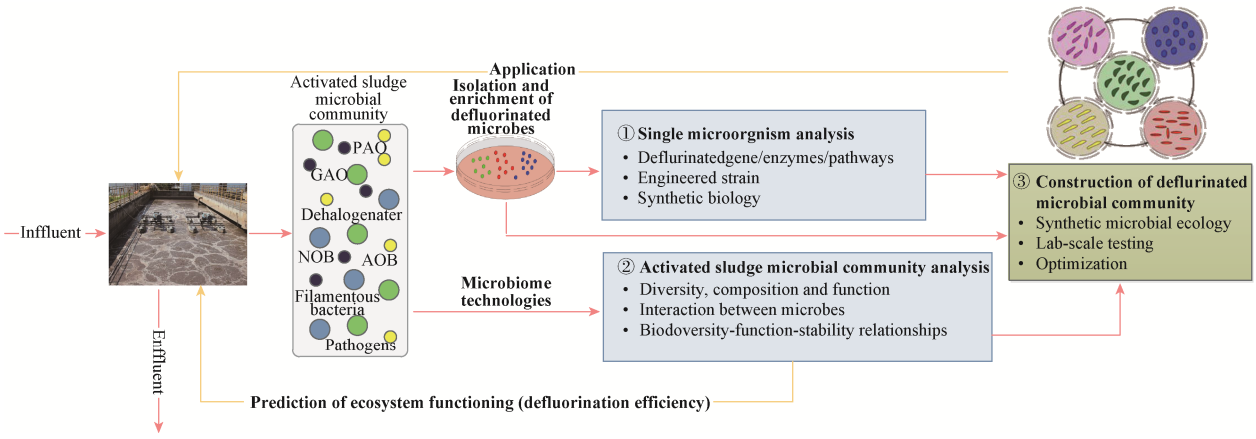

图 4　利用活性污泥微生物组技术提高含氟有机废水处理效果的概念图

Figure 4　A concept scheme for activated sludge microbiome technologies to improve fluoride-containing wastewater process performance

(2) 系统研究活性污泥中各类微生物的互作网络及其机制

在污染物降解方面，废水中污染物的降解通常由多种微生物互作完成。一方面，微生物组学(如宏基因组，宏代谢组)分析能获得含氟化合物降解微生物及功能基因、代谢产物和代谢途径的信息，为探索活性污泥微生物群落互作网络及其机制提供了数据；另一方面，运用计算机工具、数学模型、生物信息学技术和数据库平台[128]，可系统地模拟活性污泥微生物群落的动态变化，分析和预测关键微生物在时间和空间上对环境的响应，阐明活性污泥微生物群落的互作网络及其机制，明确其关键微生物和功能基因，为靶向富集分离提供依据。

(3) 富集分离降解/转化有机氟化物的关键功能微生物并揭示其机制

通过了解降解/转化氟化的关键功能微生物，继而利用相关基因组信息来设计[129]高效的富集培养方案，进而运用转录组学、蛋白组学、代谢组学等技术，探索其降解/转化有机氟化物的机理[130-131]。同时，通过对微生物遗传回路、代谢途径和酶进行工程设计，利用合成生物学技术进一步增强其功能[132]。

(4) 设计和构建高效脱氟的微生物群落，提高含氟有机废水处理效率

结合微生物生态学及合成微生物生态学理论和方法，选择具有降解含氟物质的功能菌株和相关菌群，以合适比例构建高效脱氟的微生物群落，从而改善活性污泥性能，提高微生物群落的功能，增强含氟有机物的去除效率。

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