微生物学通报
Microbiology China
http://journals.im.ac.cn/wswxtbcn

Jul. 20, 2023, 50(7): 3104−3121
DOI: 10.13344/j.microbiol.china.220983

专论与综述

黏细菌资源及其系统分类

杜欣然，王晶晶*，冉柒，李越中*

山东大学微生物技术研究院 微生物技术国家重点实验室，山东 青岛 266237

杜欣然, 王晶晶, 冉柒, 李越中. 黏细菌资源及其系统分类[J]. 微生物学通报, 2023, 50(7): 3104-3121.
DU Xinran, WANG Jingjing, RAN Qi, LI Yuezhong. Resources and taxonomy of myxobacteria: a review[J]. Microbiology China, 2023, 50(7): 3104-3121.

摘 要：黏细菌是一类捕食性革兰氏阴性菌，广泛分布在土壤、海洋和淡水等生境中，是多类环境的优势类群。根据 16S rRNA 基因序列，黏细菌被归属于变形菌门的 δ 分支黏细菌目(*Myxococcales*)。新近根据 120 个保守性的单拷贝标识基因和 16S rRNA 基因序列，对变形菌门的系统分类学研究将黏细菌类群单列为黏细菌门(*Myxococcota*)。本文介绍了黏细菌资源的特性，并围绕从目到门的分类地位变迁，系统简述了黏细菌分类学研究的历史演变，对黏细菌资源的应用和发展进行了展望。
关键词：黏细菌；黏细菌门；分类地位；系统发生；微生物资源

Resources and taxonomy of myxobacteria: a review

DU Xinran, WANG Jingjing*, RAN Qi, LI Yuezhong*

State Key Laboratory of Microbial Technology, Institute of Microbiology Technology, Shandong University, Qingdao 266237, Shandong, China

Abstract: Myxobacteria are predatory Gram-negative bacteria ubiquitous and often predominant in soil, ocean, and freshwater environments. According to the 16S rRNA gene sequences, myxobacteria were classified as an order *Myxococcales* affiliated to the class *δ-Proteobacteria*. The recent phylogenetic studies based on 120 conserved single-copy marker genes and the 16S rRNA gene sequences have upgraded *Myxococcales* to the phylum *Myxococcota*. This review briefly summarizes the characteristics of myxobacteria and the history of the phylogenetic research and then makes a perspective on the future studies and applications of myxobacterial resources.
Keywords: myxobacteria; *Myxococcota*; taxonomy; phylogeny; microbial resources

---

资助项目：科技基础资源调查专项(2022FY101100)；国家自然科学基金(32070030)；山东省自然科学基金(ZR2022QC100)
This work was supported by the Science and Technology Fundamental Resources Investigation Program (2022FY101100), the National Natural Science Foundation of China (32070030), and the Natural Science Foundation of Shandong Province (ZR2022QC100).
*Corresponding authors. E-mail: WANG Jingjing, wangjingjing@sdu.edu.cn; LI Yuezhong, lilab@sdu.edu.cn
Received: 2022-10-09; Accepted: 2023-03-01; Published online: 2023-04-12

黏细菌是一类广泛分布于各种自然生境的革兰氏阴性杆状细菌,以其复杂的多细胞群体行为特性和庞大的基因组而著称。除类普通杆菌(*Vulgatibacter*)[1]、嗜纤维素菌(*Byssovorax*)[2]和厌氧黏细菌(*Anaeromyxobacter*)[3-4]外，已培养的其他黏细菌基因组大小为 9.0−16.5 Mb,基因组 GC 含量为 64%−75%[5]。黏细菌的复杂多细胞群体行为表现在生活周期的各个阶段,如细胞生长密度依赖、多细胞子实体发育、细胞群体运动模式及细胞的群体方式捕食等[6]。

黏细菌最显著的形态特征是能够形成形态各异、肉眼可见(50−500 μm)的多细胞子实体(fruiting body)结构,其中包裹具有抗逆性的黏孢子[7]。子实体等形态特征也是黏细菌多相分类的重要指标。根据单生境未培养黏细菌的多样性和已培养黏细菌的局限性推测,自然生境中应存在大量的无子实体(non-fruiting)或子实体发育不典型的黏细菌类群[8]。已经被近年来发现的多个不能形成子实体的黏细菌新类群证实,如类普通杆菌、丝状滑行黏细菌(*Labilithrix*)[1]、幽灵孢子菌(*Simulacricoccus*)[9]及金色多囊菌(*Polyangium aurulentum*)[10]等。除厌氧黏细菌[1]外，其他已培养黏细菌均为好氧细菌。

黏细菌细胞通常能够在固体表面上以两种机制进行滑行运动[11]：冒险运动(adventurous motility，A-运动)和群体运动(social motility，S-运动)，冒险运动是指菌落边缘个体细胞向着新环境进行探索式的滑行运动,群体运动是依赖于四型菌毛固着和收缩的大规模细胞的集体运动。这两种运动模式共同协助黏细菌完成捕食、子实体发育等多细胞群体行为,黏细菌因其复杂的多细胞行为而成为研究微生物社会学行为的模式生物[11]。值得一提的是，由于黏细菌在液体中的聚团生长或不生长特性,给黏细菌的研究和应用带来很大的困难。目前黏细菌研究所用的模式菌株黄色黏球菌(*Myxococcus xanthus*) DK1622 是原始分离菌(FB 菌株)在子实体形态突变丢失后通过恢复突变获得的兼具形成子实体和液体分散生长特性的菌株,为后续的各种遗传操作提供了可能和便利[12-13]。

黏细菌的捕食策略被称为“狼群捕食”(wolf-pack attack)，即通过细胞大量聚集的方式，提升胞外裂解酶浓度，实现“猎物”细胞裂解的“群体捕食”[14]。捕食性细菌的捕食策略还有附着在猎物细胞表面吸收养分的“表生型捕食”和通过分泌水解酶给猎物细胞壁打孔或改造而进入猎物细胞周质空间或细胞质的“侵入型捕食”[15]。黏细菌能够捕食各类细菌和真菌。然而并不是所有黏细菌都能够捕食其他微生物,黏细菌中也存在不能捕食活的微生物的溶纤维素类群，目前已知的仅有两个属，即堆囊菌属(*Sorangium*)和嗜纤维素菌属,它们不仅降解利用纤维素和糖类的能力突出,并能以无机氮化合物(NH_4^+, NO_3^-)或有机氮化合物作为唯一氮源[16]。此外,近年来报道的一些黏细菌新类群既不能分解纤维素也不能捕食，如类普通杆菌、丝状滑行黏细菌和幽灵孢子菌等[1,9]。

黏细菌另一吸引人之处在于其能够产生多种具有生物活性的次级代谢产物,是公认的重要的药源微生物新类群之一[17]。在过去的 40 年里,从黏细菌中已鉴定出 100 多种新的碳骨架代谢物和 600 多种衍生物[18-19],这些代谢产物具有抗真菌、抗细菌、抗病毒、抗疟疾、抗肿瘤和免疫调节等活性[20]。部分黏细菌化合物已用于临床,如从纤维堆囊菌(*S. cellulosum*)发现的埃博霉素(epothilones)具有抗肿瘤活性[21-23]，其类似物伊沙匹隆(ixabepilone)和优替德隆(utidelone)分别于 2007 年和 2021 年获批上市,用于癌症的临床

治疗。此外，由于捕食特性，黏细菌在生态中具有重要作用，有可能用于农业生物防治[24-25]和污水处理[26-27]等。因此，黏细菌是一类具有重要基础研究价值和应用价值的微生物资源。

根据 16S rRNA 基因序列，黏细菌在系统分类上隶属于变形菌门中 δ 分支的黏细菌目(*Myxococcales*)[28]。目前基于基因组系统发育关系的分类标准，已将黏细菌目提升为黏细菌门(*Myxococcota*)[29]。随着已培养黏细菌类群的不断增多和微生物系统分类的发展，对黏细菌的系统分类也在逐步完善。本文以黏细菌系统分类学的发展为主线，介绍黏细菌资源的特性和研究现状，以期为黏细菌资源研究和开发利用提供参考。

1 黏细菌系统分类历史演变

黏细菌系统分类学大致经历了以下 3 个阶段：早期的依赖于黏细菌形态的分类，16S rRNA 基因序列相似性分析和形态分类并举的黏细菌系统分类，以及基于 120 个保守的单拷贝标识基因和 16S rRNA 基因的分类。

1.1 基于黏细菌子实体形态的早期分类学体系：黏细菌目

对黏细菌的描述可以追溯到 1892 年，对黏细菌的最早认知是其复杂多样的子实体结构，这也是早期黏细菌分类的基础[30]。在 16S rRNA 基因序列相似性引入系统发育学研究之前，黏细菌的分类体系几乎完全依赖子实体等的形态学特征，并辅以抗生素、酶活等生理生化指标；早期对黏细菌的保存主要是干燥法，黏细菌的子实体也曾被当作植物标本进行干燥保藏；根据黏细菌子实体孢子囊颜色、数量、是否有柄，黏孢子形状等特征，将具有相似子实体特征的菌株进行聚类、等级划分。实际上这些“代表菌株”并不是严格意义上的“模式菌株”，更像是“模式材料”[31]。

1989 年，*Bergey's manual of systematic bacteriology*[32]首先根据营养细胞形状、是否形成小孢囊将多囊菌科(*Polyangiaceae*)划分出来；再根据小孢囊形状及小孢囊是否在孢子囊中，将黏球菌科(*Myxococcaceae*)、原囊菌科(*Archangiaceae*)和孢囊杆菌科(*Cystobacteraceae*)区分开。此时黏细菌目共分为 8 个属：黏球菌属(*Myxococcus*)、原囊菌属(*Archangium*)、孢囊杆菌属(*Cystobacter*)、蜂窝囊菌属(*Melittangium*)、标桩菌属(*Stigmatella*)、小囊菌属(*Nannocystis*)、软骨霉状菌属(*Chondromyces*)和多囊菌属(*Polyangium*)。1992 年，*The Prokaryotes*[33]根据细胞形态、黏孢子发育、菌落表型、细胞脂肪酸谱、类胡萝卜素谱、菌落黏液是否吸附刚果红，将黏细菌目划分为孢囊杆菌亚目(*Cystobacterineae*)和堆囊菌亚目(*Sorangineae*)。科级的划分主要依据黏孢子的形态。属和种的划分是基于形态特征和一些生理特征。如黏球菌科的黏孢子是光滑的球形；黏球菌属子实体通常是柔软黏滑的球状，球形底部收束或不收束；而珊瑚球菌属子实体通常是坚韧的圆柱体或垫状，有的会形成珊瑚或珊瑚枝状。

在早期分类体系下，黏球菌目分为黏球菌科(*Myxococcaceae*)、原囊菌科(*Archangiaceae*)、孢囊杆菌科(*Cystobacteraceae*)和堆囊菌科(*Sorangiaceae*)这 4 个科和 12 个属约 40 个种[33]。尽管如此，仍有很多属或种处于争议或者不确定的范围。例如，孢囊杆菌属(*Cystobacter*)到底有多少个种并不能确定，只能根据孢子囊的形态划分为 4 个“模式种”[33]。分类学家们曾尝试引入纤维素降解能力、几丁质降解能力、紫外线激发荧光等特性对黏细菌进行分类学研究，但都未完全成功[34-35]。黏细菌的子实体特征由于容易在分离纯化和培养的过程中退化或丢失，从而出现纯培养黏细菌子实体不典型或不形成子实体的现象，

之后的系统发育学研究证实,有很多形态学特征十分“相似”的菌株并不是同一类[36]。因此，早期的系统分类是含糊的，尤其是“种”间的区分。以黏细菌形态为基础、辅以生理特征进行逐级划分的早期分类体系存在较大的不准确性。

1.2 16S rRNA 基因相似性和形态分类并举的系统分类：黏细菌目

随着测序技术的发展,微生物系统分类研究进入了新阶段。1999 年，Spröer 等对 54 株黏细菌进行了 16S rRNA 基因的系统发育分析，证实了黏细菌中的 3 个深度分支,并肯定了黏细菌的形态和系统发育之间的相关性,但有少数黏细菌在系统发育上与形态分类不一致[37]。2010 年，Garcia 等对 101 株黏细菌的 16S rRNA 基因序列进行了系统发育分析,明确了 3 个亚目成员之间的分歧，并且发现了 9 个新的分类单元[38]。因此，引入 16S rRNA 基因序列相似性对细菌系统发育进行矫正之后,黏细菌的系统分类学变得更为清晰。以 2005 年 *Bergey's manual of systematic bacteriology*[36]和 2006 年 *The Prokaryotes*[28]为代表，根据 16S rRNA 基因序列相似性，将黏细菌归为 δ 变形菌纲的黏细菌目[39],与之亲缘关系相近的是蛭弧菌属(*Bdellovibrio*)和一些绝对厌氧的脱硫菌[40]。不同黏细菌亚目通过营养细胞、黏孢子和菌落形态来进行分类。菌落是否吸附刚果红作为菌落黏液的化学特性指标也被用作一个分类标准[35]。此时的黏细菌分类仍然是以形态学特征为主、16S rRNA 基因序列相似性分析为辅。黏细菌目共分为 3 亚目 5 个科 17 个属 52 个种[38]。值得一提的是，黏细菌的形态学分类体系和 16S rRNA 基因系统分类体系在高级分类单元上有较好的一致性,但在种属分类时有较大的差异。这也导致了一些不同属黏细菌的 16S rRNA 基因序列相似性>97%的现象。此外，根据 *Bacteriological Code* (1990 年版)的命名规范[41]，截止到 2007 年，有 16 个黏细菌种暂属于有效报道(effectively published)状态，因为命名不规范或缺少保藏证明等未生效发表(not validly)[42]。

1.3 基于保守单拷贝标识基因的现代分类体系：黏细菌门

随着基因组测序、宏基因组拼装和单细胞测序技术的飞速发展,目前更容易从纯培养和未培养微生物中获取大量的高质量基因组序列。从基因组序列中筛选多个蛋白标识基因进行系统发育学分析已经变得越来越普遍[43-44]。2018 年 Parks 等[45]通过数据库现有的细菌基因组及宏基因组分装得到的数据筛选出用于细菌系统发育学分析的 120 个单拷贝标识蛋白序列(bac120)。2020 年基于 bac120 的系统发育学分析发现 *Deltaproteobacteria* 纲、*Oligoflexia* 纲与热脱硫杆菌门(*Thermodesulfobacteria*)并非单系同源,并对其重新分类，成立了 4 个新的细菌门：黏细菌门(*Myxococcota*)、脱硫菌门(*Desulfobacterota*)、蛭弧菌门(*Bdellovibrionota*)和未培养的 SAR324[29]。基于 bac120 和 16S rRNA 基因的黏细菌现代分类体系正式建立;与单个保守基因的分类相比,基于基因组的分类系统覆盖更多的信息,因此能够更好地反映生物的真实系统进化关系[29]。目前黏细菌门的分类系统兼顾了传统的分类系统和新的系统发育学研究,并将系统发育与黏细菌功能特点结合起来。

黏细菌门现有 2 个已培养纲：黏球菌纲(*Myxococcia*)和多囊菌纲(*Polyangia*)。此外，系统发育分析显示黏细菌门至少有一个纲处于未培养状态，包含未培养黏细菌的宏基因组拼装，如 c_UBA727 和 c_UBA796 等[29]。值得注意的是，有些已发表的黏细菌类群，由于缺乏基因组信息，其归类是根据 16S rRNA 基因序列构建系统发育进化树[29]。例如，原豆囊菌科

(*Phaselicystaceae*)[46]被暂归为多囊菌科(*Polyangiaceae*)下的豆囊菌属(*Phaselicystis*)；科夫勒菌科(*Kofleriaceae*)中科夫勒菌属(*Kofleria*)与海生囊菌属(*Haliangium*)同在16S rRNA基因序列进化树的一个分支，被归于多囊菌纲海生囊菌目，这与2006年*The Prokaryotes*[28]将海生囊菌属和科夫勒菌属同归于黏球菌目下科夫勒菌科相悖。以国际原核生物命名法为标准的在线统计[47]，科夫勒菌属和海生囊菌属仍同在黏球菌目下的科夫勒菌科。

自黏细菌现代分类体系建立以来，黏细菌有效发表的新类群有柠檬色球菌属(*Citreicoccus*)[48]、珊瑚球菌属9个新种[49-50]、黏球菌属3个新种[51]和厌氧黏细菌属3个新种[3]。截至目前，黏细菌门共有效发表3纲4目8科31属，详见表1。在低分类单元“属”“种”水平上，现代分类体系主要是对新发现的一些形态学特征如子实体不典型类群的分类，如淡黄色丝状滑行黏细菌(*Labilithrix luteola*)和朴素类普通杆菌(*Vulgatibacter incomptus*)[1]。此外，区分了形态学特征差异不显著但16S rRNA基因序列相似性达到新物种鉴定阈值(98.65%)的菌株。自1970年Colwell提出多相分类(polyphasic taxonomy)[52]的概念以来，利用微生物表型、基因型等多方面不同信息的综合系统分类已经成为主流。在目前的黏细菌分类体系中，黏细菌的形态学特征依然是新分类单元需要描述的重要内容。

2 已培养黏细菌的系统分类及特征简述

黏细菌是兼性捕食类群的典型代表，因其进化关系和捕食策略的不同，将黏细菌与专性捕食类群蛭弧菌分别单列成为2个独立的门[29]。现已培养的黏细菌门下包含2个纲：黏球菌纲(*Myxococcia*)和多囊菌纲(*Polyangia*)，分别代表了黏细菌系统发育的两大分支[29]。以下对2个纲的相关分类特征进行了描述，包含的具体科、属见表1。黏细菌新类群系统发育的研究报道不多，表2总结了近20年黏细菌新菌鉴定的相关报道。这些黏细菌新菌大多分离自土壤相关生境，其次是海洋生境。值得注意的是，近两年报道的某些新种或新属与已知模式菌16S相似性水平均较高，如*Corallococcus soli* ZKHCc1 1396^{T}与已知模式菌*C. terminator* CA054A^{T}的相似性高达99.67%[53]；*Corallococcus silvisoli* c25j21^{T}与已知模式菌*C. aberystwythensis* DSM 108846^{T}的相似性为99.3%[50]；*Citreicoccus inhibens* M34^T(新属)与已知珊瑚球菌属模式菌*Corallococcus exercitus* AB043A^{T}的相似性为98.18%[48]。

2.1 黏球菌纲

黏球菌纲下只有一个黏球菌目(*Myxococcales*)。该目均为溶细菌型菌株，一般能够裂解细菌细胞，但不能分解纤维素。共包含5个科，黏球菌科(*Myxococcaceae*)、原囊菌科(*Archangiaceae*)、类普通杆菌科(*Vulgatibacteraceae*)、厌氧黏杆菌科(*Anaeromyxobacteraceae*)和科夫勒菌科(*Kofleriaceae*)。营养细胞细长杆状，黏孢子短圆且成熟后具有光学折射特性(图1A、1B)。菌落能够吸附刚果红。但也有特殊的黏细菌类群如类普通杆菌属(*Vulgatibacter*)，无运动性，既不能裂解细菌细胞，也不能分解纤维素且无子实体形成[1]。幽灵孢子属(*Simulacricoccus*)不形成子实体但能够形成球状黏孢子[9]。厌氧黏细菌科(*Anaeromyxobacteraceae*)是黏细菌中唯一已知的兼性厌氧菌类群，能够进行滑行运动、无典型子实体形成[4]。新发现的柠檬色球菌属(*Citreicoccus*)能够显著抑制丝状真菌和裂解病原菌[8]。

表 1　黏细菌门有效发表属分类地位变迁

Table 1　Proposed taxonomy of the phylum *Myxococcota* with changes from the past taxonomy marked below the rank of family

纲 Class	目 Order	科 Family	属 Genus	2006-《原核生物》(科)[28] 2006-*The Prokaryotes* (family)[28]	1992-《原核生物》(科)[33] 1992-*The Prokaryotes* (family)[33]
黏球菌纲 *Myxococcia*	黏球菌目 *Myxococcales*	黏球菌科 *Myxococcaceae*	匣状球菌属 *Pyxidicoccus* (2)	–	nov
			黏球菌属 *Myxococcus* (9)	–	–
			珊瑚球菌属 *Corallococcus* (12)	–	–
			聚团球菌属 *Aggregicoccus* (1)	nov	nov
			幽灵孢子属 *Simulacricoccus* (1)	nov	nov
			柠檬色球菌属 *Citreicoccus* (1)	nov	nov
		原囊菌科 *Archangiaceae*	孢囊杆菌属 *Cystobacter* (7)	孢囊杆菌科 *Cystobacteraceae*	孢囊杆菌科 *Cystobacteraceae*
			原囊菌属 *Archangium* (4)	孢囊杆菌科 *Cystobacteraceae*	–
			标桩菌属 *Stigmatella* (3)	孢囊杆菌科 *Cystobacteraceae*	孢囊杆菌科 *Cystobacteraceae*
			玻璃囊菌属 *Hyalangium* (1)	孢囊杆菌科 *Cystobacteraceae*	nov
			蜂窝囊菌属 *Melittangium* (3)	孢囊杆菌科 *Cystobacteraceae*	孢囊杆菌科 *Cystobacteraceae*
			无孔菌属 *Vitiosangium* (2)	nov	nov
		类普通杆菌科 *Vulgatibacteraceae*	类普通杆菌属 *Vulgatibacter* (1)	nov	nov
		厌氧黏细菌科 *Anaeromyxobacteraceae*	厌氧黏细菌属 *Anaeromyxobacter* (3)	nov	nov
多囊菌纲 *Polyangia*	多囊菌目 *Polyangiales*	多囊菌科 *Polyangiaceae*	多囊菌属 *Polyangium* (9)	–	堆囊菌科 *Sorangiaceae*
			堆囊菌属 *Sorangium* (8)	–	堆囊菌科 *Sorangiaceae*
			软骨霉状菌属 *Chondromyces* (6)	–	堆囊菌科 *Sorangiaceae*
			小孢囊属 *Minicystis* (1)	nov	nov
			豆囊菌属 *Phaselicystis* (1)	nov	nov
			丝状滑行黏细菌属 *Labilithrix* (1)	nov	nov
			卓恩属 *Jahnella* (1)	–	nov
			嗜纤维素菌属 *Byssovorax* (1)	–	nov
			透明蠕杆菌属 *Aetherobacter* (2)	nov	nov

(续表)

(待续 1)

纲 Class	目 Order	科 Family	属 Genus	2006-《原核生物》(科)[28] 2006-*The Prokaryotes* (family)[28]	1992-《原核生物》(科)[33] 1992-*The Prokaryotes* (family)[33]
			簇囊菌属 *Racemicystis* (2)	nov	nov
		橙杆菌科 *Sandaracinaceae*	橙杆菌属 *Sandaracinus* (1)	nov	nov
	小囊菌目 *Nannocystales*	小囊菌科 *Nannocystaceae*	小囊菌属 *Nannocystis* (3)	–	堆囊菌科 *Sorangiaceae*
			邻囊菌属 *Plesiocystis* (1)	nov	nov
			水黏细菌属 *Enhygromyxa* (1)	nov	nov
			假水黏细菌属 *Pseudenhygromyxa* (1)	nov	nov
	海生囊菌目 *Haliangiales*	海生囊菌科 *Haliangiaceae*	科夫勒菌属 *Kofleria* (1)	科夫勒菌科 *Kofleriaceae*	nov
			海生囊菌属 *Haliangium* (2)	科夫勒菌科 *Kofleriaceae*	nov

–：科级分类地位未发生改变；nov：在原分类体系中该属处于"未有效发表"状态或不存在；括号中数字表示该属现有有效发表种的数量；因属名书写不规范更名：原"*Jahnia*"更名为 *Jahnella*，原"*Byssophaga* "更名为 *Byssovorax*；因种属合并取消的属名：原囊球菌属(*Angiococcus*)模式菌 *Angiococcus disciformis* 归为原囊菌属 *Archangium disciforme*；原单囊菌属(*Haploangium*)[28]归为多囊菌属(*Polyangium*)

–: No change in classification at the family level; nov: "Nonexistent" or "not validly"; Numbers in parentheses following genus names denote the number of currently valid published species of the genus; Some genus names have been changed due to abnormal spelling: *Jahnia* changed to *Jahnella*; *Byssophaga* changed to *Byssovorax*; The canceled genus names due to amalgamation: The type species of *Angiococcus*, *Angiococcus disciformis* classified as *Archangium disciforme*; *Haploangium*[28] classified as *Polyangium*.

表 2 近 20 年黏细菌新菌的系统分类

Table 2 Systematic classification of novel myxobacteria in the last 20 years

科学命名 Scientific name	菌株 Strains	菌株来源 Habitats	分离方法 Isolation methods	菌株特性 Biological characteristics	基因组大小 Genome size (Mb)	GC 含量 GC contents (%)	参考文献 Reference
Anaeromyxobacter oryzae *A. diazotrophicus* *A. paludicola*	Red232[T] Red267[T] Red630[T]	稻田土 Paddy soil	–	兼性厌氧 Facultative anaerobic	6.72 4.83 4.59	73.5 74.5 74.1	[3]
Corallococcus soli	ZKHCc1 1396[T]	土壤 Soil	大肠杆菌诱导法 *Escherichia coli* baiting method	–	9.44	70.6	[53]
Corallococcus silvisoli	c25j21[T]	森林土 Forest soil	大肠杆菌诱导法 *Escherichia coli* baiting method	–	9.23	70.7	[50]
Citreicoccus inhibens	M34[T]	森林土 Forest soil	大肠杆菌诱导法 *Escherichia coli* baiting method	抗真菌活性、裂解病原细菌 Antifungal activity and bacteriolytic property against phytopathogens	9.05	69.5	[48]

(待续)

(续表 2)

科学命名 Scientific name	菌株 Strains	菌株来源 Habitats	分离方法 Isolation methods	菌株特性 Biological characteristics	基因组大小 Genome size (Mb)	GC 含量 GC contents (%)	参考文献 Reference
Polyangium aurulentum *P. jinanense*	SDU3-1^{T} SDU14^{T}	土壤 Soil	大肠杆菌诱导法 *Escherichia coli* baiting method	不形成子实体 Non-fruiting	12.32 13.81	69.4 68.4	[10]
Myxococcus spp. *Pyxidicoccus* spp.	5 species*	土壤 Soil	大肠杆菌诱导法 *Escherichia coli* baiting method	–	–	–	[51]
Corallococcus spp.	8 species**	土壤 Soil	标准分离方法 Standard isolation methods	–	–	–	[49]
Sorangium spp.	7 species***	土壤 Soil	–	降解纤维素 Cellulose-decomposing	–	–	[54]
Nannocystis konarekensis	MNa11734^{T}	沙漠土 Desert soil	标准分离方法 Standard isolation methods	–	–	–	[55]
Simulacricoccus ruber	MCy10636^{T}	土壤 Soil	在 MS21 琼脂覆盖滤纸片平板形成微菌落 Tiny swarming colony on MS21 agar baited with a filter paper	微耐氧，不形成子实体、形成黏孢子 Microaerotolerant, non-fruiting, myxospore-forming	–	–	[9]
Vitiosangium cumulatum *V. subalbum*	MCy10943^{T} MCy10944^{T}	土壤 Soil	土壤浸提液琼脂涂抹灭活的大肠杆菌 Adding 1% (v/v) soil extract, autoclaved *Escherichia coli*	–	–	–	[56]
Racemicystis persica	MSr11462^{T}	沙滩沙土 Sand sample of beach	无机盐 ST21 培养基加无菌滤纸片诱导 Mineral salt ST21 agar, overlaid with sterile filter papers	–	–	–	[57]
Aetherobacter fasciculatus *A. rufus*	SBSr002^{T} SBSr003^{T}	土壤 Soil	标准分离方法 Standard isolation methods	含有独特的多不饱和脂肪酸生物合成途径 The unique PUFA biosynthetic pathways	–	–	[58]
Racemicystis crocea	MSr9521^{T}	土壤 Soil	无机盐 ST21 培养基加无菌滤纸片诱导 Mineral salt ST21 agar, overlaid with sterile filter papers	–	–	–	[59]
Aggregicoccus edonensis	MCy1366^{T}	土壤 Soil	标准分离方法 Standard isolation methods	菌体特殊的聚集现象 Unusually aggregating	–	–	[60]
Minicystis rosea	SBNa008^{T}	土壤 Soil	大肠杆菌诱导法 *Escherichia coli* baiting method	富含不饱和脂肪酸，产甾类化合物 Polyunsaturated fatty acid-rich-and steroid-producing	16.04	69.1	[61]

(待续)

(续表 2)

科学命名 Scientific name	菌株 Strains	菌株来源 Habitats	分离方法 Isolation methods	菌株特性 Biological characteristics	基因组大小 Genome size (Mb)	GC 含量 GC contents (%)	参考文献 Reference
Vulgatibacter incomptus *Labilithrix luteola*	B00001^{T} B00002^{T}	森林土 Forest soil	稀释涂布平板法 Plate dilution method	无子实体聚集现象，不能裂解菌体，不能分解纤维素 No fruiting body-like cell aggregates, non-bacteriolytic and non-cellulolytic type of nutrition	4.35 12.19	68.9 66.1	[1]
Pseudenhygromyxa salsuginis	SYR-2^{T}	河口湿地淤泥 Estuarine marsh	改良版海洋黏细菌分离方法 Modified isolation methods for marine myxobacteria	适应低浓度的盐环境(0.0–2.5%)	–	–	[62]
Sandaracinus amylolyticus	NOSO-4^{T}	土壤 Soil	标准分离方法 Standard isolation methods	分解淀粉 Starch-degrading	10.33	72.0	[63]
Phaselicystis flava	SBKo001^{T}	森林土 Forest soil	标准分离方法 Standard isolation methods	含有花生油酸 Arachidonic acid-containing	–	–	[46]
Byssovorax cruenta	By c2^{T}	土壤 Soil	标准分离方法 Standard isolation methods	降解纤维素 Cellulose-degrading	5.99	66.6	[2]
Enhygromyxa salina	SHK-1^{T}	海洋 Coastal samples (mud, sands and algae)	海洋黏细菌分离方法 Isolation methods for marine myxobacteria	微嗜盐黏细菌 Slightly halophilic myxobacterium	–	–	[64]
Plesiocystis pacifica	SIR-1^{T}	海洋 Pacific coasts	海洋黏细菌分离方法 Isolation methods for marine myxobacteria	含有脱氢甲基萘醌 Contains dihydrogenated menaquinone	10.59	70.7	[65]
Haliangium ochraceum *H. tepidum*	SMP-2^{T} SMP-10^{T}	海洋 Seaweed samples	海洋黏细菌分离方法 Isolation methods for marine myxobacteria	中度嗜盐；水解淀粉、DNA 和明胶 Moderately halophilic; Hydrolyze starch, DNA, casein and gelatin	9.45 –	69.5 –	[66]
Anaeromyxobacter dehalogenans	2CP-1^{T}	土壤和沉积物 Soils and sediments	醋酸盐作为唯一碳源和能源 Acetate as the sole carbon and energy source	兼性厌氧 Facultative anaerobic	5.03	74.7	[4]

–：参考文献中未显示此信息

–: This information is not displayed in the reference. *: Five species of *Myxococcus eversor*, *M. llanfairpwllgwyngyllgogerychwyrndrobwllllantysiliogogogochensis*, *M. vastator*, *Pyxidicoccus caerfyrddinensis* and *P. trucidator*. **: Eight species of *Corallococcus aberystwythensis*, *C. carmarthensis*, *C. exercitus*, *C. interemptor*, *C. llansteffanensis*, *C. praedator*, *C. sicarius* and *C. terminator*. ***: Seven species of *Sorangium ambruticinum*, *S. arenae*, *S. bulgaricum*, *S. dawidii*, *S. kenyense*, *S. orientale* and *S. reichenbachii*.

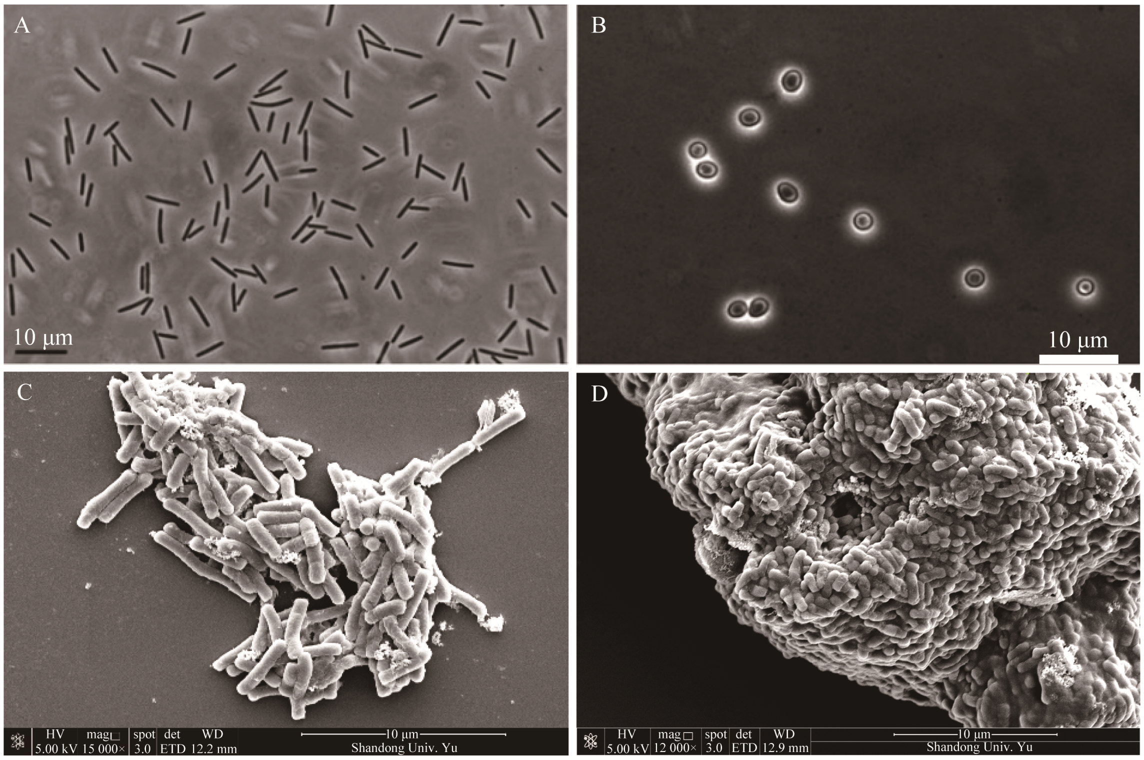

图 1　黏球菌纲、多囊菌纲的营养细胞和黏孢子形态照片　A：黏球菌纲营养细胞长杆状[67]. B：黏孢子大而圆且具有折光性[67]. C：多囊菌纲营养细胞短杆状[10]. D：黏孢子短杆状、钝圆，与营养细胞相似[10]

Figure 1　Morphologies of *Myxococcia* and *Polyangia*. A: Vegetative long-rod cells of *Myxococcia*[67]. B: Optically refractile, large, and rounded myxospores[67]. C: Vegetative short-rod cells of *Polyangia*[10]. D: Short rod shaped and blunt round myxospore-like cells[10].

2.2　多囊菌纲

多囊菌纲包含多囊菌目(*Polyangiales*)、小囊菌目(*Nannocystales*)和海生囊菌目(*Haliangiales*)。营养细胞粗短，圆柱形、末端钝圆，黏孢子在形态上与营养细胞的区别较小(图1C、1D)，菌落不吸附刚果红。多囊菌科的堆囊菌属(*Sorangium*)和嗜纤维素菌属(*Byssovorax*)是目前已知的以纤维素为主要碳源的黏细菌类群。软骨霉状菌是最早被培养的黏细菌类群,能够形成“树形”的复杂子实体结构[68]。但第一株被发现的软骨霉状菌(*Chondromyces lichenicolus*)[30]现已被归为原囊菌科的蜂窝囊菌属(*Melittangium*)[69]。堆囊菌属是最早发掘生物活性次级代谢产物的黏细菌类群之一,也是目前报道次级代谢产物最多的黏细菌类群。多囊菌属(*Polyangium*)形成的子实体通常包含多个聚在一起的小孢囊，但新报道的金色多囊菌(*P. aurulentum*)无子实体结构，而济南多囊菌(*P. jinanense*)的子实体只含有一个小孢囊[10]。橙杆菌科(*Sandaracinaceae*)目前只有一个模式种(*Sandaracinus amylolyticus*)[63]，其子实体形态不典型：类子实体无孢子囊、在琼脂平板上散落分布。小囊菌科具有蚀刻琼脂但不使琼脂液化的特点，其中邻囊菌属(*Plesiocystis*)[65]和水黏细菌属(*Enhygromyxa*)[64]分离自海洋环境。海生囊菌目包含科夫勒菌属和海生囊菌属(*Haliangium*)，海生囊菌属目前仅有 2 个模式种,是分离自海洋环境的耐盐黏细菌类群[66]。

3 未培养黏细菌

由于黏细菌的胞外黏液、液体培养细胞易聚集难分散、难以形成单菌落等限制，使用稀释涂布平板法、拮抗平板筛选法等传统的微生物分离技术几乎不能获得黏细菌。近年来，微生物分离技术已经逐步向高通量培养、针对性分离方法方向发展，并衍生出一些高效分离方法，如拉曼活细胞分选[70]、反向基因组学[71]等。但遗憾的是这些新分离技术也未成功应用于黏细菌的分离培养。目前分离黏细菌的方法主要是通过底物富集诱导法(大肠杆菌、酵母、兔粪和滤纸都是经典的底物)挑取子实体，再反复转接纯化[28,72]。黏细菌分离方法学研究一直都在进行，但基本离不开底物富集诱导法[73-77]。目前尚未实现高通量培养和对某类黏细菌的特异性富集，建立高效的黏细菌培养方法任重而道远。

长久以来，黏细菌被认为是土壤细菌。实际上黏细菌是地球上已知的最多样化、分布最为广泛的细菌类群之一，温带、热带、北极苔原、沙漠、酸性土壤、海洋及淡水都是其合适的栖息地[29,66,78-79]，显示了黏细菌对环境的广泛适应能力。我们前期基于全球微生物组(earth microbiome project, EMP)数据对黏细菌类群的分析显示，已培养黏细菌 OTU 和已测序的黏细菌 OTU 只占全部黏细菌 OTU 的 10.01%和 7.29%，属于已培养率和基因组测序率均较低的类群[79]。2019 年对 GenBank 中的全部黏细菌 16S rRNA 基因序列分析显示，黏细菌目可分为 20 个亚目，有 17 个新亚目尚未得到纯培养[80]。基于 bac120 对黏细菌门的系统发育分析显示黏细菌门仍有至少一个纲处于未培养状态[29]。综上所述，环境中仍有大量的黏细菌处于未培养状态。近年来，组学技术的发展产生了大量的微生物基因组数据[81-82]。经宏基因组组装基因组(metagenome-assembled genomes, MAG)数据预测，黏细菌的捕食和子实体形成等群体行为与对土壤生境的适应性密切相关，而未培养黏细菌的高分类单元多半来自非土壤生境或是厌氧类群[83]。在已培养黏细菌基因组和 MAGs 数据中预测到反硝化、芳烃降解、甲胺降解、好氧甲基营养和氢营养呼吸等方面的代谢基因，黏细菌在与其他甲基营养降解菌的竞争中可能发挥着意想不到的作用，并参与全球碳和氮循环[84]。此外，我们发现利用细菌通用引物对黏细菌进行多样性分析并不准确和全面，可能会忽略掉很多环境中的稀有黏细菌类群[8]。利用黏细菌半特异性引物对深海沉积物和海洋热泉口样品进行系统发育分析，结果表明黏细菌在海洋环境也普遍大量存在，且海洋黏细菌与陆生黏细菌在高分类地位上出现分化[85]。虽然来自海洋环境的黏细菌菌株已有纯培养(如海生囊菌)，但由于缺乏更多数据和系统的研究，海洋黏细菌的生理特点与基因进化等信息我们还知之甚少[86-88]。

4 总结与展望

捕食性黏细菌是一类具有重要应用潜力的微生物资源。然而受限于分离培养和纯化的困难，黏细菌资源和系统发育研究发展相对缓慢[89]。黏细菌分布极为广泛，但属于培养率较低的原核生物类群[79]。自 2000 年以来黏细菌新类群的报道绝大多数为新属和新种级别，而根据 16S rRNA 基因序列分析显示自然界存在的 20 个黏细菌亚目中有 17 个尚未得到纯培养[80]。目前黏细菌类群绝大多数分离自陆地土壤相关生境，海洋生境的黏细菌仅有小囊菌目和海生囊菌目下的 4 个属，并且来源较为单一。但细菌多样性及宏基因组分析显示海洋生境蕴藏大量海洋专属黏细菌类群，且多为未培养的高分类单元[82,90]。此外，厌氧黏细菌由于生长较为缓慢和分离培养条件更为复杂，也是一类关注度较少的黏细菌资源。

因此,改良和创新黏细菌分离培养技术显然是获取未培养黏细菌资源的关键所在。黏细菌的次级代谢产物挖掘和基因调控次级代谢产物等方面一直以来都是黏细菌应用研究中的热点[91-92]。除了具有药物先导化合物筛选价值,黏细菌还能够产生多种水解酶[93]，包括淀粉酶、几丁质酶、脂肪酶、木聚糖酶等[24,94-97]，这些降解大分子的酶具有应用潜力。有些水解酶还具有降解毒素的作用，如从黏球菌属黏细菌(*Myxococcus fulvus*)的蛋白粗提物中获得的黄曲霉素降解酶[98]。此外,研究表明黏细菌在污水处理过程中能够稳定存在且是一类优势菌,可能在污水有害物质降解的过程中发挥着重要的作用[26-27]。MAGs 数据中预测到来自热泉的黏细菌中存在聚羟基脂肪酸酯解聚酶基因，是潜在的塑料降解菌[99]。黏细菌因捕食其他微生物、形成孢子和耐受恶劣环境等生防特性,被用来尝试治理很多顽固的农业病害[100]。如珊瑚球菌属黏细菌 EGB 菌株能够抑制稻瘟病真菌(*Magnaporthe oryzae*)的孢子萌发[24]和调控黄瓜根系的菌群结构防治黄瓜枯萎病[25]等。因此，黏细菌在工业、农业、生物医学和环境保护中均具有广泛的应用潜力。但黏细菌资源的应用尚有待于对黏细菌性质的深入了解和认识，如黏细菌基因组中多拷贝分子伴侣[101-102]、黏细菌之间如何相互识别[103-104]、黏细菌的毒素分泌与免疫系统[105-107]，以及捕食机制[11]等方面正在被深入探索。此外，缺乏有效的遗传操作方法也是黏细菌研发的重要限制。

近年来,微生物培养组学的发展极大地促进了未培养和难培养微生物的分离培养,丰富了微生物资源库。未培养黏细菌的分离培养离不开组学技术的进步，基因组学研究已经为黏细菌生态、社会行为和次级代谢产物形成等方面提供了重要的理论依据，间接促进了黏细菌资源的挖掘[108]。充分利用宏基因组学、培养组学等多组学技术，结合黏细菌捕食、形成黏孢子等生活习性及生理生化特点,开展未培养黏细菌的定向富集分离和尝试高通量培养,建立起黏细菌的培养组学以及资源评估体系,已成为黏细菌资源研究和利用的迫切需求。

REFERENCES

[1] YAMAMOTO E, MURAMATSU H, NAGAI K. *Vulgatibacter incomptus* Gen. nov., sp. nov. and *Labilithrix luteola* Gen. nov., sp. nov., two myxobacteria isolated from soil in Yakushima Island, and the description of *Vulgatibacteraceae* fam. nov., *Labilitrichaceae* fam. nov. and *Anaeromyxobacteraceae* fam. nov.[J]. International Journal of Systematic and Evolutionary Microbiology, 2014, 64(Pt 10): 3360-3368.

[2] REICHENBACH H, LANG E, SCHUMANN P, SPRÖER C. *Byssovorax cruenta* Gen. nov., sp. nov., nom. rev., a cellulose-degrading myxobacterium: rediscovery of ‘*Myxococcus cruentus*’ thaxter 1897[J]. International Journal of Systematic and Evolutionary Microbiology, 2006, 56(Pt 10): 2357-2363.

[3] ITOH H, XU ZX, MISE K, MASUDA Y, USHIJIMA N, HAYAKAWA C, SHIRATORI Y, SENOO K. *Anaeromyxobacter oryzae* sp. nov., *Anaeromyxobacter diazotrophicus* sp. nov. and *Anaeromyxobacter paludicola* sp. nov., isolated from paddy soils[J]. International Journal of Systematic and Evolutionary Microbiology, 2022, 72(10).

[4] SANFORD RA, COLE JR, TIEDJE JM. Characterization and description of *Anaeromyxobacter dehalogenans* gen. nov., sp. nov., an aryl-halorespiring facultative anaerobic myxobacterium[J]. Applied and Environmental Microbiology. 2002, 68(2): 893-900.

[5] 李曙光, 周秀文, 吴志红, 李越中. 粘细菌的种群生态及其生存策略[J]. 微生物学通报, 2013, 40(1): 172-179. LI SG, ZHOU XW, WU ZH, LI YZ. Population ecology and survival strategy of myxobacteria[J]. Microbiology China, 2013, 40(1): 172-179 (in Chinese).

[6] SHIMKETS LJ. Social and developmental biology of the myxobacteria[J]. Microbiological Reviews, 1990, 54(4): 473-501.

[7] MOHR KI. Diversity of myxobacteria-we only see the tip of the iceberg[J]. Microorganisms, 2018, 6(3): 84.

[8] JIANG DM, WU ZH, ZHAO JY, LI YZ. Fruiting and non-fruiting myxobacteria: a phylogenetic perspective of cultured and uncultured members of this group[J]. Molecular Phylogenetics and Evolution, 2007, 44(2): 545-552.

[9] GARCIA R, MÜLLER R. *Simulacricoccus ruber* Gen. nov., sp. nov., a microaerotolerant, non-fruiting, myxospore-forming soil myxobacterium and emended description of the family *Myxococcaceae*[J]. International Journal of Systematic and Evolutionary Microbiology, 2018, 68(10): 3101-3110.

[10] WANG JJ, RAN Q, DU XR, WU SG, WANG JN, SHENG DH, CHEN Q, DU ZJ, LI YZ. Two new *Polyangium* species, *P. aurulentum* sp. nov. and *P. jinanense* sp. nov., isolated from a soil sample[J]. Systematic and Applied Microbiology, 2021, 44(6): 126274.

[11] MUÑOZ-DORADO J, MARCOS-TORRES FJ, GARCÍA-BRAVO E, MORALEDA-MUÑOZ A, PÉREZ J. Myxobacteria: moving, killing, feeding, and surviving together[J]. Frontiers in Microbiology, 2016, 7: 781.

[12] CHEN H, KESELER IM, SHIMKETS LJ. Genome size of *Myxococcus xanthus* determined by pulsed-field gel electrophoresis[J]. Journal of Bacteriology, 1990, 172(8): 4206-4213.

[13] MCVITTIE A, MESSIK F, ZAHLER SA. Developmental biology of *Myxococcus*[J]. Journal of Bacteriology, 1962, 84(3): 546-551.

[14] THIERY S, KAIMER C. The predation strategy of *Myxococcus xanthus*[J]. Frontiers in Microbiology, 2020, 11: 2.

[15] PÉREZ J, MORALEDA-MUÑOZ A, MARCOS-TORRES FJ, MUÑOZ-DORADO J. Bacterial predation: 75 years and counting![J]. Environmental Microbiology, 2016, 18(3): 766-779.

[16] ROSENBERG E, DELONG E F, LORY S, STACKEBRANDT E, THOMPSON F. The Family *Polyangiaceae*[M]. The Prokaryotes. New York, NY: Springer New York, 2014, (Chapter 308): 247-279.

[17] WENZEL SC, MÜLLER R. Myxobacteria: 'microbial factories' for the production of bioactive secondary metabolites[J]. Molecular BioSystems, 2009, 5(6): 567-574.

[18] HOFFMANN T, KRUG D, BOZKURT N, DUDDELA S, JANSEN R, GARCIA R, GERTH K, STEINMETZ H, MÜLLER R. Correlating chemical diversity with taxonomic distance for discovery of natural products in myxobacteria[J]. Nature Communications, 2018, 9: 803.

[19] LANDWEHR W, WOLF C, WINK J. Actinobacteria and myxobacteria-two of the most important bacterial resources for novel antibiotics[J]. Current Topics in Microbiology and Immunology, 2016, 398: 273-302.

[20] BHAT MA, MISHRA AK, BHAT MA, BANDAY MI, BASHIR O, RATHER IA, RAHMAN S, SHAH AA, JAN AT. Myxobacteria as a source of new bioactive compounds: a perspective study[J]. Pharmaceutics, 2021, 13(8): 1265.

[21] HERRMANN J, FAVAD AA, MÜLLER R. Natural products from myxobacteria: novel metabolites and bioactivities[J]. Natural Product Reports, 2017, 34(2): 135-160.

[22] SCHÄBERLE TF, LOHR F, SCHMITZ A, KÖNIG GM. Antibiotics from myxobacteria[J]. Natural Product Reports, 2014, 31(7): 953-972.

[23] WEISSMAN KJ, MÜLLER R. Myxobacterial secondary metabolites: bioactivities and modes-of-action[J]. Natural Product Reports, 2010, 27(9): 1276-1295.

[24] LI ZK, XIA CY, WANG YX, LI X, QIAO Y, LI CY, ZHOU J, ZHANG L, YE XF, HUANG Y, CUI ZL. Identification of an endo-chitinase from *Corallococcus* sp. EGB and evaluation of its antifungal properties[J]. International Journal of Biological Macromolecules, 2019, 132: 1235-1243.

[25] YE XF, LI ZK, LUO X, WANG WH, LI YK, LI R, ZHANG B, QIAO Y, ZHOU J, FAN JQ, WANG H, HUANG Y, CAO H, CUI ZL, ZHANG RF. A predatory myxobacterium controls cucumber *Fusarium* wilt by regulating the soil microbial community[J]. Microbiome, 2020, 8(1): 49.

[26] ZHOU Z, QIAO W, XING C, SHEN X, HU D, WANG L. A micro-aerobic hydrolysis process for sludge *in situ* reduction: performance and microbial community structure[J]. Bioresource Technology, 2014, 173: 452-456.

[27] WU LW, NING DL, ZHANG B, LI Y, ZHANG P, SHAN XY, ZHANG QT, BROWN MR, LI ZX, van NOSTRAND JD, LING FQ, XIAO NJ, ZHANG Y, VIERHEILIG J, WELLS GF, YANG YF, DENG Y, TU QC, WANG AJ, ZHANG T, et al. Global diversity and

biogeography of bacterial communities in wastewater treatment plants[J]. Nature Microbiology, 2019, 4(7): 1183-1195.

[28] SHIMKETS LJ, DWORKIN M, REICHENBACH H. The Myxobacteria[M]. The Prokaryotes. New York, NY: Springer New York, 2006: 31-115.

[29] WAITE DW, CHUVOCHINA M, PELIKAN C, PARKS DH, YILMAZ P, WAGNER M, LOY A, NAGANUMA T, NAKAI R, WHITMAN WB, HAHN MW, KUEVER J, HUGENHOLTZ P. Proposal to reclassify the proteobacterial classes *Deltaproteobacteria* and *Oligoflexia*, and the phylum *Thermodesulfobacteria* into four phyla reflecting major functional capabilities[J]. International Journal of Systematic and Evolutionary Microbiology, 2020, 70(11): 5972-6016.

[30] THAXTER R. On the *Myxobacteriaceae*, a new order of schizomycetes[J]. Botanical Gazette, 1892, 17(12): 389-406.

[31] BUCHANAN RE, GIBBONS NE. 伯杰细菌鉴定手册[M]. 中国科学院微生物研究所, 译. 8 版. 北京: 科学出版社, 1984
BUCHANAN RE, GIBBONS NE. Bergey's Manual of Determinative Bacteriology[M]. Institute of Microbiology, Chinese Academy of Sciences, trans. 8th ed. Beijing: Science Press, 1984 (in Chinese).

[32] MCCURDY HD. Order *Myxococcales*. Tchan, Pochon, Prevot 1948, 398 (with contributions of BROCKMAN ER, REICHENBACH H, WHITE D). In: STALEY JT, BRYANT MP, PFENNIG N, HOLT JG (Eds.)[M]// Bergey's Manual of Systematic Bacteriology. Baltimore: The Williams & Wilkins Co., 1989: vol. 3, 2139-2170.

[33] REICHENBACH H, DWORKIN M. The myxobacteria[M]// The Prokaryotes. New York, NY: Springer New York, 1992: 3416-3487.

[34] LAMPKY JR, BROCKMAN ER. Note: fluorescence of *Myxococcus stipitatus*[J]. International Journal of Systematic Bacteriology, 1977, 27(2): 161.

[35] MCCURDY HD. Studies on the taxonomy of the *Myxobacterales*. I. Record of Canadian isolates and survey of methods[J]. Canadian Journal of Microbiology, 1969, 15(12): 1453-1461.

[36] REICHENBACH H. The *Myxococcales*. Part 3: the *Beta*-, *Delta*-, and *Epsilonproteobacteria*.[M]// Bergey's Manual of Systematic Bacteriology. Garrity GM (ed.). New York, USA: Springer Verlag, 2005, 2: 1059-1143.

[37] SPRÖER C, REICHENBACH H, STACKEBRANDT E. The correlation between morphological and phylogenetic classification of myxobacteria[J]. International Journal of Systematic Bacteriology, 1999, 49 Pt 3: 1255-1262.

[38] GARCIA R, GERTH K, STADLER M, DOGMA I J, MÜLLER R. Expanded phylogeny of myxobacteria and evidence for cultivation of the 'unculturables'[J]. Molecular Phylogenetics and Evolution, 2010, 57(2): 878-887.

[39] STACKEBRANDT E, MURRAY RGE, TRUPER HG. Proteobacteria classis nov., a name for the phylogenetic taxon that includes the "purple bacteria and their relatives"[J]. International Journal of Systematic Bacteriology, 1988, 38(3): 321-325.

[40] OYAIZU H, WOESE CR. Phylogenetic relationships among the sulfate respiring bacteria, myxobacteria and purple bacteria[J]. Systematic and Applied Microbiology, 1985, 6(3): 257-263.

[41] LAPAGE S, PHA S, LESSEL E, VBD S, HPR S, CLARK WAV. International code of nomenclature of bacteria: bacteriological code, 1990 revision[J] Washington DC: American Society for Microbiology Press, 1992.

[42] EUZÉBY J. List of new names and new combinations previously effectively, but not validly, published[J]. International Journal of Systematic and Evolutionary Microbiology, 2007, 57(Pt 5): 893-897.

[43] TONINI J, MOORE A, STERN D, SHCHEGLOVITOVA M, ORTÍ G. Concatenation and species tree methods exhibit statistically indistinguishable accuracy under a range of simulated conditions[J]. PLoS Currents, 2015, 7: ecurrents.tol.34260cc27551a527b124ec5f6334b6be.

[44] GADAGKAR SR, ROSENBERG MS, KUMAR S. Inferring species phylogenies from multiple genes: concatenated sequence tree versus consensus gene tree[J]. Journal of Experimental Zoology Part B: Molecular and Developmental Evolution, 2005, 304B(1): 64-74.

[45] PARKS DH, CHUVOCHINA M, WAITE DW, RINKE C, SKARSHEWSKI A, CHAUMEIL PA, HUGENHOLTZ P. A standardized bacterial taxonomy based on genome phylogeny substantially revises the tree of life[J]. Nature Biotechnology, 2018, 36(10): 996-1004.

[46] GARCIA RO, REICHENBACH H, RING MW,

MÜLLER R. *Phaselicystis flava* Gen. nov., sp. nov., an arachidonic acid-containing soil myxobacterium, and the description of *Phaselicystidaceae* fam. nov.[J]. International Journal of Systematic and Evolutionary Microbiology, 2009, 59(Pt 6): 1524-1530.

[47] PARTE AC, SARDÀ CARBASSE J, MEIER-KOLTHOFF JP, REIMER LC, GÖKER M. List of Prokaryotic names with Standing in Nomenclature (LPSN) moves to the DSMZ[J]. International Journal of Systematic and Evolutionary Microbiology, 2020, 70(11): 5607-5612.

[48] ZHOU Y, YI SX, ZANG Y, YAO Q, ZHU HH. The predatory myxobacterium *Citreicoccus inhibens* Gen. nov. sp. nov. showed antifungal activity and bacteriolytic property against phytopathogens[J]. Microorganisms, 2021, 9(10): 2137.

[49] LIVINGSTONE PG, INGLEBY O, GIRDWOOD S, COOKSON AR, MORPHEW RM, WHITWORTH DE. Predatory organisms with untapped biosynthetic potential: descriptions of novel *Corallococcus* species *C. aberystwythensis* sp. nov., *C. carmarthensis* sp. nov., *C. exercitus* sp. nov., *C. interemptor* sp. nov., *C. llansteffanensis* sp. nov., *C. praedator* sp. nov., *C. sicarius* sp. nov., and *C. terminator* sp. nov[J]. Applied and Environmental Microbiology, 2020, 86(2): e01931-e01919.

[50] ZHANG XJ, FENG GD, LIU Y, ZHOU Y, DENG XQ, YAO Q, ZHU HH. *Corallococcus silvisoli* sp. nov, a novel myxobacterium isolated from subtropical forest soil[J]. Archives of Microbiology, 2022, 204(2): 141.

[51] CHAMBERS J, SPARKS N, SYDNEY N, LIVINGSTONE PG, COOKSON AR, WHITWORTH DE. Comparative genomics and pan-genomics of the *Myxococcaceae*, including a description of five novel species: *Myxococcus eversor* sp. nov., *Myxococcus llanfairpwllgwyngyllgogerychwyrndrobwllllantysiliogogogochensis* sp. nov., *Myxococcus vastator* sp. nov., *Pyxidicoccus caerfyrddinensis* sp. nov., and *Pyxidicoccus trucidator* sp. nov.[J]. Genome Biology and Evolution, 2020, 12(12): 2289-2302.

[52] COLWELL RR. Polyphasic taxonomy of bacteria[J]. Culture Collections of Microorganisms, 1970, 104 (1): 421-436.

[53] BABADI ZK, GARCIA R, EBRAHIMIPOUR GH, RISDIAN C, KÄMPFER P, JAREK M, MÜLLER R, WINK J. *Corallococcus* soli sp. nov., a soil myxobacterium isolated from subtropical climate, chalus County, Iran, and its potential to produce secondary metabolites[J]. Microorganisms, 2022, 10(7): 1262.

[54] MOHR KI, WOLF C, NÜBEL U, SZAFRAŃSKA AK, STEGLICH M, HENNESSEN F, GEMPERLEIN K, KÄMPFER P, MARTIN K, MÜLLER R, WINK J. A polyphasic approach leads to seven new species of the cellulose-decomposing genus *Sorangium*, *Sorangium ambruticinum* sp. nov., *Sorangium arenae* sp. nov., *Sorangium bulgaricum* sp. nov., *Sorangium dawidii* sp. nov., *Sorangium kenyense* sp. nov., *Sorangium orientale* sp. nov. and *Sorangium reichenbachii* sp. nov.[J]. International Journal of Systematic and Evolutionary Microbiology, 2018, 68(11): 3576-3586.

[55] MOHR KI, MORADI A, GLAESER SP, KÄMPFER P, GEMPERLEIN K, NÜBEL U, SCHUMANN P, MÜLLER R, WINK J. *Nannocystis konarekensis* sp. nov., a novel myxobacterium from an Iranian Desert[J]. International Journal of Systematic and Evolutionary Microbiology, 2018, 68(3): 721-729.

[56] AWAL RP, GARCIA R, GEMPERLEIN K, WINK J, KUNWAR B, PARAJULI N, MÜLLER R. *Vitiosangium cumulatum* Gen. nov., sp. nov. and *Vitiosangium subalbum* sp. nov., soil myxobacteria, and emended descriptions of the genera *Archangium* and *Angiococcus*, and of the family *Cystobacteraceae*[J]. International Journal of Systematic and Evolutionary Microbiology, 2017, 67(5): 1422-1430.

[57] MORADI A, EBRAHIMIPOUR GH, MOHR KI, KÄMPFER P, GLAESER SP, HENNESSEN F, GEMPERLEIN K, AWAL RP, WOLF C, MÜLLER R, WINK J. *Racemicystis persica* sp. nov., a myxobacterium from soil[J]. International Journal of Systematic and Evolutionary Microbiology, 2017, 67(2): 472-478.

[58] GARCIA R, STADLER M, GEMPERLEIN K, MÜLLER R. *Aetherobacter fasciculatus* Gen. nov., sp. nov. and *Aetherobacter rufus* sp. nov., novel myxobacteria with promising biotechnological applications[J]. International Journal of Systematic and Evolutionary Microbiology, 2016, 66(2): 928-938.

[59] AWAL RP, GARCIA R, MÜLLER R. *Racemicystis crocea* Gen. nov., sp. nov., a soil myxobacterium in the family *Polyangiaceae*[J]. International Journal of

Systematic and Evolutionary Microbiology, 2016, 66(6): 2389-2395.

[60] SOOD S, AWAL RP, WINK J, MOHR KI, ROHDE M, STADLER M, KÄMPFER P, GLAESER SP, SCHUMANN P, GARCIA R, MÜLLER R. *Aggregicoccus edonensis* Gen. nov., sp. nov., an unusually aggregating myxobacterium isolated from a soil sample[J]. International Journal of Systematic and Evolutionary Microbiology, 2015, 65(Pt 3): 745-753.

[61] GARCIA R, GEMPERLEIN K, MÜLLER R. *Minicystis rosea* Gen. nov., sp. nov., a polyunsaturated fatty acid-rich and steroid-producing soil myxobacterium[J]. International Journal of Systematic and Evolutionary Microbiology, 2014, 64(Pt 11): 3733-3742.

[62] IIZUKA T, JOJIMA Y, HAYAKAWA A, FUJII T, YAMANAKA S, FUDOU R. *Pseudenhygromyxa salsuginis* Gen. nov., sp. nov., a myxobacterium isolated from an estuarine marsh[J]. International Journal of Systematic and Evolutionary Microbiology, 2013, 63(Pt 4): 1360-1369.

[63] MOHR KI, GARCIA RO, GERTH K, IRSCHIK H, MÜLLER R. *Sandaracinus amylolyticus* Gen. nov., sp. nov., a starch-degrading soil myxobacterium, and description of *Sandaracinaceae* fam. nov.[J]. International Journal of Systematic and Evolutionary Microbiology, 2012, 62(Pt 5): 1191-1198.

[64] LIZUKA T, JOJIMA Y, FUDOU R, TOKURA M, HIRAISHI A, YAMANAKA S. *Enhygromyxa salina* Gen. nov., sp. nov., a slightly halophilic myxobacterium isolated from the coastal areas of Japan[J]. Systematic and Applied Microbiology, 2003, 26(2): 189-196.

[65] IIZUKA T, JOJIMA Y, FUDOU R, HIRAISHI A, AHN JW, YAMANAKA S. *Plesiocystis pacifica* Gen. nov., sp. nov., a marine myxobacterium that contains dihydrogenated menaquinone, isolated from the Pacific coasts of Japan[J]. International Journal of Systematic and Evolutionary Microbiology, 2003, 53(Pt 1): 189-195.

[66] FUDOU R, JOJIMA Y, IIZUKA T, YAMANAKA S. *Haliangium ochraceum* Gen. nov., sp. nov. and *Haliangium tepidum* sp. nov.: novel moderately halophilic myxobacteria isolated from coastal saline environments[J]. The Journal of General and Applied Microbiology, 2002, 48(2): 109-116.

[67] GARCIA R, MÜLLER R. The family *Myxococcaceae*[M]// In: ROSENBERG E, DELONG EF, LORY S, STACKEBRANDT E, THOMPSON F (editors). The Prokaryotes, 4th ed, vol. 10. Heidelberg: Springer; 2014: 191-212.

[68] THAXTER R. Contributions from the cryptogamic laboratory of Harvard University. XXXIX. further observations on the *Myxobacteriaceae*[J]. Botanical Gazette, 1897, 23(6): 395-411.

[69] MCCURDY HD. Studies on the taxonomy of the *Myxobacterales*: IV. *Melittangium*[J]. International Journal of Systematic Bacteriology, 1971, 21(1): 50-54.

[70] LEE KS, PEREIRA FC, PALATINSZKY M, BEHRENDT L, ALCOLOMBRI U, BERRY D, WAGNER M, STOCKER R. Optofluidic Raman-activated cell sorting for targeted genome retrieval or cultivation of microbial cells with specific functions[J]. Nature Protocols, 2021, 16(2): 634-676.

[71] CROSS KL, CAMPBELL JH, BALACHANDRAN M, CAMPBELL AG, COOPER CJ, GRIFFEN A, HEATON M, JOSHI S, KLINGEMAN D, LEYS E, YANG Z, PARKS JM, PODAR M. Targeted isolation and cultivation of uncultivated bacteria by reverse genomics[J]. Nature Biotechnology, 2019, 37(11): 1314-1321.

[72] 李越中, 李健. 粘细菌的分离与纯化[J]. 微生物学通报, 1997, 24(4): 237-240.
LI YZ, LI J. Isolation and purification of myxobacteria[J]. Microbiology China, 1997, 24(4): 237-240 (in Chinese).

[73] 张宜涛, 惠明, 田青. 粘细菌的分离筛选方法及其应用前景[J]. 生物技术, 2010, 20(6): 95-98.
ZHANG YT, HUI M, TIAN Q. Screening of myxobacteria and its application prospects[J]. Biotechnology, 2010, 20(6): 95-98 (in Chinese).

[74] 常宁宁, 欧一新, 徐庆妍, 钱晓鸣, 郑忠辉, 黄耀坚. 粘细菌的分离鉴定及活性检测[J]. 厦门大学学报(自然科学版), 2012, 51(1): 112-116.
CHANG NN, OU YX, XU QY, QIAN XM, ZHENG ZH, HUANG YJ. The isolation, identification and activity assays of the myxobacteria[J]. Journal of Xiamen University (Natural Science Edition), 2012, 51(1): 112-116 (in Chinese).

[75] 王婷. 新型生防粘细菌 *Myxococcus* sp. BS 的分离及粘细菌对细菌性软腐病菌的捕食机理研究[D]. 南京: 南京农业大学硕士学位论文, 2018.
WANG T. Isolation of a new biocontrol *Myxococcus* sp.

BS and the myxobacterial predation mechanism against bacterial soft rot[D]. Nanjing: Master's Thesis of Nanjing Agricultural University, 2018 (in Chinese).

[76] 周杨，蚁烁星，张鲜姣，姚青，朱红惠. 基于细菌共现网络的土壤粘细菌分离[J]. 生物资源，2020，42(5): 531-539.
ZHOU Y, YI SX, ZHANG XJ, YAO Q, ZHU HH. Isolation of soil myxobacteria based on bacterial co-occurrence network[J]. Biotic Resources, 2020, 42(5): 531-539 (in Chinese).

[77] 蚁烁星，周杨，张鲜姣，姚青，李华平，朱红惠. 不同分离方法对子实体形成和粘细菌分离的影响[J]. 微生物学报, 2021, 61(4): 923-934.
YI SX, ZHOU Y, ZHANG XJ, YAO Q, LI HP, ZHU HH. Effects of different methods on the formation of fruiting bodies and isolation of myxobacteria[J]. Acta Microbiologica Sinica, 2021, 61(4): 923-934 (in Chinese).

[78] DAWID W. Biology and global distribution of myxobacteria in soils[J]. FEMS Microbiology Reviews, 2000, 24(4): 403-427.

[79] WANG JJ, WANG JN, WU SG, ZHANG Z, LI YZ. Global geographic diversity and distribution of the myxobacteria[J]. Microbiology Spectrum, 2021, 9(1): e0001221.

[80] LIU Y, YAO Q, ZHU HH. Meta-16S rRNA gene phylogenetic reconstruction reveals the astonishing diversity of cosmopolitan myxobacteria[J]. Microorganisms, 2019, 7(11): 551.

[81] ANANTHARAMAN K, BROWN CT, HUG LA, SHARON I, CASTELLE CJ, PROBST AJ, THOMAS BC, SINGH A, WILKINS MJ, KARAOZ U, BRODIE EL, WILLIAMS KH, HUBBARD SS, BANFIELD JF. Thousands of microbial genomes shed light on interconnected biogeochemical processes in an aquifer system[J]. Nature Communications, 2016, 7: 13219.

[82] PARKS DH, RINKE C, CHUVOCHINA M, CHAUMEIL PA, WOODCROFT BJ, EVANS PN, HUGENHOLTZ P, TYSON GW. Recovery of nearly 8, 000 metagenome-assembled genomes substantially expands the tree of life[J]. Nature Microbiology, 2017, 2(11): 1533-1542.

[83] MURPHY CL, YANG R, DECKER T, CAVALLIERE C, ANDREEV V, BIRCHER N, CORNELL J, DOHMEN R, PRATT CJ, GRINNELL A, HIGGS J, JETT C, GILLETT E, KHADKA R, MARES S, MEILI C, LIU J, MUKHTAR H, ELSHAHED MS, YOUSSEF NH. Genomes of novel *Myxococcota* reveal severely curtailed machineries for predation and cellular differentiation[J]. Applied and Environmental Microbiology, 2021, 87(23): e0170621.

[84] LANGWIG MV, de ANDA V, DOMBROWSKI N, SEITZ KW, RAMBO IM, GREENING C, TESKE AP, BAKER BJ. Large-scale protein level comparison of *Deltaproteobacteria* reveals cohesive metabolic groups[J]. The ISME Journal, 2022, 16(1): 307-320.

[85] LI ZF, LI X, LIU H, LIU X, HAN K, WU ZH, HU W, LI FF, LI YZ. Genome sequence of the halotolerant marine bacterium *Myxococcus fulvus* HW-1[J]. Journal of Bacteriology, 2011, 193(18): 5015-5016.

[86] LI YZ, HU W, ZHANG YQ, QIU ZJ, ZHANG Y, WU BH. A simple method to isolate salt-tolerant myxobacteria from marine samples[J]. Journal of Microbiological Methods, 2002, 50(2): 205-209.

[87] ZHANG YQ, LI YZ, WANG B, WU ZH, ZHANG CY, GONG X, QIU ZJ, ZHANG Y. Characteristics and living patterns of marine myxobacterial isolates[J]. Applied and Environmental Microbiology, 2005, 71(6): 3331-3336.

[88] JIANG DM, KATO C, ZHOU XW, WU ZH, SATO T, LI YZ. Phylogeographic separation of marine and soil myxobacteria at high levels of classification[J]. The ISME Journal, 2010, 4(12): 1520-1530.

[89] 王春玲，吕颖颖，姚青，李安章，朱红惠. 粘细菌资源挖掘与多相分类研究进展[J]. 微生物学通报，2021, 48(8): 2870-2880.
WANG CL, LÜ YY, YAO Q, LI AZ, ZHU HH. Research progress in resources mining and polyphase classification of myxobacteria[J]. Microbiology China, 2021, 48(8): 2870-2880 (in Chinese).

[90] BRINKHOFF T, FISCHER D, VOLLMERS J, VOGET S, BEARDSLEY C, THOLE S, MUSSMANN M, KUNZE B, WAGNER-DÖBLER I, DANIEL R, SIMON M. Biogeography and phylogenetic diversity of a cluster of exclusively marine myxobacteria[J]. The ISME Journal, 2012, 6(6): 1260-1272.

[91] HU JQ, WANG JJ, LI YL, ZHUO L, ZHANG A, SUI HY, LI XJ, SHEN T, YIN YZ, WU ZH, HU W, LI YZ, WU CS. Combining NMR-based metabolic profiling and genome mining for the accelerated discovery of archangiumide, an allenic macrolide from the

myxobacterium *Archangium violaceum* SDU8[J]. Organic Letters, 2021, 23(6): 2114-2119.

[92] LI YL, ZHUO L, LI XB, ZHU YQ, WU SG, SHEN T, HU W, LI YZ, WU CS. Myxadazoles, myxobacterium-derived isoxazole-benzimidazole hybrids with cardiovascular activities[J]. Angewandte Chemie (International Ed in English), 2021, 60(40): 21679-21684.

[93] 徐欣, 李安章, 徐帅帅, 姚青, 朱红惠. 粘细菌产生的水解酶类研究进展[J]. 微生物学通报, 2021, 48(1): 253-265.
XU X, LI AZ, XU SS, YAO Q, ZHU HH. Research progress on hydrolytic enzymes produced by Myxobacteria[J]. Microbiology China, 2021, 48(1): 253-265 (in Chinese).

[94] SÁNCHEZ-SUTIL MC, GÓMEZ-SANTOS N, MORALEDA-MUÑOZ A, MARTINS LO, PÉREZ J, MUÑOZ-DORADO J. Differential expression of the three multicopper oxidases from *Myxococcus xanthus*[J]. Journal of Bacteriology, 2007, 189(13): 4887-4898.

[95] CHENG YY, QIAN YK, LI ZF, WU ZH, LIU H, LI YZ. A novel cold-adapted lipase from *Sorangium cellulosum* strain So0157-2: gene cloning, expression, and enzymatic characterization[J]. International Journal of Molecular Sciences, 2011, 12(10): 6765-6780.

[96] WANG SY, HU W, LIN XY, WU ZH, LI YZ. A novel cold-active xylanase from the cellulolytic myxobacterium *Sorangium cellulosum* So9733-1: gene cloning, expression, and enzymatic characterization[J]. Applied Microbiology and Biotechnology, 2012, 93(4): 1503-1512.

[97] SHARMA G, KHATRI I, SUBRAMANIAN S. Complete genome of the starch-degrading myxobacteria *Sandaracinus amylolyticus* DSM 53668^T[J]. Genome Biology and Evolution, 2016, 8(8): 2520-2529.

[98] ZHAO LH, GUAN S, GAO X, MA QG, LEI YP, BAI XM, JI C. Preparation, purification and characteristics of an aflatoxin degradation enzyme from *Myxococcus fulvus* ANSM068[J]. Journal of Applied Microbiology, 2011, 110(1): 147-155.

[99] VILJAKAINEN VR, HUG LA. The phylogenetic and global distribution of bacterial polyhydroxyalkanoate bioplastic-degrading genes[J]. Environmental Microbiology, 2021, 23(3): 1717-1731.

[100] 李周坤, 叶现丰, 杨凡, 黄彦, 范加勤, 王辉, 崔中利. 黏细菌捕食生物学研究进展及其在农业领域的应用潜力[J]. 南京农业大学学报, 2021, 44(2): 208-216.
LI ZK, YE XF, YANG F, HUANG Y, FAN JQ, WANG H, CUI ZL. The predation biology of myxobacteria and its application in agricultural field[J]. Journal of Nanjing Agricultural University, 2021, 44(2): 208-216 (in Chinese).

[101] ZHUO L, ZHANG Z, PAN Z, SHENG DH, HU W, LI YZ. *CIRCE* element evolved for the coordinated transcriptional regulation of bacterial duplicate *groEL*s[J]. Biochimica et Biophysica Acta (BBA) - Gene Regulatory Mechanisms, 2018, 1861(10): 928-937.

[102] PAN Z, ZHANG Z, ZHUO L, WAN TY, LI YZ. Bioinformatic and functional characterization of Hsp70s in *Myxococcus xanthus*[J]. mSphere, 2021, 6(3): e00305-21.

[103] GONG Y, ZHANG Z, ZHOU XW, ANWAR MN, HU XZ, LI ZS, CHEN XJ, LI YZ. Competitive interactions between incompatible mutants of the social bacterium *Myxococcus xanthus* DK1622[J]. Frontiers in Microbiology, 2018, 9: 1200.

[104] GONG Y, ZHANG Z, LIU Y, ZHOU XW, ANWAR MN, LI ZS, HU W, LI YZ. A nuclease-toxin and immunity system for kin discrimination in *Myxococcus xanthus*[J]. Environmental Microbiology, 2018, 20(7): 2552-2567.

[105] LIU Y, WANG JN, ZHANG Z, WANG F, GONG Y, SHENG DH, LI YZ. Two PAAR proteins with different C-terminal extended domains have distinct ecological functions in *Myxococcus xanthus*[J]. Applied and Environmental Microbiology, 2021, 87(9): e00080-e00021.

[106] ZHANG Z, LIU Y, ZHANG P, WANG JN, LI DD, LI YZ. PAAR proteins are versatile clips that enrich the antimicrobial weapon arsenals of prokaryotes[J]. mSystems, 2021, 6(6): e0095321.

[107] 刘亚. 黄色黏球菌PAAR蛋白功能及其携带毒素机制研究[D]. 济南: 山东大学博士学位论文, 2021.
LIU Y. Study on the function of PAAR protein of *Myxococcus flavus* and its toxin-carrying mechanism[D]. Ji'nan: Doctoral Dissertation of Shandong University, 2021 (in Chinese).

[108] 王春玲, 冯广达, 姚青, 李安章, 朱红惠. 粘细菌基因组学研究进展[J]. 微生物学通报, 2019, 46(9): 2394-2403.
WANG CL, FENG GD, YAO Q, LI AZ, ZHU HH. Research progress in genomics of myxobacteria[J]. Microbiology China, 2019, 46(9): 2394-2403 (in Chinese).