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Review 综 述

获取有机物厌氧降解产甲烷过程中关键功能类群——互营细菌培养物

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摘要：互营代谢是微生物之间的重要种间互作关系之一，参与互营代谢的微生物广泛存在于土壤、淡水和海水沉积物、厌氧消化反应器、动物肠道和极端环境中(如地下油藏)，在有机物厌氧降解转化为二氧化碳和甲烷的过程中发挥着关键性的作用。研究互营细菌的物质代谢和能量传递的分子机制，对认识缺氧环境中的元素生物地球化学循环具有重要意义，也为解决全球能源危机、缓解气候变暖提供理论指导。但是，互营细菌生长缓慢、对氧气敏感，其分离培养的难度大。本文主要回顾了互营细菌的分离策略及其生理生化特征，展望了互营细菌分离培养的发展趋势，并指出以高通量筛选与定向分离相结合的方法，获得具有特定生理生态学功能的互营细菌，是互营微生物资源和分类学研究的发展方向。

关键词：互营细菌，产甲烷，高通量筛选，定向分离

“互营”是微生物“互惠共生”的一种互作方式，传统上特指厌氧产氢产乙酸菌和耗氢的产甲烷古菌共代谢、克服化学反应过程中不可逾越能差的步骤，是有机物厌氧降解为二氧化碳和甲烷的过程的关键环节[1]。互营代谢普遍发生在土壤、厌氧反应器、动物肠道、淡水和海水沉积物、泥炭、盐碱湖和油藏等缺氧环境中[2–5]。深入研究互营细菌的微生物学特征，对于认识元素生物地球化学循环、缓解温室效应和解决能源危机等，都具有重要的理论和实践意义，而获得纯培养物是开展互营细菌分子代谢机理研究的重要前提。

地球上微生物总数可能达到了4×10^{30}–6×10^{30}个[6]。随着高通量测序技术的发展，科学家推测微生物的物种数可能高达10^{6}–10^{12}个[7–9]，构成了1500个门[9]。但由于营养条件的限制，大部分微生物尚未获得纯培养物[10]。受限于生化反应的热力学限制，互营细菌分离培养的难度更大，迄今只报道了40多个物种(图1)[11]。因此，本文总结了互营细菌的生

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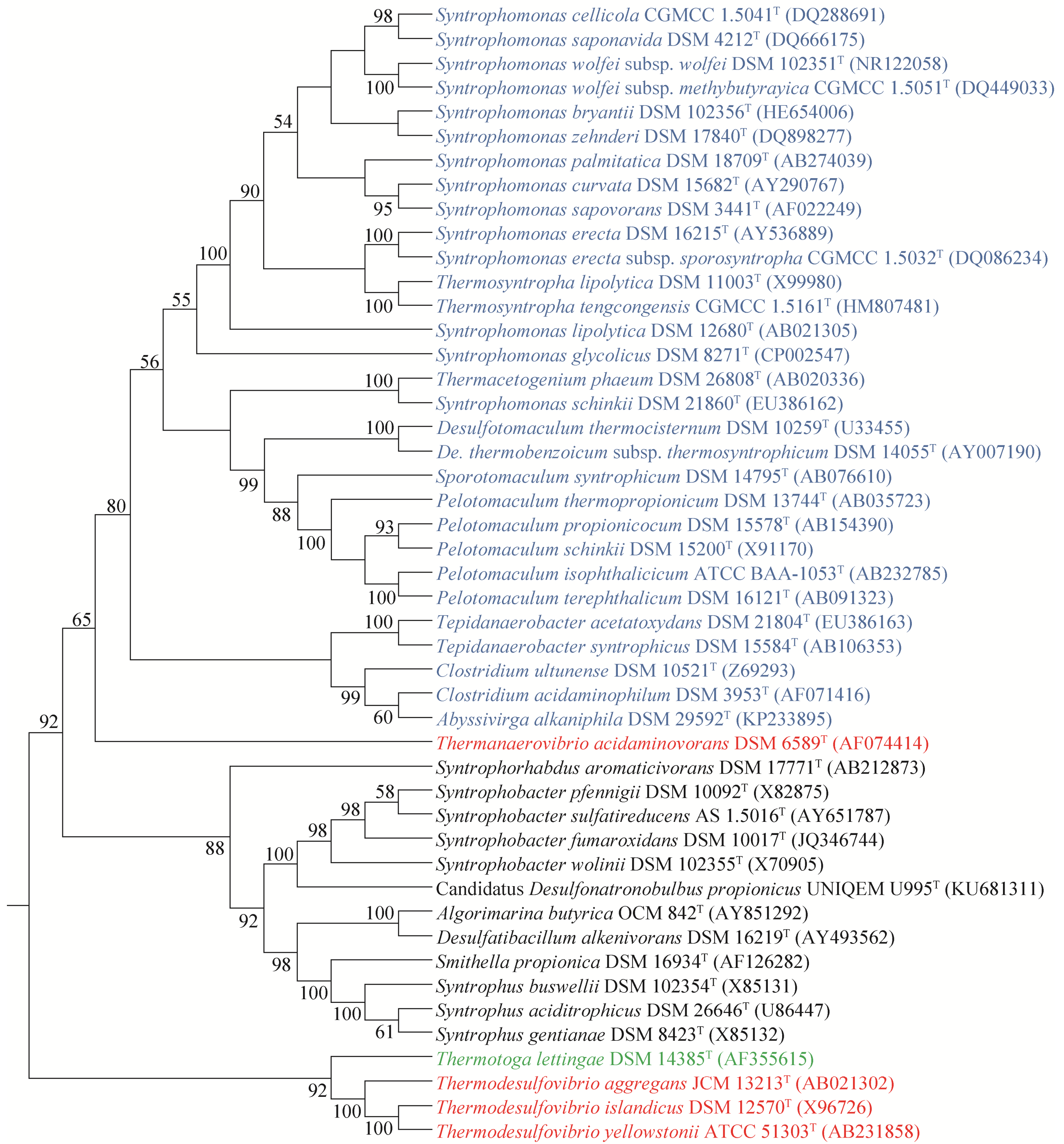

图 1. 基于 16S rRNA 基因的互营细菌系统发育树

Figure 1. Phylogenetic tree of syntrophic bacteria based on 16S rRNA genes of type strains.

理生化特征和分离方法，分析了限制互营细菌分离培养的主要因素，提出在微生物分子生态学技术的指导下，应用高通量筛选和定向分离方法分离互营菌是未来互营微生物资源和分类学研究的发展趋势。

1 互营代谢产甲烷过程的热力学特征

互营代谢最早用来定义光合绿硫细菌和化能自养硫还原细菌合作利用硫化物[12]，随后这个概念被 Mclnerney 等引用到脂肪酸降解产甲烷过程中，表示脂肪酸氧化细菌和氢营养型产甲烷古菌之间合作利用氢和甲酸的过程[13]。现在的主流观点认为互营代谢是指厌氧细菌和产甲烷古菌紧密合作，通过种间氢/甲酸转移突破热力学屏障，完成脂肪酸厌氧氧化代谢过程[3,14]。从生化反应的热力学角度分析，当不存在外源电子受体时，脂肪酸等高度还原性有机物的"厌氧发酵"产氢产乙酸过程，在标准热力学条件下的吉布斯自由能(ΔG^{0}')几乎均为正值(表 1)，不能自发进行(即吸能反应)。但是当这些产氢产乙酸反应产生的氢气被产甲烷古菌消耗后则可降低至帕级氢分压，脂肪酸互营代谢产甲烷反应的 ΔG 转变为负值，反应自发进行。这种通过"种间氢转移"的互营代谢产甲烷过程，是有机质厌氧代谢的经典方式。此外，互营细菌和产甲烷古菌之间，还可以通过种间电子传递的方式进行产甲烷代谢[11,15]。当然，也有科学家认为这种关系不能仅限于种间氢、甲酸或电子转移，还应该包括有机含氮、有机硫化合物的降解，可以定义为"严格共生代谢"[16]。本文阐述的互营代谢，是指互营细菌降解脂肪酸、烃、醇类、芳香族化合物和氨基酸等物质的产甲烷过程。

表 1. 互营有机物降解产甲烷过程中的吉布斯自由能变化

Table 1. Change in Gibbs free energy values for reactions potentially involved in methanogenic degradation of organic compounds

Substrates		Reactions	ΔG^{0}'(kJ/mol)	Reference
Anaerobic oxidation				
Short chain fatty acids	CH_3COOH	$CH_3COO^- + H^+ + 2H_2O \rightarrow 2CO_2 + 4H_2$	95	[17]
	CH_3CH_2COOH	$CH_3CH_2COO^- + 2H_2O \rightarrow CH_3COO^- + CO_2 + 3H_2$	72	
	$C_4H_8O_2$	$C_4H_7O_2^- + 2H_2O \rightarrow 2CH_3COO^- + H^+ + 2H_2$	49	
Long chain fatty acids	$C_{18}H_{32}O_2$	$C_{18}H_{31}O_2^- + 16H_2O \rightarrow 9CH_3COO^- + 14H_2 + 8H^+$	272	[18]
	$C_{18}H_{34}O_2$	$C_{18}H_{33}O_2^- + 16H_2O \rightarrow 9CH_3COO^- + 15H_2 + 8H^+$	338	
	$C_{18}H_{36}O_2$	$C_{18}H_{35}O_2^- + 16H_2O \rightarrow 9CH_3COO^- + 16H_2 + 8H^+$	404	
	$C_{16}H_{32}O_2$	$C_{16}H_{31}O_2^- + 14H_2O \rightarrow 8CH_3COO^- + 14H_2 + 7H^+$	353	
Lactate	$CH_3CH(OH)COOH$	$CH_3CH(OH)COO^- + 2H_2O \rightarrow CH_3COO^- + 2H_2 + H^+ + HCO_3^-$	–4	[19]
Alcohol	CH_3CH_2OH	$CH_3CH_2OH + H_2O \rightarrow CH_3COO^- + 2H_2 + H^+$	9	[3]
Amino acid	$C_3H_7NO_2$	$C_3H_7NO_2 + 2H_2O \rightarrow CH_3COO^- + 2H_2 + CO_2 + NH_4^+$	10	[20]
Alkane	$C_{16}H_{34}$	$4C_{16}H_{34} + 64H_2O \rightarrow 32CH_3COO^- + 68H_2 + 32H^+$	471	[21]
Aromatics	C_6H_5COOH	$4C_6H_5COO^- + 6H_2O \rightarrow 3CH_3COO^- + CO_2 + 2H^+ + 3H_2$	50	[20]
	C_6H_6O	$C_6H_6O + 5H_2O \rightarrow 3CH_3COO^- + 3H^+ + 2H_2$	10	
Methanogenesis				
H_2		$4H_2 + CO_2 \rightarrow CH_4 + 2H_2O$	–131	[20]
CH_3COOH		$CH_3COOH + 2H_2O \rightarrow CH_4 + HCO_3^-$	–31	[19]
HCOOH		$4HCOOH + H_2O \rightarrow CH_4 + 3HCO_3^-$	–130	

2 互营细菌多样性研究进展

截止目前，分离报道的互营细菌仅有 47 种，主要分布在厚壁菌门(Firmicutes)和变形菌门(Proteobacteria) (图 1)。除去依赖产甲烷古菌的 4 个属共 7 个种的细菌外(*Pelotomaculum*、*Syntrophomonas*、*Algorimarina* 和 *Syntrophorhabdus*)，其他 40 个都可以单独培养，其中有 33 个利用巴豆酸或丙酮酸等高氧化还原电势化合物生长(表 2)。当与产甲烷古菌共培养，这些微生物可以互营利用有机酸、醇类、脂类、烃类以及氨基酸等生长(表 2)。其中互营代谢脂肪酸的物种最多(共有 33 个)，它们主要分离自厌氧反应器(表 2)[3]，这表明互营脂肪酸降解菌在厌氧消化过程中发挥着重要作用。互营丁酸降解菌(14 个种)能降解更长链的脂肪酸，但是不具有丙酸和乙酸降解能力。互营丙酸和乙酸降解菌分别有 12 和 5 个物种，但是也不具备另外两种短链脂肪酸降解功能(表 2)，这可能与它们利用不同的降解途径有关。此外，有 7 种互营细菌可以利用苯甲酸盐，5 种可以互营代谢醇类，各有 2 种分别互营代谢氨基酸和正构烷烃(表 2)。64%的互营细菌属于革兰氏阴性菌，28%为革兰氏阳性菌，剩余部分革兰氏染色可变(表 2)。已知的互营细菌中有 30 个物种属于中温菌(最适生长温度 20–50 °C)，12 种属于高温菌(最适生长温度>50 °C)，仅有一种互营丁酸/异丁酸降解菌 *Algorimarina butyrica* 属于低温菌，最适生长温度为 15 °C，另外有 4 个物种的生长温度未见详细报道(表 2)。已知互营细菌最低生长温度为 10 °C，最高为 75 °C，这表明极端温度条件下(如永冻土和高温油藏)的互营细菌分离工作可能更为困难。互营细菌对生长营养要求并不高，大多数互营细菌的培养不需要额外添加生长刺激因子(表 2)。

Syntrophomonas 包含的互营细菌物种数最多，有 8 个种和 2 个亚种，都具有互营长链脂肪酸(C_4 及以上)降解功能，最适生长温度在 30–40 °C 之间(表 2)。含有 4 个种的 *Syntrophobacter* 均为中温互营丙酸降解菌，当存在硫酸盐和延胡索酸盐时，它们可以单独利用丙酸生长(表 2)。*Syntrophobacter fumaroxidans* 纯培养情况下的底物代谢种类最多，可以利用氢气、苹果酸盐、琥珀酸盐、延胡索酸盐和丙酮酸盐生长[22]。*Pelotomaculum* 中有 5 种互营细菌，它们互营代谢的底物比较复杂，*Pelotomaculum isophthalicicum* 和 *Pelotomaculum terephthalicum* 互营代谢苯甲酸等芳香族化合物，*Pelotomaculum propionicicum* 和 *Pelotomaculum schinkii* 互营代谢丙酸，*Pelotomaculum thermopropionicum* 除了利用丙酸外，还可以互营代谢乳酸和醇类化合物(表 2)。*Thermodesulfovibrio* 下有 3 个种可以互营代谢乳酸，均为高温菌，当存在硫酸盐和硫代硫酸盐等电子受体时，同样可以代谢乳酸，表现为兼性互营代谢功能(表 2)。

3 互营细菌的传统分离策略

在 Hungate 厌氧操作技术发明以前，科学家在卵型试管或培养皿中倾入融化的琼脂培养基，冷却后形成深层固体培养基，培养基底部的氧气被还原剂消耗，可维持缺氧状态，这种称之为“Agar shake cultures method”技术[67]，是早期分离厌氧微生物(包括互营细菌)的经典方法，如互营乙酸氧化菌 *Clostridium ultunense* 的分离(表 2)。但是用这个方法挑取单菌落时容易受到污染，对氧气的隔绝效果也不好。Hungate 厌氧操作技术的发明，解决了厌氧菌分离培养过程中的氧气干扰问

题，降低了厌氧微生物的分离难度[68]。基于Hungate厌氧操作技术的滚管法操作流程如下：预培养环境样品，接种到熔化的琼脂培养基中并进行梯度稀释，在冰水中水平滚动厌氧管(俗称“滚管”)，培养基在管内壁分散并凝固，静置培养一段时间后，可挑取单菌落进行再培养(滚管法)。对于难以形成菌落的微生物，可以在液体培养基中连续梯度稀释培养，并重复若干次获得纯培养物(液体稀释法)，如互营丙酸降解菌 *Smithella propionica* 的分离(表 2)。有时候，也会结合不同方式进行分离，如 *Syntrophomonas wolfei* subsp. *methylbutyratica* 的分离采用了“液体稀释+滚管”的方式(表 2)。

外源添加耗氢菌(如产甲烷古菌)、电子受体或更换底物，也可以提高互营细菌的分离效率。据统计，31%的互营细菌在分离时添加了外源微生物(表 2)，最为经典的外源产甲烷古菌为 *Methanospirillum hungatei*。也有报道添加硫酸盐还原菌 *Desulfovibrio* sp.作为外源促生菌，如 *Syntrophomonas bryantii* 的分离[35]。此外，大部分互营细菌表现为兼性互营，通过添加替代底物或外源电子受体可以提高分离效率。常用的替代底物有巴豆酸和丙酮酸等高氧化还原电势化合物，常用的外源电子受体主要有 SO_4^{2-}、$S_2O_3^{2-}$、SO_3^{2-} 和延胡索酸等，超过 68%的互营细菌借助这种方法获得了纯培养物(表 2)。

迄今为止报道的互营细菌物种数远低于产甲烷古菌[69]。笔者总结了限制互营细菌分离培养的因素，认为主要有以下几点：(1) 互营细菌代谢释放的能量极少，合成的 ATP 只能维持最低水平的代谢活动，用于细胞生物质合成代谢的能量分配较少，其生长繁殖的速度较低[70]，导致互营细菌的分离培养周期较长且不稳定。(2) 互营产甲烷菌系的生长代谢过程及其机制尚不清晰，参与互营代谢的微生物不仅存在种间氢、甲酸或电子转移外，可能还存在其他的营养分配，如不同微生物之间共享氨基酸[71]。当人为地切开这些未知的协作关系，又没有提供合适的培养条件，就会出现互营细菌生长缓慢，甚至不生长的现象，从而增加了分离难度。(3) 传统的液体和固体稀释分离技术，制备预还原培养基、添加各种试剂等操作繁琐、耗时长，用厌氧管作梯度稀释的通量低，且分离盲目性大，不能定向高效地分离培养互营细菌。(4) 传统微生物分离采用“先预培养后分离”的策略，通过添加选择性培养基，富集培养潜在功能菌，再进行分离纯化，但是该方法容易错过生长速度慢、对环境敏感的微生物，导致微生物可检测，但是难以分离培养(VBNC)。

4 互营细菌分离的新策略展望

首先，微生物分子生态学技术的发展和应用可以指导互营细菌的分离。Hatamoto 等应用 RNA-稳定同位素标记技术，发现 7 个长链脂肪酸降解产甲烷培养物中，有 5 个未培养细菌 *Syntrophomonadaceae* spp.，具有互营氧化棕榈酸的能力[72]。结合滚管法，他们分离获得了一个具有互营氧化 C_4–C_{18} 脂肪酸的新物种 *Syntrophomonas palmitatica* sp. nov. [42]。石油烃厌氧生物降解产甲烷研究是国内外关注的前沿领域之一，热力学分析表明参与石油烃起始降解的微生物属于互营细菌[21]。qPCR 和 DNA 稳定同位素探针技术证实 *Smithella* spp.是参与互营烷烃降解的关键功能菌[73–74]；利用宏基因组拼接、单细胞测序和 GC-MS 分析中间代谢产物，证实 *Smithella* spp.通过延胡索酸激活了烷烃的起始代谢[75–76]；通过基因组代谢网络分析，发现 *Smithella*

表 2. 互营细菌的分离策略和生理生化特征

Table 2. Isolation strategies and physio-biochemical characteristics of sytrophic bacteria

No.	Isolation methods		G	*T* (opt) / °C			E	Substrate utilization under pure culture conditions												Substrate utilization under co-culture conditions								GF	Is	Re
	I	P		Lo	M	T		H2	VF	LF	Al	Ar	CC	Ho	Su	Ot	Tc	Aa	Nn	VF	LF	Al	Ar	Hy	Su	Tc	Aa			
1	S	–	+		+		+				+		+		+									+	+			–	–	[23]
2	S	+	+		+		+					+		+		+		+								+	+	+	–	[24]
3	A+S	–	+		+		–		+		+			+	+	+		+		+								+	+	[25]
4	S	–	+			+	+		+	+	+			+			+			+								–	+	[26]
5	L	–	+			+	+	+	+	+	+			+						+								+	–	[27]
6	S	–	–		+		–												+				+					–	+	[28]
7	L	–	+		+		–												+	+								–	+	[29]
8	L+C	+	+		+		–												+	+								–	+	[30]
9	L	+	–		+		–					+		+									+					–	+	[28]
10	L	+	–			+	+							+			+			+		+						+	+	[31]
11	L	+	+		+		+							+									+					–	+	[32]
12	A	–	V		ND		–		+		+					+				+								+	+	[33]
13	S	–	+		+		–										+									+		–	+	[34]
14	A	+	+		+		–							+						+	+							–	–	[35]
15	S	+	V		+		–							+							+							–	–	[35]
16	S	+	–		+		–							+							+							–	+	[36]
17	S	+	–		+		+		+					+							+							–	+	[37]
18	S	+	–		+		+		+					+							+							–	–	[38]
19	L	+	–		ND		+							+							+							–	+	[39]
20	S	+	–		+		+												+		+							+	+	[40]
21	L+S	+	V		+		–							+						+	+							–	–	[39]
22	L	+	–		+		–							+							+							–	+	[41]
23	S	–	–		+		+		+					+							+							–	+	[42]
24	S	+	V		+		–												+		+							–	+	[43]
25	S	–	–			+	–							+						+	+							–	+	[44]
26	S	–	+		ND		+				+	+			+		+	+		+								–	+	[45]
27	S	–	–		+		+						+	+	+		+			+		+						+	+	[46]
28	S	–	+			+	+	+	+		+	+		+		+		+		+								–	+	[47]
29	L+S	–	+			+	–						+	+	+	+					+							+	–	[48]
30	S	–	–			+	–							+							+							–	–	[49]
31	S	–	–			+	–				+			+	+		+	+				+			+	+	+	–	+	[50–51]
32	S	–	–			+	+	+	+					+						+								–	+	[52]
33	S	–	–			+	+	+	+					+						+								–	–	[53]
34	S	–	–			+	+	+	+					+						+								–	–	[54]
35	S	–	–	+			–												+	+								–	–	[55]
36	L+C	–	–		+		+		+		+									+		+						–	–	[56]
37	S	–	–		+		+	+	+	+				+			+							+				–	–	[57]
38	L	+	–		+		–							+						+								+	+	[58]
39	L	–	–		+		+	+	+					+			+	+		+								–	+	[22]

(待续)

(续表 2)

40	L	–	–	+		+	+														+	+	[59]
41	S+L	–	–	+		+	+				+						+		+		–	+	[60]
42	L	+	–	ND		+	+				+			+			+				–	+	[61]
43	L	–	–	+		+										+				+	–	+	[62]
44	S	–	–	+		–					+						+	+		+	–	–	[63]
45	L	–	–	+		+			+		+									+	–	+	[64]
46	S	–	–	+		–			+											+	+	+	[65]
47	S+L	–	–		+	+	+	+		+	+	+	+	+	+		+		+		+	+	[66]

1: *Abyssivirga alkaniphila*; 2: *Clostridium acidaminophilum*; 3: *Clostridium ultunense*; 4: *Desulfotomaculum thermobenzoicum* subsp. *thermosyntrophicum*; 5: *Desulfotomaculum thermocisternum*; 6: *Pelotomaculum isophthalicicum*; 7: *Pelotomaculum propionicicum*; 8: *Pelotomaculum schinkii*; 9: *Pelotomaculum terephthalicum*; 10: *Pelotomaculum thermopropionicum*; 11: *Sporotomaculum syntrophicum*; 12: *Syntrophaceticus schinkii*; 13: *Syntrophobotulus glycolicus*; 14: *Syntrophomonas bryantii*; 15: *Syntrophomonas cellicola*; 16: *Syntrophomonas curvata*; 17: *Syntrophomonas erecta*; 18: *Syntrophomonas erecta* subsp. *sporosyntropha*; 19: *Syntrophomonas saponavida*; 20: *Syntrophomonas sapovorans*; 21: *Syntrophomonas wolfei* subsp. *methybutyratica*; 22: *Syntrophomonas wolfei* subsp. *wolfei*; 23: *Syntrophomonas palmitatica*; 24: *Syntrophomonas zehnderi*; 25: *Syntrophothermus lipocalidus*; 26: *Tepidanaerobacter acetatoxydans*; 27: *Tepidanaerobacter syntrophicus*; 28: *Thermacetogenium phaeum*; 29: *Thermosyntropha lipolytica*; 30: *Thermosyntropha tengcongensis*; 31: *Thermanaerovibrio acidaminovorans*; 32: *Thermodesulfovibrio aggregans*; 33: *Thermodesulfovibrio islandicus*; 34: *Thermodesulfovibrio yellowstonii*; 35: *Algorimarina butyrica*; 36: Candidatus *Desulfonatronobulbus propionicus*; 37: *Desulfatibacillum alkenivorans*; 38: *Smithella propionica*; 39: *Syntrophobacter fumaroxidans*; 40: *Syntrophobacter pfennigii*; 41: *Syntrophobacter sulfatireducens*; 42: *Syntrophobacter wolinii*; 43: *Syntrophorhabdus aromaticivorans*; 44: *Syntrophus aciditrophicus*; 45: *Syntrophus buswellii*; 46: *Syntrophus gentianae*; 47: *Thermotoga lettingae*.

A: Solid dilution method; B: Liquid dilution method; C: Agar shake method; P: Methanogens and/or *Desulfovibrio* sp. were added during isolation process. G: Gram-staining positive; L: Optimum growth occurred at <20 °C; M: Optimum growth temperature ranging from 20 °C to 50 °C; T: Optimum growth occurred at >50 °C; E: Pure culture growing with external electron acceptors; H_2: H_2+CO_2/acetate; Vf: Volatile fatty acids; Lf: Long chain fatty acids. Ai: Alcohols; Ar: Aromatic compounds; Cc: Complex organic compounds; Ho: Crotonate or pyruvate; Su: Sugars, Ot: Other compounds; Tc: Organic compounds associated with TCA cycle; Aa: Amino acids; Hy: Hydrocarbons; No: No growth under pure culture condition; Gf: Growth required factors; Gd: Whole/draft genome sequence; Is: Isolated from anaerobic digesting reactors; Re: References. +: positive; –: negative; blank: not reported.

spp.在降解烷烃降解过程，与其他细菌共享氨基酸的合成代谢途径[71]。虽然迄今为止还没有分离出互营烷烃降解菌 *Smithella* spp.，但是这些基于未培养的研究进展，对互营烷烃降解菌的分离工作有很强的指导作用。

其次，近年来新发展起来的微生物分离培养技术，可以为我们分离互营细菌提供新的思路：(1) 借鉴扩散盒培养技术[77]、细胞微囊包埋技术[78]和 iChip 芯片技术[79]，尽可能地模拟互营细菌的原位条件，避免互营细菌缺少未知的营养物质而无法生长；(2) 借鉴高通量培养[80]和微流控液滴技术[81]，在微孔板上高通量选择性培养互营细菌。特别是微孔板容积大小合适(96–384 孔板的容积为 100–360 μL)，如果密封得当可培养数年时间，辅以无菌无氧手套箱和自动转移设备，操作效率更高，还可以避免大量使用厌氧管带来的繁重工作量。此外，在一块微孔板上可排列组合多种培养条件(不同的底物、生长必需/刺激因子、外源促生菌或电子受体等)，根据目标互营细菌的类型和可能的代谢特征，提供丰富多样的培养条件，提高了互营细菌的生长概率。此外，结合特异性 PCR 扩增技术，实时监测目标互营细菌的生长状况，从而解决互营细菌分离通量低、盲目性大的问题。

总之，利用稳定同位素探针技术和各种组学方法，可以在分离互营细菌之前，了解哪些是我们感兴趣的目标菌，这些微生物可能具有哪些遗

传代谢特征。在此基础上，提供丰富多样的培养条件，应用高通量培养和特异性 PCR 扩增监测技术，定向筛选互营细菌，这将是互营微生物资源和系统分类学研究的发展方向。

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Key players involved in methanogenic degradation of organic compounds: progress on the cultivation of syntrophic bacteria

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Abstract: Syntrophic metabolism is one of the important interspecies relationships among microbes. Syntrophic microorganisms not only distribute in soils, freshwater, marine anoxic sediments, anaerobic digestion and gastrointestinal tract of animals, but also present in extreme environments such as subsurface oil reservoirs. They play essential roles in anaerobic degradation of organic compounds to methane and carbon dioxide. Study on the syntrophic metabolisms of syntrophic microorganisms through culture-dependent methods, would help understand the biogeochemical cycle of elements in anoxic environments, and deal with the global energy crisis and global warming problems. However, it is difficult to isolate syntrophic microorganisms for their slow-growing and oxygen-sensitive properties. This review summarizes the recent studies on the isolation strategies of syntrophic microorganisms, and their physiological and biochemical properties. Furthermore, the future development trend of culture techniques including high throughput screening and targeted isolation of syntrophic microorganisms were discussed.

Keywords: syntrophic bacteria, methanogenesis, high throughput screen, targeted isolation

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