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·综 述·

厌氧颗粒污泥微生物群落结构与功能的研究进展

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摘 要：厌氧颗粒污泥(anaerobic granular sludge, AnGS)是由多种功能微生物组成的自固定化聚集体，具有容积负荷高、工艺简单、剩余污泥产量低等优点，在废水处理领域中显示出巨大的技术和经济潜力，被认为是一种很有前景的低碳废水处理工艺。本文系统总结了近年来厌氧颗粒污泥微生物结构和功能的研究成果，从微生物学角度讨论了厌氧颗粒污泥形成及稳定的影响因素，并对今后厌氧颗粒污泥的研究进行了展望，以期为后续厌氧颗粒污泥技术的深入研究和实际工程应用提供参考。

关键词：厌氧颗粒污泥；厌氧消化；微生物；污水处理

Recent advances in the structure and function of microbial community in anaerobic granular sludge

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Abstract: Anaerobic granular sludge (AnGS), a self-immobilized aggregate containing various functional microorganisms, is considered as a promising green process for wastewater treatment. AnGS has the advantages of high volume loading rate, simple process and low excess sludge generation, thus shows great technological and economical potentials. This review systematically summarizes the recent advances of the microbial community structure and function of anaerobic granular sludge, and discusses the factors affecting the formation and stability of anaerobic granular sludge from the perspective of microbiology. Moreover, future research directions of

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AnGS are prospected. This review is expected to facilitate the research and engineering application of AnGS.

Keywords: anaerobic granular sludge; anaerobic digestion; microorganism; wastewater treatment

厌氧颗粒污泥(anaerobic granular sludge, AnGS)是微生物细胞自发聚集形成的球形生物膜，通常用于高浓度有机废水的厌氧消化[1]。广义上，厌氧颗粒污泥还包括厌氧氨氧化颗粒污泥和反硝化颗粒污泥等。近年来，厌氧颗粒污泥在生物制氢方面表现出优异潜力[2]。厌氧颗粒污泥主要由微生物、无机矿物及胞外多聚物(extracellular polymeric substance, EPS)组成，其中 EPS 可充当凝胶基质促进微生物聚集，并参与颗粒形成，保护内部微生物免受外部恶劣环境影响[3-5]。厌氧颗粒污泥与传统的絮体污泥相比，具有良好的沉降性能和相对稳定的微生物代谢活性[6]，被广泛应用于工业废水处理，已成为污水处理领域的研究热点[7-8]。

厌氧颗粒污泥具有空间分层的微生物结构和高生物保留量[1,9]，是一个复杂的小型生态系统，其形成和稳定需同时考虑水力条件、物理化学和微生物等因素[10-11]。目前已提出厌氧颗粒污泥形成和稳定的 4 步骤理论[12]：(1) 水力学、扩散力、重力、热力学和细胞流动性等物理运动促进细菌与细菌间接触或附着到固体表面；(2) 物理、化学或生物作用增强细胞与细胞或固体间相互吸引；(3) 分泌 EPS 增强微生物间相互黏附；(4) 水力剪切力进一步稳定颗粒的三维结构。

在过去几十年中，研究学者开展了许多关于厌氧颗粒污泥培养条件、影响因素及实际应用的研究，基于此开发出许多先进的厌氧颗粒污泥反应器，例如上流式厌氧污泥床(upflow anaerobic sludge blanket, UASB)反应器、内循环(internal circulation, IC)反应器和膨胀颗粒污泥床(expand granular sludge bed, EGSB)反应器[13]。然而，厌氧颗粒污泥的形成是一个长期且不稳定的过程，反应器的运行还需考虑温度、pH、水力停留时间(hydraulic retention time, HRT)、水力剪切力和基质浓度等操作参数对颗粒污泥去除性能和稳定性的影响，且目前对于厌氧颗粒污泥中微生物学信息仍缺乏系统的认知，这限制了人们对于厌氧颗粒污泥群落结构和功能的进一步了解。因此，本文对厌氧颗粒污泥中微生物群落结构和功能的研究现状进行综述，以期为厌氧颗粒污泥技术的深入研究和工程应用提供最新认识和技术支持。

1 接种污泥——厌氧颗粒污泥微生物群落的来源

由于厌氧颗粒污泥的可获得性十分有限，因此厌氧颗粒污泥通常通过接种絮体污泥来培养，而采用破碎生物膜和絮体污泥的混合接种可促进颗粒污泥的形成[14]。多数情况下，启动用的种泥应采用待处理废水进行驯化，如无法进行驯化，种泥的微生物多样性应尽可能高。且种泥的类型会直接影响厌氧消化中有机物的降解和甲烷化过程，采用多种接种物可提高厌氧消化中的甲烷产量[7,15]。例如，采用甲醇培养的污泥用于UASB接种可缩短厌氧颗粒污泥系统的启动时间；采用厌氧污泥和好氧污泥的混合污泥进行接种，可较早地启动厌氧消化反应器并促进造粒[16-17]，这可能是由于好氧微生物可去除废水中的溶解氧，有助于建立严格的厌氧环境。以上研究表明，微生物多样性越高的种泥似乎既可促进造粒，又可增强反应器性能。

此外，接种污泥在塑造整个微生物群落结

构和特定的生态系统功能方面也具有决定性的贡献[18]。Bovio 等[19]的研究发现，塑造绿弯菌门(Chloroflexi)中优势菌群的是接种污泥而不是废水成分，并会进一步影响绿弯菌门的群落多样性，而绿弯菌门细菌被认为与厌氧颗粒污泥的形成高度相关。Jannat 等[20]通过微生物网络分析不同微生物种泥对鱼类垃圾厌氧消化的影响，结果表明，种泥中存在的产甲烷菌决定了鱼类垃圾厌氧消化过程的微生物功能，选择适当的种泥有助于构建更加特异且稳定的微生物群落结构，从而获得更高的甲烷产量。也有报道称，同一类型的反应器在接种不同来源的污泥后会形成不同的微生物群落结构，但都含有处理该废水特定的功能菌和基因[21]。因此如果接种污泥中含有更多与厌氧污泥颗粒化或处理特定废水相关的功能菌，可能会加快厌氧污泥颗粒化过程。

总的来说，接种污泥为厌氧颗粒污泥提供微生物来源，并与待处理废水的性质共同影响厌氧颗粒污泥的形成过程，因此在厌氧污泥颗粒化的进一步研究中应考虑反应器接种污泥微生物群落的一致性，这可能是影响厌氧颗粒污泥群落结构的一个重要因素[22]。

2 厌氧颗粒污泥形成过程中微生物群落结构动态变化

尽管在厌氧污泥颗粒化方面已进行了大量研究，研究学者提出了许多描述颗粒形成的假说和模型，但颗粒形成的机理仍未达成共识，厌氧污泥颗粒化似乎只是一种自发的微生物进化过程，在其生长过程中微生物群落结构会发生显著变化[7]。初始的厌氧颗粒污泥主要由丝状或杆状菌组成，这类细菌可首先形成骨架来维持颗粒结构，而成熟的厌氧颗粒污泥主要由球状菌构成[23]。且基于不同生长期的厌氧颗粒污泥微生物群落研究发现，不同功能作用的微生物在颗粒形成的不同时期占据主导地位，在颗粒形成末期可检测出许多不活跃的微生物，但它们可能在颗粒生长的某个时期是活跃的，也是颗粒结构完整性所必须的[24]。例如，含有高比例产酸微生物[如链球菌科(Streptococcaceae)]的群落和陶厄氏菌属(*Thauera*)，前者可为产甲烷菌和共生群落提供更简单的底物，后者可参与 EPS 的产生，这些细菌主要存在于厌氧颗粒污泥形成初期，被认为在厌氧颗粒污泥形成初期发挥重要作用[24-25]。

以往关于厌氧颗粒污泥微生物群落结构变化的研究主要集中在颗粒污泥形成(污泥颗粒化)过程，但颗粒形成后不可能长时间存在，它们会不断生长并分裂解体[26]，因此颗粒全生命周期(即颗粒形成、解体和再颗粒化)的微生物群落结构变化研究需进一步加深。事实上，厌氧颗粒污泥解体导致的内部微生物释放很大程度上会影响颗粒形成和微生物多样性，且合作和互惠关系被认为是厌氧颗粒污泥微生物群落多样性的驱动因素，这种相互作用也可促进物种的高丰富度并增强群落稳定性[27-28]。通常这种互补代谢关系需初级消费者(如产酸/发酵菌)的定殖并促进次级消费者(如产甲烷菌)的演替，逐渐形成群落多样性，而在再颗粒化过程中，老颗粒和解体颗粒重新聚集在一起形成新的颗粒，似乎可以加快群落演替过程，更快地形成稳定的微生物群落。

对厌氧颗粒污泥形成过程中微生物群落的动态变化很少有生态学方面的解释，此前对复杂微生物群落演替模式的相关研究表明，微生物群落对营养物改变(即种泥接种到新反应器中)的响应主要由随机性过程控制，即确切的演替轨迹是不可预测的，但由于随机性过程和确定性过程在群落演替中都发挥着重要作用，且它

们的相对重要性与时间相关，如果确定性过程在演替的最后阶段发挥更大作用，则最终的群落状态似乎可得到预测[29]。也有研究表明，在初始厌氧颗粒污泥形成后，微生物群落的确定性影响会随着颗粒大小的增大而增大[24]。总之，厌氧颗粒污泥形成过程中群落演替受到多方面的影响，如何通过调整系统条件(包括接种污泥、废水性质及运行条件)加强确定性过程并预测其演替轨迹还有待后续深入研究。

3　厌氧颗粒污泥中微生物群落组成

通常来说，来自不同污水处理厂的厌氧颗粒污泥微生物群落结构存在显著差异，这可能是由于废水性质、反应器构造及运行工况不同所造成的[30]。厌氧颗粒污泥中微生物在细菌门水平主要包含绿弯菌门、变形菌门(Proteobacteria)、拟杆菌门(Bacteroidetes)及厚壁菌门(Firmicutes)[31-32]。其中，丝状绿弯菌门细菌可在其他微生物周围的层间生长，促进厌氧颗粒污泥的形成和稳定[33]，且由于其作为网状结构被其他微生物包围，这使得它们在颗粒生长过程中得以保留，这也是厌氧颗粒污泥中绿弯菌门细菌含量比絮体高的主要原因[19]；此外，绿弯菌门细菌的丰度与反应器有机负荷呈正相关，因此过高的有机负荷可能会导致绿弯菌门细菌的过量生长，并进一步诱发污泥膨胀[34]。变形菌门细菌主要与小分子化合物的利用有关[33]，其中动胶菌属(*Zoogloea*)细菌还可分泌EPS，有利于厌氧颗粒污泥的形成[35]。拟杆菌门中主要有产酸菌、糖发酵菌、糖酵解菌和蛋白质水解菌，主要生成丙酸盐、乙酸盐和琥珀酸盐，被认为在有机物的水解和酸化过程中起着重要作用[36]，其丰度与有机物的浓度高度相关，在厌氧消化反应器的丰度可达到 50%以上，而在厌氧氨氧化反应器中的丰度只有 10%左右[37-38]；此外，拟杆菌门还可附着在厌氧颗粒污泥外层，以增强颗粒结构[39]。厚壁菌门细菌主要与复杂聚合物的降解有关，是厌氧消化过程水解阶段的重要参与者，其数量与水力剪切力高度相关，相较于其他微生物，厚壁菌门细菌更易在较高水力剪切力下被冲走，适当的水力剪切力有利于厚壁菌门细菌的生长[40]。

厌氧消化反应器中还有一类含量较高的微生物，即产甲烷菌，隶属于广古菌门(Euryarchaeota)，主要分为氢营养型、甲基营养型和乙酸营养型(表 1)[41-47]，其中鬃毛甲烷菌属(*Methanosaeta*)和甲烷杆菌属(*Methanobacterium*)是厌氧消化反应器中常见的产甲烷菌属[48]，前者属于乙酸营养型产甲烷菌，可在健康的厌氧颗粒污泥中形成簇，有助于固定功能微生物[49]，还可通过产生 EPS 来捕获其他微生物，在厌氧污泥颗粒化中发挥重要作用[50-51]；后者属于氢营养型产甲烷菌，其丰度越高，反应器对外界不利条件的耐受性也越强[48]。

为了更具体地描述厌氧颗粒污泥中的微生物种群，作者收集了近些年关于厌氧颗粒污泥研究在科水平上的群落数据，使用Gephi软件[52]对收集的信息进行网络分析(图 1)[30,36,53-61]。从图 1可以看出，紫单胞菌科(Porphyromonadaceae)、厌氧生菌科(Anaerolineaceae)、螺旋体科(Spirochaetaceae)、拟杆菌科(Bacteroidaceae)、脱硫弧菌科(Desulfovibrionaceae)、瘤胃菌科(Ruminococcaceae)和互营菌科(Syntrophaceae)等细菌科在厌氧颗粒污泥中出现的频次最高，但即使是出现频次最高的 Porphyromonadaceae 其占比也不超过总体样本的 50%，说明不同的厌氧颗粒污泥具有不同的细菌群落核心，这与好氧颗粒污泥不同：不同运行条件下的好氧颗粒通常拥有 1 个共同的核心细菌群落，并具有相

似的功能[62]。这可能是由于厌氧条件下，颗粒的形成与稳定更依赖于细菌与古菌间的互营共生作用，而不同的运行条件会形成不同的优势古菌，从而形成不同的细菌群落核心。因此，后续对厌氧颗粒污泥形成与稳定的研究应关注不同条件下核心功能微生物的群落差异，这将有助于探究厌氧颗粒污泥形成及稳定的作用机理。

4 厌氧颗粒污泥中微生物群落的空间分布

厌氧颗粒污泥的微生物空间结构对颗粒生长起着至关重要的作用，一般而言，生长于中温条件下的厌氧颗粒污泥具有 3 层微生物结构(图 2A)，外层由大小不一的杆状、球状和丝状菌组成，主要功能菌是产酸菌和氢营养型产甲烷菌；中间层主要由杆状菌组成，主要功能菌为产氢产乙酸菌、氢营养型产甲烷菌及乙酸营养型产甲烷菌；内层则以球状乙酸营养型产甲烷菌为主[63-65]。厌氧颗粒污泥的空间分层现象可使微生物的不同营养组在其生态位上更好地发挥作用，这些生态位可沿着生物膜中电子供体和受体产生的氧化还原梯度及其他溶质产生的不同渗透深度和梯度来实现，不同营养组可沿着这些生态位生长、合作、互动或竞争，这种合作、互动或竞争能够促进厌氧颗粒污泥的形成和生物量的增加[1,66]。这种分层现象也存在于厌氧氨氧化颗粒污泥中，一般而言，厌氧氨氧化菌无法在纯培养体系中获得，它们通常与厌氧氨氧化颗粒污泥中的其他微生物处于共生关系，例如在单级短程硝化-厌氧氨氧化颗粒污泥体系中，氨氧化菌主要聚集在氧气较多的颗粒外层，而厌氧氨氧化菌则主要集中在严格厌氧的内层(图 2B)[67-68]。总之，相对于其他类型污泥，厌氧颗粒污泥实现了最有效的互营共生关系，污泥空间结构在促进良好的互营共生关系中发挥重要作用，而这种多维相互作用能够增强群落稳定性并提高反应器性能[27-28]。

表 1　参与厌氧消化过程的主要古菌及其类别

Table 1　Main archaea and their categories involved in anaerobic digestion

Order	Family	Genus	Category
Methanosarcinales	Methanosaetaceae	*Methanothrix* (*Methanosaeta*)	Acetoclastic
	Methanosarcinaceae	*Methanosarcina*	Acetoclastic/Hydrogenotrophic/Methylotrophic
		Methanimicrococcus	Methylotrophic
		Methanolobus	Methylotrophic
		Methanomethylovorans	Methylotrophic
Methanomicrobiales	Methanomicrobiaceae	*Methanoculleus*	Hydrogenotrophic
	Methanoregulaceae	*Methanosphaerula*	Hydrogenotrophic
		Methanolinea	Hydrogenotrophic/Methlotrophic
	Methanocorpusculaceae	*Methanocorpusculum*	Hydrogenotrophic
Methanomassiliicoccales	Methanomassiliicoccaceae	*Methanomassiliicoccus*	Hydrogenotrophic/Methlotrophic
Methanobacteriales	Methanosprillaceae	*Methanospirillum*	Hydrogenotrophic
	Methanobacteriaceae	*Methanobacterium*	Hydrogenotrophic
		Methanobrevibacter	Hydrogenotrophic
		Methanothermobacter	Hydrogenotrophic
		Methanosphaera	Hydrogenotrophic/Methlotrophic

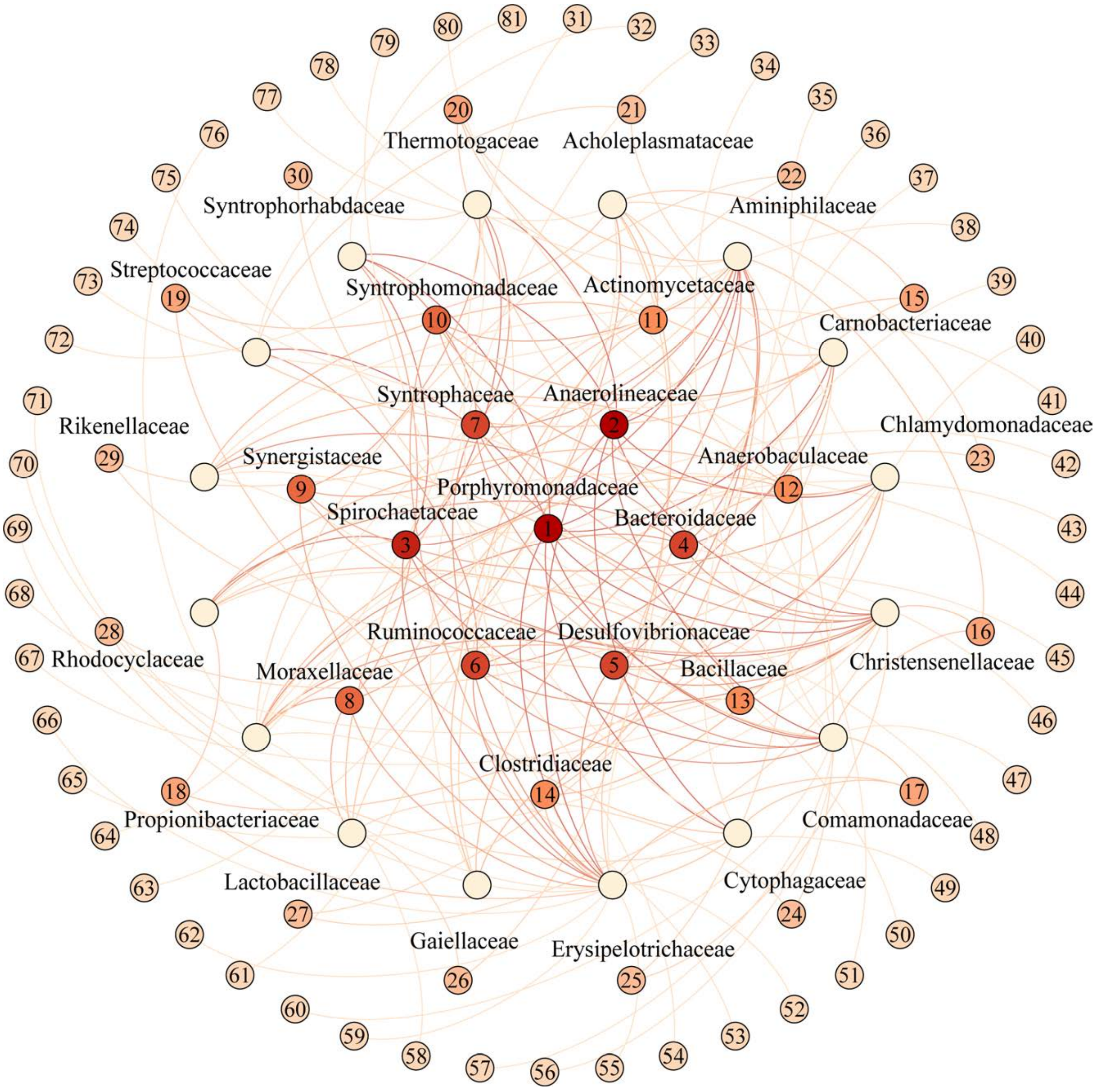

图 1　厌氧颗粒污泥的微生物群落组成示意图　图中显示厌氧颗粒污泥样本中每个细菌科存在的网络，不带数字的圆代表样本，带数字的圆代表细菌科，两圆间的连线表示样本中存在该细菌科. 圆颜色强度与连接的数量成正比，细菌科 31–81 的名称不予显示

Figure 1　Schematic overview of microbial community composition of anaerobic granular sludge. The figure shows the network of each bacterial family in anaerobic granular sludge sample. The circle without numbers represents the sample, the circle with numbers represents the bacterial family, and the line between the two circles represents the bacterial family in the sample. The color intensity of the circle is proportional to the number of connections, and the name of bacterial family 31−81 is not shown.

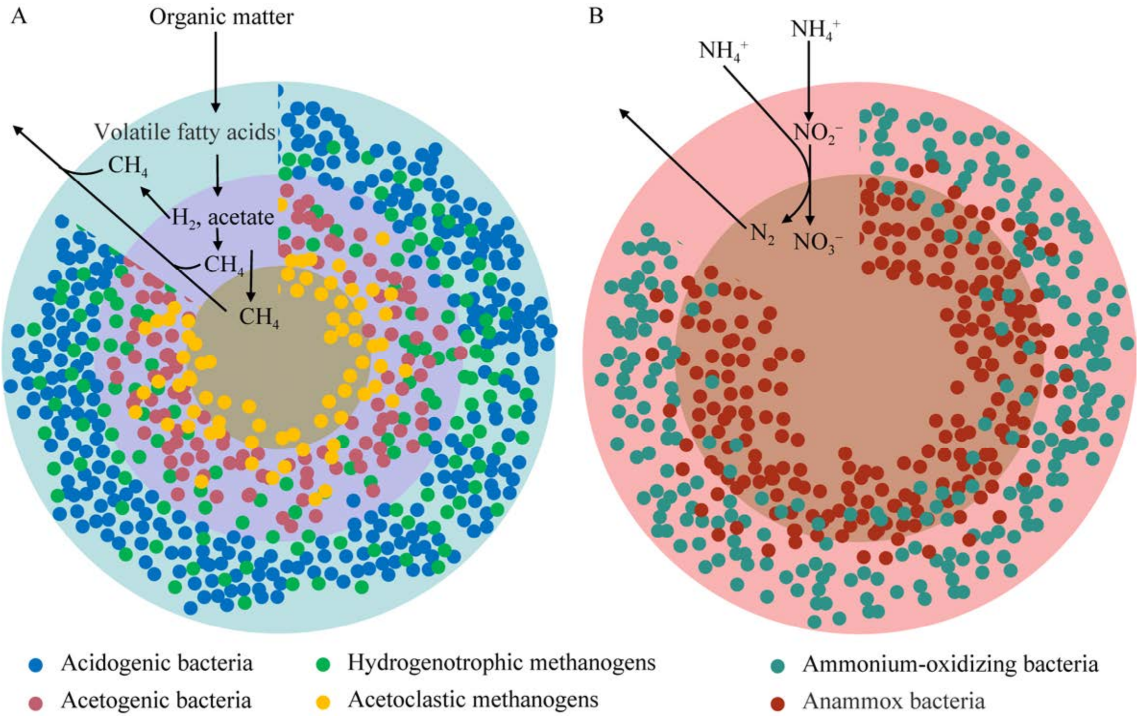

图 2　厌氧颗粒污泥微生物空间结构示意图　A：产甲烷颗粒污泥. B：短程硝化-厌氧氨氧化颗粒污泥
Figure 2　Schematic overview of spatial structure of microorganisms in anaerobic granular sludge. A: Methanogenic granular sludge. B: Partial nitrification-anammox granular sludge.

然而，有文献报道在高有机负载下，UASB 反应器中厌氧颗粒污泥并没有表现分层结构，微生物组成大多是同质的[69]，此外，Hou 等[70]的研究表明，序批次反应器(sequencing batch reactor, SBR)中形成的厌氧颗粒污泥具有独特的团簇结构，即大量产乙酸菌和产甲烷菌形成的互营微生物群落随机分布在颗粒内部，且颗粒内部存在的空腔便于基质传递和气体释放，这种团簇结构被认为是一种对互营微生物群落极佳的厌氧颗粒污泥空间结构。这些结果表明，不同运行条件下(如反应器构型、基质类型、有机负荷、温度和水力剪切力等)的厌氧颗粒污泥可能具有不同的空间结构。目前，对微生物群落空间分布影响因素的认知仍相对有限，未来还需进行更深入的研究。

5　影响厌氧颗粒污泥形成与稳定的因素——微生物学原理

5.1　有机负荷

有机负荷是厌氧污泥颗粒化最重要的控制参数之一，多项证据表明，厌氧污泥颗粒化是通过在反应器启动期间逐渐增加有机负荷来实现的，此外，在启动时选择适当的高有机负荷对厌氧颗粒污泥的稳定性也至关重要[71]。在厌氧颗粒污泥形成过程中增加有机负荷可促进 EPS 的积累，进而影响颗粒的强度和稳定性，增大污染物的去除效率[69,72]，相反，低有机负荷则会产生严重的传质限制，从而导致大颗粒的解体[73]。

此外，有机负荷的改变对厌氧颗粒污泥的微生物群落(包括古菌和细菌)也有显著影响，

微生物丰富度和均匀度会随着有机负荷的增加而急剧下降，表明微生物群落组成在受到高有机负荷冲击的压力下会变得更具特异性[74]。且在反应器受到高有机负荷冲击导致性能下降时，可通过调节有机负荷控制内源酰基高丝氨酸内酯(acylated homoserine lactones, AHLs)的产生，进而通过群体感应机制调节微生物的社会行为，协调各种功能微生物的相互作用，恢复受冲击反应器的性能[75-76]。此外，通过扫描电子显微镜观察发现，在低负荷反应器中，丝状菌在厌氧颗粒污泥中占据优势地位，而在高负荷反应器中，无论是在颗粒表面还是内部，都仅能发现杆状菌[59]。在古菌中，有机负荷的增加会导致乙酸营养型产甲烷菌(*Methanosaeta*)转变为甲烷八叠球菌属(*Methanosarcina*)，且与氢营养型产甲烷菌高度相关的厚壁菌门的丰度不断上升。这些结果说明，有机负荷对厌氧颗粒污泥反应器中微生物群落的变化具有实质性影响[77-78]。

从广义的厌氧颗粒污泥角度来看，厌氧氨氧化反应器似乎具有与厌氧消化反应器类似的核心功能微生物群落变化特性。已有研究表明，在不同氮负荷下，厌氧氨氧化颗粒污泥中的优势厌氧氨氧化菌属不同，*Candidatus* Kunenia 在高底物浓度下占优势，而 *Candidatus* Brocadia 在低底物浓度下占优势[79]，这与氢营养型产甲烷菌和乙酸营养型产甲烷菌在厌氧颗粒污泥中相对丰度的变化趋势类似。此外，Yuan 等[80]的研究表明，高氮负荷环境可能会抑制对游离铵和游离亚硝酸敏感细菌的生长，与这类敏感细菌互作的厌氧氨氧化菌的丰度也随之下降，从而导致优势厌氧氨氧化菌的转变，而在厌氧颗粒污泥中也存在类似的互作关系，有机负荷的变化也会导致产甲烷菌互营微生物丰度的变化，进而导致不同类型产甲烷菌丰度的变化。

此外，有机物成分也会显著影响厌氧颗粒污泥的微生物群落结构，包括变形菌门、厚壁菌门和拟杆菌门细菌占比的显著变化及优势产甲烷菌属的转变[81]。例如采用脂肪、油及油脂作为有机物进行厌氧消化时会产生较多乙酸盐，这将导致拥有更高半饱和常数(K_s)和最大比生长速率(μ_{max})的 *Methanosarcina* 产甲烷菌丰度逐渐超过 *Methanosaeta* 产甲烷菌；在细菌门水平上，变形菌门细菌的丰度显著下降，厚壁菌门和拟杆菌门细菌的丰度显著上升，这可能是由于厚壁菌门中包含多种可以降解不同底物并产生挥发性脂肪酸(volatile fatty acids, VAFs)的互营细菌，而拟杆菌门中的微生物含有多种能降解复杂有机物的酶[82-83]。

然而，采用单一底物厌氧消化的反应器通常存在气体产量低和稳定性差等问题。近年来，研究发现多种有机底物混合似乎能为厌氧颗粒污泥提供更加丰富且均衡的营养，能有效缓解这一问题，因此含有多种有机底物的厌氧共消化(anaerobic co-digestion, AcoD)理论逐渐成为研究热点[84]。通常情况下，采用富含蛋白质有机底物生产沼气时，由于其氨的过量生产会引发微生物抑制作用[85-86]，通过在屠宰场废水厌氧消化反应器中添加木质纤维素可维持氢营养型产甲烷菌的高丰度，从而缓解氨抑制导致的不稳定现象，且单一底物厌氧消化下较高的古菌多样性并不能保证厌氧消化的稳定性，更重要的是需要维持特定产甲烷菌及其互营细菌的高丰度[87]。此外，采用城市污泥和葡萄糖共消化的 UASB 反应器中甲烷生成量相对于城市污泥单独消化提高了 90%，大麦秸秆和猪粪共消化的最高产气量分别是大麦秸秆和猪粪单独消化的 1.7 倍和 1.6 倍[88-89]。总之，用于厌氧消化反应器的有机物需充分考虑其蛋白质、碳水化合物及脂质的配

比，可有效提高厌氧消化中产甲烷菌与互营细菌间的协同效应，减少中间代谢抑制物的积累，维持良好的产甲烷群落生态结构，进而提高甲烷产量和颗粒稳定性。

5.2 水流和产气的剪切力

在上流式反应器中，厌氧颗粒污泥的形成和稳定都会受到上升水流和气体表观速率的影响(如厌氧氨氧化颗粒污泥产生氮气、厌氧消化污泥产生甲烷)[90]。在选择压力理论中，上升水流产生的水力剪切力是主要的选择压力，通过不断增加选择压力，分散和不易沉降的污泥会被冲出反应器，较重的生物质则会被保留并聚集形成稳定的颗粒，因此适当的水力剪切力对厌氧颗粒污泥反应器的性能至关重要[91]。过高的水力剪切力会引起厌氧颗粒污泥的解体，进而导致污泥流失[92-93]；而较低的水力剪切力则会抑制传质，减少挥发性脂肪酸积累，从而导致厌氧消化反应器性能恶化[93]。此外，高有机负荷下剧烈的气体释放产生的剪切力也可导致颗粒部分解体，降低颗粒密度，诱发污泥上浮[94]。

由于厌氧颗粒污泥的性能与微生物群落结构具有强烈的关联作用，因此探究水力剪切力对厌氧颗粒污泥反应器微生物群落形成与维持的影响也至关重要。厌氧颗粒污泥在不同水力剪切力下通常具有相似的核心功能微生物群落组成，但它们的相对丰度会随着水力剪切力的变化而变化[95]，适当的水力剪切力可维持具有更高多样性和均匀性的微生物群落，特别是互营细菌丰度的增加，这与良好的反应器性能密切相关[96]。一般而言，水力剪切力的降低会导致变形菌门细菌富集并抑制绿弯菌门细菌生长，而绿弯菌门细菌对厌氧颗粒污泥的稳定性非常重要。而高水力剪切力(>8 m/h)会破坏细菌和产甲烷菌间的互营共生作用，被认为是反应器性能不佳的主要原因。当水流上升速度增加到 10 m/h 时，会发生显著的微生物群落绝对丰度和多样性的降低及群落结构的改变，包括乙酸营养型产甲烷菌丰度的降低和氢营养型产甲烷菌占比的提高[97-98]。

此外，研究表明细菌群落相比古菌群落对剪切力更敏感，由于厌氧颗粒污泥具有层状结构，古菌存在于内层，细菌存在于外层，因此，外层细菌会由于暴露在水力剪切力下，从而导致细菌群落结构的变化[99-100]。且在古菌中，丝状结构的甲烷鬃菌科(Methanosaetaceae)相比于球状结构的甲烷八叠球菌科(Methanosarcinaceae)对水力剪切力更敏感，这可归因于它们形态结构的不同[98]。

总之，水力剪切力作为提高反应器性能最重要的控制参数之一，在厌氧颗粒污泥形成、稳定及微生物群落构建中发挥重要作用，相比于高通量测序技术，宏基因组等先进技术可揭示各种环境条件下微生物间相互作用和生态功能关系[101]，有利于水力剪切力对厌氧颗粒污泥微生物群落结构与功能影响的深入研究。

5.3 温度

在厌氧颗粒污泥反应器运行过程中，温度可显著影响厌氧颗粒污泥微生物的活性，并通过改变发酵菌和产甲烷菌的种类和相对丰度来影响厌氧消化反应器性能[102]。有研究表明，尽管厌氧颗粒污泥反应器中的总操作分类单元(operational taxonomic units, OTU)超过 400，但能影响反应器性能的关键细菌和古菌始终低于 20 个 OTU[103]。大多数厌氧颗粒污泥反应器主要是在中温(25−45 ℃)或高温(45−65 ℃)条件下运行，温度过低会造成微生物生长缓慢、活性降低及难以形成颗粒等问题[104]。此外，微生物的相互作用也会影响厌氧颗粒污泥反应器的稳定性和性能，而温度在微生物相互作用中起着

至关重要的作用。Lin 等[105]采用共生网络分析和确定性与随机性相结合的方法，研究温度对厌氧消化过程中微生物相互作用的影响，结果表明，适合的温度能促进网络模块化和塑造微生物相互作用的确定性过程，从而加强厌氧消化过程的稳定性和污染物去除效率。

在多数文献的研究中均观察到温度的升高对微生物多样性的剧烈影响，这主要体现在中温到高温的转变过程中，通常在中温条件下，温度的变化并不会引发厌氧颗粒污泥微生物组成和代谢途径的变化，只有当温度超过 45 ℃时，古菌和细菌的多样性和绝对丰度才会随着温度的升高而降低，但颗粒仍能保持其完整性[106-108]。此外，从中温升至高温会导致产甲烷群落从 *Methanosaeta* sp. 主导转变为 *Methanocorpusculum* sp.主导，而在高温添加硫酸盐作为抑制剂的反应器中观察到 *Methanobacterium* 的主导地位，表明氢营养型产甲烷菌更能适应外界施加的不利条件，这可能是由于其具有更好的能量获取效率[109-110]。此外，作为种泥时，中温颗粒污泥能提供更快和更稳定的启动，且不同温度下形成的厌氧颗粒污泥似乎具有不同的空间结构，还需进一步研究[106,111]。

然而，大多数工业废水温度较低(≤18 ℃)，导致在中温或高温下运行厌氧消化反应器的加热成本过高，因此需探究低温下厌氧颗粒污泥的形成及稳定，特别是低温条件下培养的厌氧颗粒污泥中微生物社会行为及相互作用机制[112]。通常，只要保持核心功能微生物良好的活性及稳定的共生群落，就可维持颗粒的稳定性。然而，在低温条件下，厌氧颗粒污泥微生物群落多样性低，产甲烷菌活性难以维持，且这类微生物通常处在颗粒内部，其衰亡也会导致其他互营微生物的死亡，颗粒就容易在长期运行过程中解体，最终导致反应器性能恶化[103,113]。研究表明，低温条件下的微生物群落和代谢途径与中温条件下显著不同，由于甲烷微菌目(Methanomicrobiales)中氢营养型产甲烷菌对不利条件的高耐受性，可能在低温厌氧颗粒污泥系统中发挥重要作用，可通过促进这一群体的增长和保留来提高低温下反应器的运行稳定性；此外，低温还会导致紫单胞菌科(Porphyromonadaceae)和拟杆菌属(*Bacteroides*)等细菌的增加以及互营单胞菌属(*Syntrophomonas*)和梭菌属(*Clostridium*)等细菌的减少[114-116]。总的来说，低温下产甲烷菌丰度、活性及微生物之间互营共生作用的降低是厌氧颗粒污泥难以形成与稳定的主要原因，因此，如何在低温下保持核心功能微生物的活性和群落的稳定是将来研究的重点。

6 总结与展望

厌氧颗粒污泥工艺经过长时间的发展已广泛应用于工业废水处理，具有良好的经济效益和生态效益，是一种很有前景的低碳废水处理工艺。总结前人关于厌氧颗粒污泥微生物群落结构的研究发现，接种污泥可能在塑造整个微生物群落结构和特定的生态系统功能方面作出了决定性贡献，微生物间的互营共生作用对厌氧颗粒污泥的形成和稳定具有重要作用，高水力剪切力、有机负荷或低温会破坏厌氧颗粒污泥中微生物的互营共生作用，从而导致反应器性能下降，因此维持适当的微生物群落结构对厌氧颗粒污泥的稳定和反应器的高效运行至关重要。对于厌氧颗粒污泥的研究，目前仍有如下问题值得深入探究。

(1) 厌氧颗粒污泥微生物间存在复杂的互营共生作用，特别是产甲烷菌和周边微生物的互营共生作用对颗粒形成和稳定具有重要作

用。然而，在不同运行条件下，哪些微生物会发生互营共生作用及其对厌氧颗粒污泥的影响仍有待进一步研究。

(2) 核心功能微生物的生长在厌氧污泥颗粒化过程中发挥重要作用。因此，如何促进颗粒化前期核心功能微生物的快速生长及提高其活性值得后续深入研究。

(3) 虽然已有研究报道了厌氧颗粒污泥中微生物群落的基本信息，但仍需进一步了解厌氧颗粒污泥中的微生物生态学原理及厌氧污泥颗粒化的确切机制。

(4) 反应器运行条件(如有机负荷、温度、水力剪切力等)会显著影响厌氧颗粒污泥的形成、稳定及污染物去除效率。在实践中，需在了解微生物生态学原理的基础上，设计适合不同进水条件的生物反应器，以促进厌氧颗粒污泥技术在实际工程中的应用。

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