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Review 综　述

厌氧氨氧化菌火山口结构

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摘　要：厌氧氨氧化(anaerobic ammonium oxidation, anammox)是微生物学、地质学和环境学领域的重要反应，厌氧氨氧化菌(anaerobic ammonium-oxidizing bacteria, AnAOB)是厌氧氨氧化的驱动器，探明 AnAOB 的生物学性状对厌氧氨氧化的应用具有重要意义。火山口结构是 AnAOB 的标志性微观结构，也是 AnAOB 的重要识别特征。由于迄今没有获得 AnAOB 纯培养物，相关研究进展缓慢。本文对 AnAOB 及其所归属的浮霉状菌的火山口结构研究进展作了综述，探讨了火山口结构的形态特征、生理功能和生态意义，得出以下结论：(1) AnAOB 的火山口结构均匀分布在细胞表面，其直径约 5 nm；(2) AnAOB 的火山口结构推测向外可连通细胞外膜和内膜，向内可与厌氧氨氧化体膜相连，对于物质转运及转化具有重要意义；(3) 火山口结构具有遗传稳定性，其形成可能与鞭毛脱落相关；(4) AnAOB 的火山口结构可能通过促进细胞物质交流、信息通讯等在维持其生态位稳定方面起作用。

关键词：厌氧氨氧化菌；浮霉状菌；火山口结构；生理功能；生态意义

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Crateriform structure of anaerobic ammonium-oxidizing bacteria

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Abstract: Anaerobic ammonium oxidation (anammox) is an important reaction in microbiology, geology, and environmental science, and anaerobic ammonium-oxidizing bacteria (AnAOB) are usually regarded as the driver of anammox. Demonstrating the biological characteristics of AnAOB is a vital issue for the application of anammox. Crateriform structure is a special microstructure and has been identified as one of the key features of AnAOB. However, little is known about the crateriform structure of AnAOB due to the failure to isolate AnAOB. In this study, the research advances about the crateriform structure of AnAOB and *Planctomycetes* were reviewed in terms of morphological characteristics, physiological functions, and ecological effects. Conclusions can be drawn as follows: (1) The crateriform structure of AnAOB is uniformly distributed over the cell surface, with a diameter of about 5 nm. (2) The crateriform structure of AnAOB may connect cytoplasmic membrane, outer membrane, and anammoxosome membrane, and play a role in substrate transport. (3) The crateriform structure has genetic stability, and its formation may be related to flagellum degeneration. (4) The crateriform structure may serve to maintain the niche stability of AnAOB by promoting material exchange and communication between microorganisms.

Keywords: anaerobic ammonium-oxidizing bacteria (AnAOB); *Planctomycetes*; crateriform structure; physiological function; ecological effects

厌氧氨氧化菌(anaerobic ammonium-oxidizing bacteria, AnAOB)是一类在厌氧条件下将铵(NH_4^+)和亚硝酸盐(NO_2^-)转化为氮气(N_2)的化能自养型细菌[1]。AnAOB 广泛存在于自然和人工生态系统中，在地球氮素循环中发挥着重要作用[2]。据估计，AnAOB 所致的厌氧氨氧化(anaerobic ammonium oxidation, anammox)反应对全球氮素循环通量的贡献可达 50%以上[3]。另一方面，全球已成功运行的厌氧氨氧化脱氮工程已超过数百座，显示了巨大的应用价值[4]。

然而，AnAOB 生长缓慢，对环境条件敏感，迄今尚未获得纯培养物，严重制约了人们对其生物学性能研究的深入开展。AnAOB 是厌氧氨氧化的基石和驱动者，探明其生物学特性，无疑具有重要的科学和应用价值。目前，针对 AnAOB 细胞壁形态、细胞膜组成和细胞内结构的研究，已取得诸多进展[5-12]。然而，对 AnAOB 研究中常被视为重要识别特征的火山口结构却依然缺乏全面了解。

据伯杰氏细菌手册报道[13]，火山口结构仅发现于浮霉菌门的部分菌种中。因此，本文拟

以现有的文献报道为基础，探讨火山口结构的形态特征、生理功能和生态意义，以深化对AnAOB生物学性能的认识，推进厌氧氨氧化技术的应用。

1 火山口结构

细菌细胞壁通常表面平整，但少数细菌细胞壁上产生类似火山口的结构。火山口结构外大内小，呈漏斗状、碗状或筒状凹陷于细胞壁内，其直径一般为纳米级(小至5–7 nm，大至20–30 nm，甚至85 nm)。火山口结构可通过细胞表面负染后采用电子显微镜观察(图1)。

据文献报道，火山口结构是浮霉状菌细胞壁上的特征性结构，其直径和分布与浮霉状菌的种类有关[14]。在大小方面，大多数菌种的火山口结构只有一种尺寸，如大部分*Planctomyces*属的火山口结构呈碗状，口部直径为30–36 nm，底部直径为12 nm；*Singulisphaera acidiphila*的火山口结构呈筒状，直径25 nm[13]；也有少数菌种的火山口结构兼有两种尺寸，如*Tuwongella immobilis*细胞壁上同时分布着直径约为25 nm的小型筒状火山口结构以及口部直径85 nm、底部直径55 nm的大型碗状火山口结构[16]。在分布方面，一部分菌种的火山口结构均匀分布在细胞壁表面，如*Planctomyces bekefii*[17]和*Gemmata obscuriglobus*[18]；一部分菌种的火山口结构则集中分布在细胞一端，如*Blastopirellula marina*[19]和*Pirellula staleyi*[15]；还有一部分兼有两种尺寸火山口结构的菌种，如*Tuwongella immobilis*，小型火山口结构均匀分布在细胞壁上，密度约为50个/μm^2，而大型火山口结构则位于细胞一端且仅有1个[16]。部分浮霉状菌火山口结构的分布状况汇总于表1。

AnAOB隶属于浮霉状菌门，具有诸多独特的表观性状。据文献报道，AnAOB形态多样，多呈不规则的球状、卵状；大小在(0.7–1.1) μm×(1.1–1.3) μm[13]；具有异于常见细菌的区室结构。如图2所示，细胞从外到内被细胞质膜(cytoplasmic membrane)、胞浆内膜(intracytoplasmic membrane)和厌氧氨氧化体膜(anammoxosome membrane)分隔成3个部分，分别称为外室细胞质(paryphoplasm)、核糖细胞质(riboplasm)和厌氧氨氧化体(anammoxosome)[26]。细胞质膜外侧为细胞壁，S-层通过与细胞壁外膜的脂多糖偶联固定于细胞

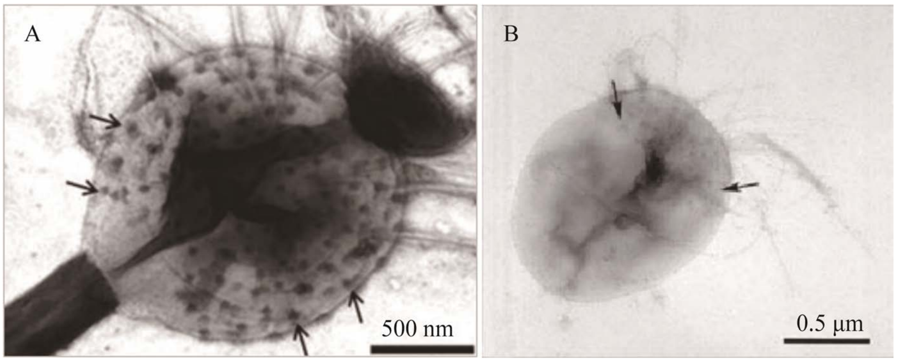

图1 透射电镜下经负染处理的浮霉状菌火山口结构[14-15]

Figure 1 Crateriform structures of *Planctomycetes* cells with negative stain under transmission electron microscopy[14-15]. A: Uniformly distributed crateriform structures of *Planctomyces bekefii*. B: Polarly distributed crateriform structures of *Pirellula staleyi*. The crateriform structures were indicated by the arrows.

表 1 浮霉状菌目(*Planctomycetales*)各种细菌的火山口结构分布状况

Table 1 Distribution of crateriform structure in *Planctomycetales*

Genus	Species	Distribution of crateriform structure	References
Planctomyces	*bekefii*	Uniformly distributed over the cell surface	[17]
Gemmata	*obscuriglobus*	Uniformly distributed over the cell surface	[18]
Isosphaera	*pallida*	Uniformly distributed over the cell surface	[19]
Zavarzinella	*formosa*	Uniformly distributed over the cell surface	[20]
Singulisphaera	*acidiphila*	Uniformly distributed over the cell surface	[21]
Pirellula	*staleyi*	Distributed over the upper half of the cell	[15]
Schlesneria	*paludicola*	Polarly distributed and covered approximately one-third of the cell surface	[22]
Blastopirellula	*marina*	Distributed at the reproductive pole	[23]
Rhodopirellula	*baltica*	Distributed at the reproductive pole	[24]
Tuwongella	*immobilis*	A single, large crateriform structure is distributed at one pole, while the small crateriform structures are uniformly distributed over the cell surface	[16]

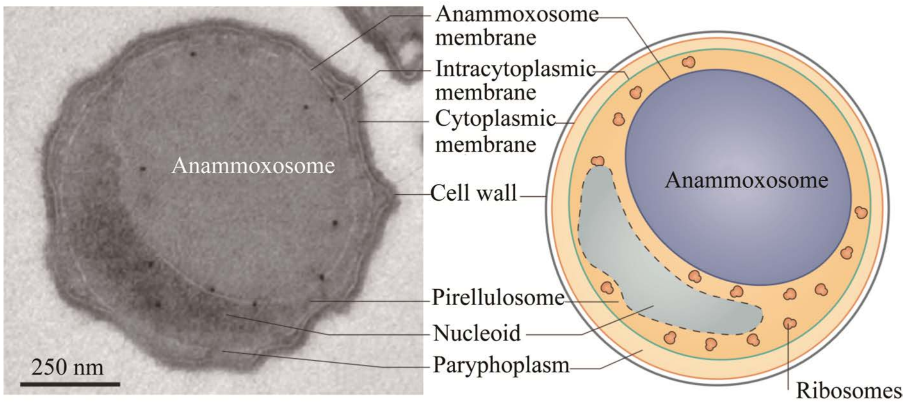

图 2 厌氧氨氧化菌的细胞形态及结构模型[25]

Figure 2 Cell morphology and structural model of AnAOB[25].

壁的最外层[27]。除此之外，部分 AnAOB 细胞表面均匀分布着纤维状附属物，诸如 *Candidatus* Scalindua 的部分菌种表面长有菌毛[28]。

类似其他浮霉状菌，AnAOB 细胞壁表面亦分布着火山口结构。1999 年，Strous 等[5]通过细胞表面负染，在 AnAOB 细胞壁上首次观察到火山口结构(图 3)，其直径约 5 nm，均匀分布在细胞表面。自此以后，火山口结构在研究中常被当作识别 AnAOB 的重要特征，但关于 AnAOB 细胞表面火山口结构的研究却鲜有报道。

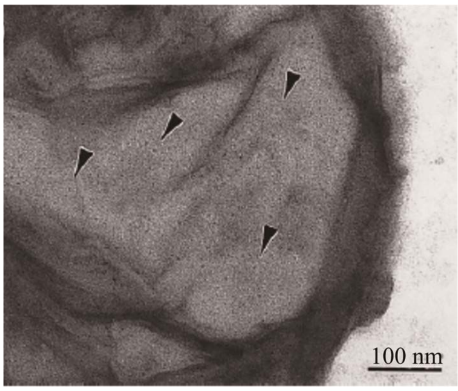

图 3 厌氧氨氧化菌的火山口结构(黑色箭头标识)[5]

Figure 3 Crateriform structures of AnAOB (indicated by the arrows)[5].

2 厌氧氨氧化菌火山口结构的生理功能

浮霉状菌细胞结构复杂，细胞质膜向内凹陷将细胞划分为不同的区室，形成类细胞器结构；细胞多以出芽方式繁殖，生长缓慢，倍增时间从6 h到1个月不等[29]。AnAOB是浮霉状菌门中分支很深的科，细胞结构更为复杂(图2)，以二分裂方式繁殖，倍增时间长达7–20 d[30]。

Boedeker等[31]对典型的浮霉状菌*Planctomyces limnophilus*进行了研究，借助超分辨率光学显微镜、低温电子断层扫描、生物信息学预测和蛋白质组分析等，重构了浮霉状菌的细胞结构模型。如图4A所示，火山口结构底部与细胞质膜紧密相连，向外可连通细胞外膜和内膜；在没有火山口结构的部位，细胞膜出现明显的内陷，形成较大的周质空间。据此分析，火山口结构可能与细胞的物质转运有关。如图4B所示，营养物质可通过火山口结构直接进入细胞质，参与代谢活动；也可先通过火山口结构进入扩大的周质空间中，再跨过细胞质膜进入细胞质参与代谢活动。由于包括AnAOB在内的浮霉状菌多为寡营养型细菌，推测火山口结构可辅助细胞在低浓度下对营养物质的吸收和对代谢废物的排泄。

值得特别关注的是，在AnAOB中，火山口结构的底部可向内与厌氧氨氧化体膜直接相连(图5)，该现象类似其他浮霉状菌火山口结构与细胞质膜的连通，起着类似真核细胞内质网的转运通道功能[32]。AnAOB内的厌氧氨氧化体则类似真核细胞内的线粒体，是能量转化的主要场所[33]。火山口结构的底部与厌氧氨氧化体膜直接连通对能源物质的转运及转化更具特殊意义。

浮霉状菌细胞壁上的火山口结构具有遗传稳定性。据报道，对于大多数浮霉状菌，其芽体火山口结构的形态和分布类同于母体[13]，仅有少数浮霉状菌表现出差异。例如，在*Rhodopirellula baltica*、*Blastopirellula marina*芽体上，火山口结构分布于整个细胞表面，而在母体上，火山口结构则仅分布于细胞生殖极一端[14]；但随着芽体的长大和成熟，其火山口结构逐渐增大，其分布也趋同于母体细胞[34]。值得一提的是，AnAOB的繁殖方式为二分裂，不同于传统浮霉状菌的出芽生殖。在AnAOB繁殖过程中，火山口结构起着什么作用？有待探索。

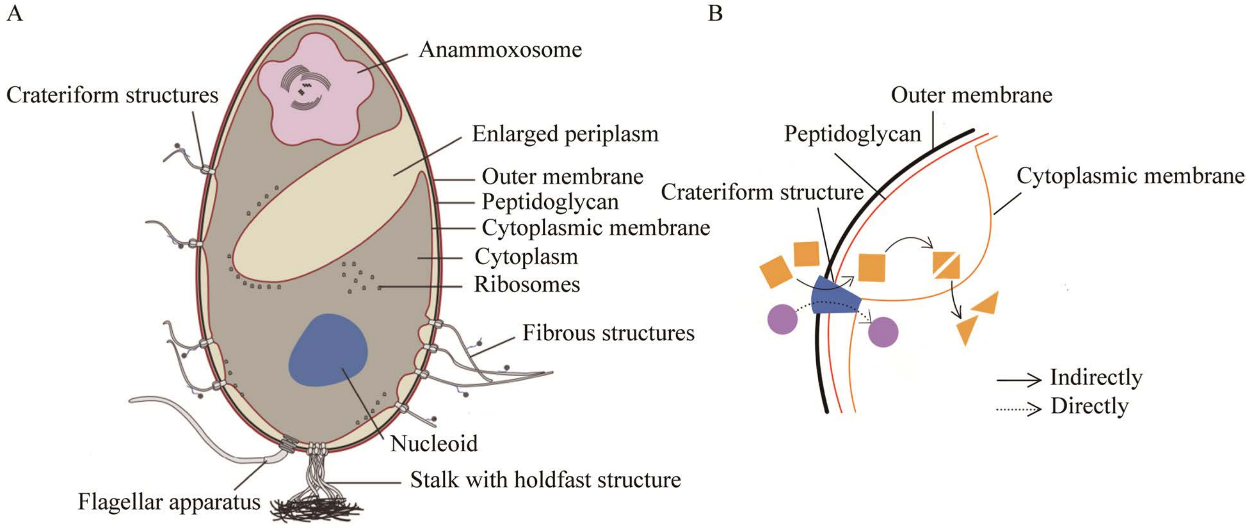

图4 浮霉状菌的细胞结构模型[31] (A)及火山口结构物质转运的假设模式(B)

Figure 4 Cell structure model of *Planctomycetes*[31] (A) and hypothesis model for the function of substrate transport by crateriform structure (B).

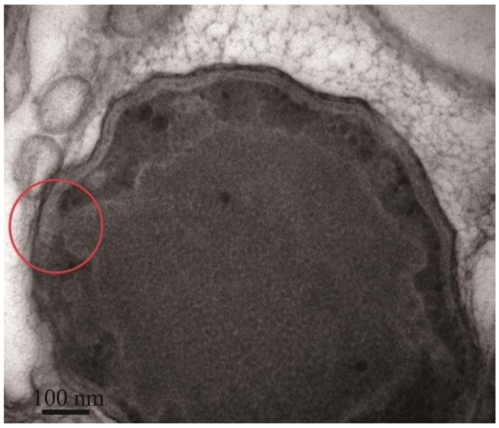

图 5　透射电镜下厌氧氨氧化菌的火山口结构(红圈标识)
Figure 5　Transmission electron microscopy (TEM) image of the crateriform structure in AnAOB (indicated by the red circle).

此外，据 Mahajan 等[16]报道，浮霉状菌 *Tuwongella immobilis* 的细胞表面同时分布着直径 25 nm 的火山口结构以及贯穿细胞质膜和细胞壁外膜的膜孔蛋白，且两者的位置均邻近鞭毛着生区域。这种火山口结构与鞭毛脱落有关吗？值得深究。

3　厌氧氨氧化菌火山口结构的生态意义

浮霉状菌广泛分布于海洋、淡水、陆地、极端和污染生境中，并与许多原核或真核生物伴生[35]。在自然界，AnAOB 也已发现于海洋[36]、淡水[37-38]、红树林[39]、水稻田[40]等一般生境中，以及海底热泉[41]、海洋冰块[42]、高温油藏[43]等极端生境中。为了应对自然生境的寡营养和极端条件，AnAOB 常聚集生活。据报道，只有在细胞密度高于 10^{10}–10^{11} 个/mL 时，AnAOB 才表现出显著的厌氧氨氧化活性[9]，即 AnAOB 存在密度依赖型群体感应(quorum sensing)[44]。另一方面，在富集培养过程中，AnAOB 常自我聚集而形成颗粒污泥[45]，颗粒增大到一定尺寸时又会解聚，即 AnAOB 存在生物团聚型群体感应[44]。

在 AnAOB 中，N-酰基-高丝氨酸内酯(acyl-homoserine lactone, AHLs)[46]和环二鸟苷酸(c-di-GMP)[47]是 2 种典型的群体感应信号分子，其中 AHLs 属于自诱导物，用于感受细胞密度，c-di-GMP 是第二信使分子，可调控胞外多聚物的合成，两者相互作用形成信号网络，起到调节细胞生理功能的作用。具体来说，在低细胞密度下，AHLs 浓度达不到与受体蛋白结合的阈值，受体蛋白会激活群体感应操纵子(AmxO)，促进编码群体感应监控核糖核酸(Qrr small regulatory RNAs, Qrr sRNAs)基因表达，Qrr sRNAs 抑制群体感应主导调节器(HapR，能抑制 c-di-GMP 功能)，c-di-GMP 激活翻译多糖 RNA，最终增强胞外多聚物的合成和分泌，引发 AnAOB 团聚；随着细胞密度增加，胞外 AHLs 浓度提高至阈值，与受体蛋白结合形成 AmxR-AHL 复合物，终止 Qrr sRNAs 转录，开启厌氧氨氧化相关基因表达[48-49]。

在 AnAOB 团聚体中，外部细胞对内部细胞具有屏蔽效应，导致内部细胞的生长繁殖受限，在寡营养生境中，这种屏弊效应将更为严重。分析认为火山口结构与植物细胞的胞间连丝、动物细胞的间隙连接和纳米管、真菌的隔膜等结构有一定的相似性[50]，其存在可有助于相邻细胞间的物质交流，传递并平衡遗传物质、蛋白、氨基酸、营养物质和化学信号等的含量，利于细胞之间的协同代谢，缓解外部细胞对内部细胞的屏蔽效应，维持其生态位稳定。火山口结构具体如何在 AnAOB 生态位选择上、生态效应调节上发挥作用亟待探究。

4　小结与展望

火山口结构是 AnAOB 的标志性结构，基于浮霉状菌的火山口结构，可理解浮霉状菌的物质

转运和细胞之间的物质交流，并由此解析AnAOB 的寡营养生长和细胞团聚现象。但对AnAOB 的火山口结构，仍有诸多方面值得深入研究：(1) 利用精确的分析技术，测定火山口结构的组成；(2) 借助先进的显微技术，确定细胞壁火山口结构及其与细胞内其他结构的联系；(3) 凭借特异性的分子标记技术，探明火山口结构的物质转运和信息交流功能。获得 AnAOB 新知，推进厌氧氨氧化的研究和应用。

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