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Review 综述

二态性柄细菌的生活史与环境适应策略

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摘　要：二态性柄细菌(dimorphic prosthecate bacteria, DPB)是一类通过不对称分裂方式繁殖的原核生物，可产生2种在形态与功能上高度分化的子代细胞。这一独特的生活史策略使其在营养匮乏环境中占据竞争优势，并成为研究细菌发育调控、形态进化与生态适应的理想模型。本文系统梳理了该类群的分类学进展、生活史调控的分子机这一独特的生活史策略，使其在营养匮乏环境中占据竞争优势，并因而成为研究细菌发育调控、形态进化与生态适应的理想模型。本文系统梳理了该类群的分类学进展、生活史调控的分子机制、广泛的生态分布及其环境适应策略，并探讨了其在环境修复与生物技术领域的应用潜力。最后，本文结合当前研究现状，对未来研究方向进行了展望，为深入理解该类细菌的生物学特性与开发其应用价值提供参考。

关键词：二态性柄细菌；生活史；生态分布；环境适应；生物技术应用

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Lifestyle and environmental adaptation strategies of dimorphic prosthecate bacteria

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Abstract: Dimorphic prosthecate bacteria (DPB) are a group of prokaryotes that reproduce through asymmetric division, producing two morphologically and functionally highly differentiated daughter cells. This unique lifestyle strategy endows them with a competitive advantage in nutrient-poor environments and makes them ideal models for studying bacterial developmental regulation, morphological evolution, and ecological adaptation. This review systematically summarizes the research progress in DPB in terms of their taxonomy, molecular mechanisms of lifestyle regulation, extensive ecological distribution, and environmental adaptation strategies. Additionally, it discusses the application potential of DPB in environmental remediation and biotechnology. Finally, this review makes an outlook on future research directions, aiming to provide a reference for deeply understanding the biological characteristics of these bacteria and expanding their application value.
Keywords: dimorphic prosthecate bacteria; lifestyle; ecological distribution; environmental adaptation; biotechnology application

原核生物在长期进化过程中演化出丰富多样的形态与生活史策略，以适应复杂多变的生态环境[1]。其中，二态性柄细菌(dimorphic prosthecate bacteria, DPB)因其独特的形态和生活史而受到广泛研究[2]。与其他常见细菌通过对称分裂产生 2 个相同的子细胞不同，DPB 的一次分裂会产生 2 个命运截然不同的后代：一个是可以借助鞭毛游动、探索新环境的游动细胞，另一个则是通过一根称为“柄”的细胞附属物附着在表面并负责生长和繁殖的柄细胞[3-4]。这种“一个定居，一个远航”的策略，完美地实现了在稳定环境中进行资源利用与在不确定环境中分散风险之间的平衡，被认为是细菌在寡营养环境中取得成功的关键适应机制之一[5-6]。

1935 年，科学家首次使用“二态性”和“柄”来描述这类细菌的特征[7]。自此，DPB 不断从各种栖息地被分离出来。随着分子生物学、高分辨率显微镜及生物信息学技术的快速发展，DPB 研究已深入细胞生物学、生态学、进化生物学及生物技术等多个领域。从解析其复杂的细胞周期调控网络，到揭示其在生态系统中的功能角色，DPB 正逐渐成为理解原核生物生命过程的重要模式系统[8]。尽管已取得显著研究进展，但对 DPB 的认识仍存在大量空白。例如，其二态性生命周期的进化起源与深层动力尚不明确；其标志性结构——柄和固着器(holdfast)的精确合成机制与多功能性仍有待揭示；它们在复杂自然生态系统中的互作网络与具体功能角色也需要更深入的探索。因此，系统性地梳理该领域的研究现状对于明确未来研究方向至关重要。

本文系统总结 DPB 的分类学多样性、生态分布规律，剖析其独特生活史的细胞与分子调控基础，探讨其多样化的环境生存策略，并评

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述其潜在的生态功能与生物技术应用价值。最后，本文将基于当前研究的瓶颈，提出未来值得关注的关键科学问题与发展方向，以期为推动该领域的持续发展提供有价值的参考。

1 二态性柄细菌的多样性及分布特征

截至 2025 年 10 月，依据国际原核生物命名法规 (international code of nomenclature of prokaryotes, ICNP)及国际原核生物分类命名数据库 (list of prokaryotic names with standing in nomenclature, LPSN)，并结合已明确具备二态性生活史与典型形态特征的文献进行统计，具有正确名称(correct name)且符合 DPB 定义的类群在系统分类学上归属于假单胞菌门(*Pseudomonadota*) α-变形菌纲(*Alphaproteobacteria*)[9]。该类群分布于 5 个目(仅各目中的部分类群)：柄杆菌目(*Caulobacterales*)、生丝单胞菌目(*Hyphomonadales*)、海茎状菌目(*Maricaulales*)、根瘤菌目(*Rhizobiales*)和鞘氨醇单胞菌目(*Sphingomonadales*)；共涉及 7 个科(同样仅各科中的部分成员)：柄杆菌科(*Caulobacteraceae*)、生丝微菌科(*Hyphomicrobiaceae*)、生丝单胞菌科(*Hyphomonadaceae*)、海茎状菌科(*Maricaulaceae*)、小棒菌科(*Parvibaculaceae*)、锈色腊肠梭菌科(*Robiginitomaculaceae*)及鞘氨醇单胞菌科(*Sphingomonadaceae*)。经严格筛选，符合上述形态与生活史特征的类群共计 31 属 106 种(表 1)。基于 16S rRNA 基因序列构建的系统发育树进一步揭示了这些类群在进化过程中的亲缘关系与分化格局(图 1)。需要指出的是，本文统计范围仅限于已明确鉴定并正确命名的类群。可能尚有部分菌株具备 DPB 特征，但因缺乏详尽的形态与生活史资料而未被纳入。因此，DPB 的实际分类多样性可能高于本文所列数据，未来研究有必要结合多相分类方法进一步确认和扩充此类群的分类范围。

DPB 高度的系统发育多样性与其广泛的生态分布相对应。综合传统培养与高通量分子检测(如 16S rRNA 基因扩增子测序、宏基因组学)的数据，DPB 几乎存在于任何类型的水体环境中[10-11]。它们是典型的水生寡营养微生物，在开放的海洋[12]、河口[13]、溪流[14]、水库[15]、盐水[16]和井水[17]等淡水与海水生境中无处不在。事实上，有观点认为柄杆菌属(*Caulobacter*)在水体中的分布范围和丰度可能仅次于假单胞菌属(*Pseudomonas*)[18]。然而，DPB 的生态位远不止水体，它们同样是陆生环境的常见成员，广泛分布于各种类型的沉积物[19]和土壤[20]中。更为突出的是，DPB 常作为附生菌，存在于多种藻类[21]和动植物体表[22-23]。此外，在相对高营养含量的环境中，如活性污泥[24]、废水[25]、生物反应器[26]和植物根际[27]，或高毒性的环境，如金属矿床[28]、油藏[29]和石油污染的土壤[28]中也存在 DPB。

环境因子对 DPB 的分布格局起着关键的塑造作用。多数已培养的 DPB 倾向于中温(20−37 ℃)、中性至微碱性(pH 6.0−9.0)及中等盐度(10−50 g/L NaCl)的环境条件(表 1)，但也有部分物种如耐盐短波单胞菌(*Brevundimonas halotolerans*) MCS 24^T 对盐度的耐受能力可达 80 g/L，展现出极强的生理适应性[30]。

2 二态性柄细菌的生活史

DPB 最核心的生物学特征在于其受到精密调控的二态性生活史，这比常见的对称二分裂复杂得多。根据子细胞产生部位的不同，DPB 的生活史分为 2 种模式：非对称二分裂和出芽分裂。在统计的物种中有 63 种 DPB 采用前者，43 种采用后者(图 1)。其中，弧形柄杆菌(*Caulobacter vibrioides*) CB15[7,31]和罗马海神生丝单胞菌(*Hyphomonas neptunium*) LE670[32-33]分别是 2 种分裂方式中研究最深入的模式菌株。

表1　二态性柄细菌分类特征

Table 1　Taxonomic characteristics of dimorphic prosthecate bacteria

Order	Family	Genus	Species	Mode of division	Source	Growth temperature (optimal)/°C	Growth pH (optimal)	Growth NaCl (optimal)/ (g/L)
Caulobacterales	*Caulobacteraceae*	*Asticcacaulis*	*Asticcacaulis benevestitus*	BIN	Soil	4−28 (15−20)	4.5−8.0 (5.6−6.0)	0−20 (ND)
			Asticcacaulis biprosthecius	BIN	Freshwater	30 (ND)	ND (ND)	ND (ND)
			Asticcacaulis endophyticus	BIN	Soil	7−33 (25−28)	6.0−10.0 (7.0−8.0)	0−10 (ND)
			Asticcacaulis excentricus	BIN	Freshwater	10−40 (ND)	ND (ND)	ND (ND)
			Asticcacaulis solisilvae	BIN	Soil	10−37 (25−30)	4.5−9.5 (5.0−7.0)	0−10 (ND)
			Asticcacaulis taihuensis	BIN	Freshwater	30 (ND)	ND (ND)	0−20 (ND)
		Brevundimonas	*Brevundimonas abyssalis*	BIN	Ocean	2−41 (20)	6.5−10.0 (7.5)	10−40 (15)
			Brevundimonas alba	BIN	Soil	30 (ND)	ND (ND)	0−80 (5−20)
			Brevundimonas aurantiaca	BIN	Alga	30 (ND)	ND (ND)	0−80 (5−20)
			Brevundimonas aveniformis	BIN	Activated sludge	15−35 (30)	6.0−9.0 (8.0)	0−10 (5)
			Brevundimonas bacteroides	BIN	Freshwater	30 (ND)	ND (ND)	0−80 (5−20)
			Brevundimonas balnearis	BIN	Freshwater	10−45 (20−30)	7.0−10.0 (8.0−9.0)	0−10 (0−10)
			Brevundimonas canariensis	BIN	Soil	15−37 (30)	6.0−8.0 (7.0)	0−50 (ND)
			Brevundimonas denitrificans	BIN	Ocean	8−30 (25)	6.0−10.0 (7.0−8.0)	10−30 (10)
			Brevundimonas diminuta	BIN	Freshwater	30 (28)	ND (ND)	ND (ND)
			Brevundimonas goettingensis	BIN	Freshwater	10−40 (30)	ND (ND)	0−40 (30)
			Brevundimonas halotolerans	BIN	Freshwater	10−40 (20−30)	ND (ND)	0−80 (5−30)
			Brevundimonas intermedia	BIN	Freshwater	30 (ND)	ND (ND)	ND (ND)
			Brevundimonas poindexterae	BIN	Activated sludge	20−40 (25)	ND (ND)	0−40 (17.5)
			Brevundimonas staleyi	BIN	Activated sludge	10−40 (30)	ND (ND)	5−30 (17.5)
			Brevundimonas subvibrioides	BIN	Freshwater	30 (ND)	ND (ND)	0−20 (20)
		Caulobacter	*Caulobacter daechungensis*	BIN	Freshwater	4−32 (30)	6.0−9.0 (7.0)	0−10 (ND)

(待续)

(续表 1)

Order	Family	Genus	Species	Mode of division	Source	Growth temperature (optimal)/°C	Growth pH (optimal)	Growth NaCl (optimal)/ (g/L)
			Caulobacter flavus	BIN	Soil	10−37 (28−30)	5.0−10.0 (7.0)	0−20 (ND)
			Caulobacter fusiformis	BIN	Freshwater	30 (ND)	ND (ND)	ND (ND)
			Caulobacter ginsengisoli	BIN	Soil	20−30 (25)	5.5−8.0 (6.5−7.0)	0−10 (ND)
			Caulobacter henricii	BIN	Freshwater	30 (ND)	ND (ND)	ND (ND)
			Caulobacter profundus	BIN	Freshwater	4−30 (25−30)	6.0−9.0 (7.0)	10−50 (ND)
			Caulobacter rhizosphaerae	BIN	Soil	10−30 (ND)	6.0−9.0 (ND)	0−10 (ND)
			Caulobacter segnis	BIN	Soil	30 (ND)	ND (ND)	ND (ND)
			Caulobacter vibrioides	BIN	Freshwater	30 (ND)	5.0−10.0 (ND)	0 (ND)
		Phenylobacterium	*Phenylobacterium conjunctum*	BIN	Freshwater	20−40 (ND)	7.0−9.0 (8.0)	0−10 (5)
		Terricaulis	*Terricaulis silvestris*	BUD	Soil	10−30 (27)	6.1−8.3 (6.5−7.9)	0 (ND)
Hyphomonadales	*Hyphomonadaceae*	*Hyphomonas*	*Hyphomonas adhaerens*	BUD	Ocean	ND (25−37)	ND (5.7−8.7)	15−120 (ND)
			Hyphomonas atlantica	BUD	Ocean	10−37 (25−37)	5.0−9.0 (6.0−8.0)	5−120 (5−70)
			Hyphomonas beringensis	BUD	Ocean	4−37 (25−30)	5.0−8.0 (6.0−9.0)	5−120 (5−70)
			Hyphomonas chukchiensis	BUD	Ocean	10−37 (25−30)	6.0−9.0 (6.0−8.0)	0−150 (0−70)
			Hyphomonas hirschiana	BUD	Ocean	4−37 (25−30)	5.0−10.0 (6.0−8.0)	0−70 (0−30)
			Hyphomonas jannaschiana	BUD	Ocean	4−37 (25−30)	6.0−10.0 (6.0−8.0)	0−70 (0−30)
			Hyphomonas johnsonii	BUD	Ocean	4−37 (25−30)	6.0−9.0 (6.0−8.0)	5−90 (5−70)
			Hyphomonas neptunium	BUD	Ocean	4−37 (25−30)	5.0−10.0 (6.0−8.0)	0−120 (5−70)
			Hyphomonas oceanitis	BUD	Ocean	4−37 (25−30)	3.0−10.0 (5.0−7.0)	20−150 (5−70)
			Hyphomonas polymorpha	BUD	Ocean	4−37 (25−30)	5.0−9.0 (6.0−8.0)	0−90 (0−30)
			Hyphomonas rosenbergii	BUD	Ocean	ND (25−45)	5.7−8.9 (ND)	10−20 (ND)
		Asprobacter	*Asprobacter aquaticus*	BUD	Freshwater	15−37 (30)	7.0 (ND)	0−10 (ND)

(待续)

(续表 1)

Order	Family	Genus	Species	Mode of division	Source	Growth temperature (optimal)/°C	Growth pH (optimal)	Growth NaCl (optimal)/ (g/L)
		Henriciella	*Henriciella algicola*	BIN	Alga	10−40 (20−40)	6.0−9.0 (ND)	5−100 (20−100)
			Henriciella barbarensis	BIN	Ocean	10−40 (20−40)	6.0−9.0 (ND)	5−100 (20−80)
		Hirschia	*Hirschia baltica*	BUD	Freshwater	ND (22−28)	7.0 (ND)	ND (ND)
			Hirschia litorea	BUD	Ocean	4−37 (25)	5.5−8.0 (7.5)	5−70 (20)
			Hirschia maritima	BUD	Ocean	10−30 (30)	6.1−10.1 (8.1−9.1)	10 (ND)
		Ponticaulis	*Ponticaulis koreensis*	BIN	Ocean	10−42 (30−37)	6.1−10.1 (7.1)	0−60 (ND)
Maricaulales	*Robiginitomaculaceae*	*Robiginitomaculum*	*Robiginitomaculum antarcticum*	BIN	Ocean	3−25 (20)	5.0−10.0 (7.0)	5−50 (22.5)
		Hellea	*Hellea balneolensis*	BUD	Ocean	15−37 (30)	6.0−8.0 (7.0)	0.2−50 (30)
		Litorimonas	*Litorimonas cladophorae*	BIN	Alga	4−35 (25−28)	5.5−10.0 (7.5)	10−50 (15−20)
			Litorimonas haliclonae	BIN	Ocean	4−34 (20−34)	4.5−10.0 (7.5)	5−95 (35)
			Litorimonas taeanensis	BUD	Soil	15−40 (25−30)	6.0−9.0 (7.0−8.0)	10−60 (20−30)
		Algimonas	*Algimonas porphyrae*	BIN	Alga	10−30 (20)	6.0−9.0 (7.5)	10−50 (25)
			Algimonas ampicilliniresistens	BIN	Alga	10−30 (20)	6.0−9.0 (7.0)	10−50 (30)
			Algimonas arctica	BIN	Soil	4−30 (25)	5.0−9.0 (7.0−8.0)	5−60 (20−30)
		Fretibacter	*Fretibacter rubidus*	BUD	Ocean	15−30 (30)	6.0−10.0 (8.5)	30−50 (30)
Maricaulales	*Maricaulaceae*	*Alkalicaulis*	*Alkalicaulis satelles*	BIN	Freshwater	5−46 (35−40)	7.3−10.3 (8.0−9.0)	0−140 (20−60)
		Glycocaulis	*Glycocaulis abyssi*	BIN	Ocean	15−35 (30)	6.0−8.0 (7.0)	20−100 (40)
			Glycocaulis albus	BIN	Soil	15−40 (25−37)	7.0−8.6 (8.0)	10−50 (10−30)
			Glycocaulis alkaliphilus	BIN	Freshwater	20−37 (30−37)	8.0−10.0 (9.0)	10−50 (10−50)
		Hyphobacterium	*Hyphobacterium vulgare*	BIN	Ocean	10−45 (30)	6.5−9.0 (7.5−8.5)	10−60 (10−20)
			Hyphobacterium indicum	BIN	Ocean	10−40 (28)	5.0−8.0 (6.0−7.0)	10−60 (20−30)

(待续)

(续表 1)

Order	Family	Genus	Species	Mode of division	Source	Growth temperature (optimal)/°C	Growth pH (optimal)	Growth NaCl (optimal)/ (g/L)
		Maricaulis	*Maricaulis maris*	BIN	Ocean	15−35 (20−25)	6.0−8.0 (7.0)	0−100 (20−60)
			Maricaulis parjimensis	BIN	Ocean	10−50 (30−40)	ND (ND)	5−100 (20−80)
			Maricaulis salignorans	BIN	Ocean	10−50 (30−40)	7.0 (ND)	0−80 (20−60)
			Maricaulis virginensis	BIN	Ocean	10−20 (20−40)	7.0 (ND)	ND (5−100)
			Maricaulis washingtonensis	BIN	Ocean	10−50 (30−40)	7.0 (ND)	0−80 (20−40)
		Marinicauda	*Marinicauda algicola*	BIN	Alga	15−45 (40)	6.0−9.0 (7.0)	0−100 (20)
			Marinicauda pacifica	BIN	Ocean	6−40 (30)	6.0−9.5 (7.0)	5−120 (20)
			Marinicauda salina	BIN	Ocean	15−45 (37−40)	6.0−9.5 (7.0−7.5)	10−160 (50)
		Oceanicaulis	*Oceanicaulis alexandrii*	BIN	Ocean	4−37 (30)	7.0 (ND)	20−100 (ND)
			Oceanicaulis stylophorae	BIN	Ocean	15−45 (37.5)	6.0−10.0 (8.0)	0−90 (15)
		Woodsholea	*Woodsholea maritima*	BIN	Freshwater	20−40 (30)	6.0−8.0 (7.0)	ND (5−100)
		Photocaulis	*Photocaulis sulfatitolerans*	BIN	Freshwater	4−41 (32)	6.5−11.0 (7.0)	50−650 (250−350)
			Photocaulis rubescens	BIN	Freshwater	4−42 (28)	6.5−11.0 (8.5)	50−650 (50−150)
Rhizobiales	*Hyphomicrobiaceae*	*Filomicrobium*	*Filomicrobium fusiforme*	BUD	Freshwater	ND (20−28)	ND (ND)	ND (ND)
			Filomicrobium insigne	BUD	Soil	4−45 (28−30)	6.0−9.0 (7.0−7.5)	0−70 (ND)
		Hyphomicrobium	*Hyphomicrobium denitrificans*	BUD	ND	30 (ND)	6.0−8.0 (ND)	ND (ND)
			Hyphomicrobium nitrativorans	BUD	Ocean	15−35 (32.5)	7.0−9.5 (8.0)	0−10 (2.5)
			Hyphomicrobium sulfonivorans	BUD	Soil	15−37 (30)	ND (7.3−7.6)	0−15 (ND)
			Hyphomicrobium chloromethanicum	BUD	Soil	ND (28−30)	ND (6.5−7.5)	ND (ND)
			Hyphomicrobium coagulans	BUD	ND	ND (ND)	ND (ND)	ND (ND)

(待续)

(续表 1)

Order	Family	Genus	Species	Mode of division	Source	Growth temperature (optimal)/°C	Growth pH (optimal)	Growth NaCl (optimal)/ (g/L)
			Hyphomicrobium facile subsp. *facile*	BUD	ND	ND (ND)	ND (ND)	ND (ND)
			Hyphomicrobium facile subsp. *tolerans*	BUD	ND	ND (ND)	ND (ND)	ND (ND)
			Hyphomicrobium facile subsp. *ureaphilum*	BUD	ND	ND (ND)	ND (ND)	ND (ND)
			Hyphomicrobium hollandicum	BUD	ND	ND (ND)	ND (ND)	ND (ND)
			Hyphomicrobium methylovorum	BUD	Soil	ND (ND)	ND (ND)	ND (ND)
			Hyphomicrobium vulgare	BUD	Freshwater	ND (ND)	ND (ND)	ND (ND)
			Hyphomicrobium zavarzinii	BUD	ND	ND (ND)	ND (ND)	ND (ND)
		Pedomicrobium	*Pedomicrobium americanum*	BUD	Freshwater	15−41 (29−32)	ND (7.3−7.6)	1 (ND)
			Pedomicrobium australicum	BUD	Freshwater	15−36 (ND)	ND	ND (ND)
			Pedomicrobium ferrugineum	BUD	Freshwater	10−40 (ND)	3.5−10.0 (ND)	ND (ND)
			Pedomicrobium manganicum	BUD	Freshwater	30 (ND)	ND (ND)	ND (ND)
		Devosia	*Devosia confluentis*	BUD	Freshwater	4−35 (30)	ND (7.0−8.0)	0−30 (0−15)
			Devosia enhydra	BUD	Freshwater	30 (ND)	ND (ND)	ND (ND)
			Devosia mishustinii	BUD	Soil	ND (28−30)	ND (ND)	ND (ND)
		Rhodomicrobium	*Rhodomicrobium udaipurense*	BUD	Freshwater	10−40 (30)	5.5−8.0 (7.0)	0−5 (ND)
			Rhodomicrobium vannielii	BUD	Activated sludge	25 (ND)	ND (ND)	ND (ND)
Rhizobiales	*Hyphomicrobiaceae*	*Rhodomicrobium*	*Rhodomicrobium lacus*	BUD	Freshwater	10−35 (30)	5.0−9.0 (7.0)	0−10 (ND)
	Parvibaculaceae	*Pyruvatibacter*	*Pyruvatibacter mobilis*	BIN	Ocean	ND (ND)	ND (ND)	ND (ND)
		Tepidicaulis	*Tepidicaulis marinus*	BIN	Ocean	ND (ND)	ND (ND)	ND (ND)
Sphingomonadales	*Sphingomonadaceae*	*Sphingomonas*	*Sphingomonas canadensis*	BIN	Freshwater	ND (30)	6.0−8.0 (7.0)	0−30 (0−20)
			Sphingomonas leidyi	BIN	Freshwater	10−40 (28)	5.0−10.0 (7.0)	ND (ND)

ND: Not described; BIN: Asymmetric binary fission; BUD: Budding fission.

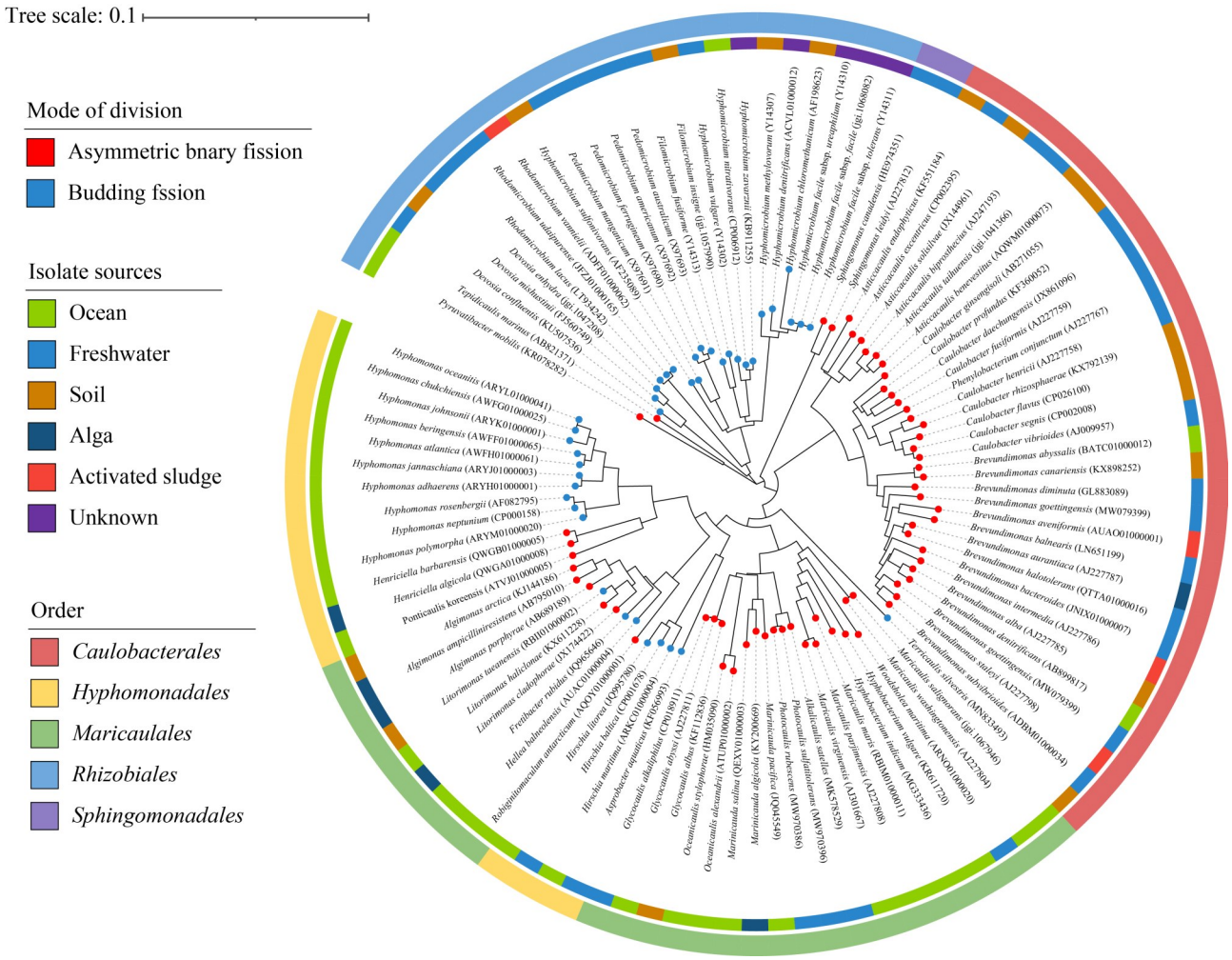

图1　基于16S rRNA基因序列构建的二态性柄细菌系统发育树

Figure 1　Phylogenetic tree of dimorphic prosthecate bacteria constructed based on 16S rRNA gene sequences. Data were obtained from 16S rRNA gene sequences of dimorphic prosthecate bacteria downloaded from the public database Ezbiocloud (https://www. ezbiocloud. net/). Multiple sequence alignment was performed using MEGA software, and gaps in the aligned sequences were removed. The phylogenetic tree was constructed by the Maximum Likelihood method based on the alignment results, with 1 000 bootstrap replicates.

2.1　非对称二分裂：以弧形柄杆菌为例

弧形柄杆菌的非对称二分裂过程呈现严格的阶段特异性，可划分为 3 个高度协同的细胞周期阶段。如图 2A 所示，弧形柄杆菌分裂的起点是游动细胞，在预合成阶段(简称 G1 相)，游动细胞会出现 2 个明显的极点，带有鞭毛的一端为旧极，相对的另一端为新极。游动细胞具有单条环状染色体，染色体的复制原点(*oriC*)位于旧极，并锚定在一个由骨架蛋白 PopZ 形成的极性微区。此微区被认为是一种生物分子凝聚物，它聚集了一系列与细胞周期相关的蛋白，限制它们的扩散从而促进它们之间的相互作用。随着细胞的发育，PopZ 微区的蛋白质组成发生变化，使得游动细胞的鞭毛脱落，在旧极合成一个以多糖为主的黏性物质称为固着器。沿着固着器的方向伸出柄，分化成柄细胞。柄开始

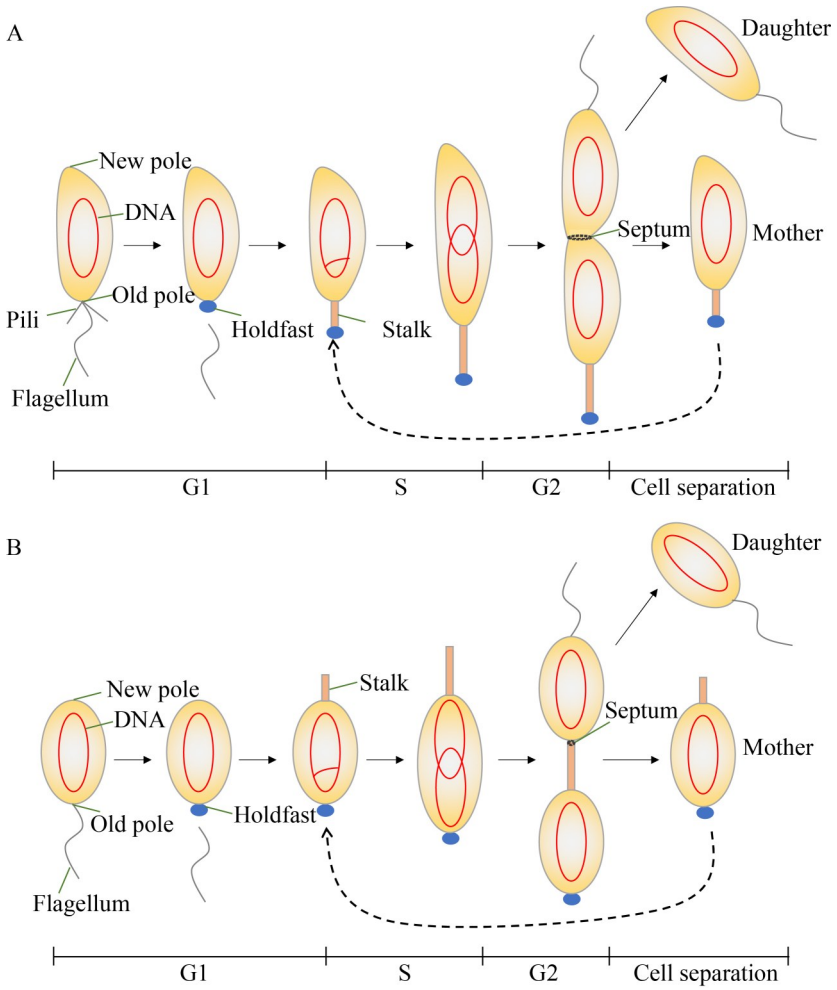

图2　二态性柄细菌的分裂方式

Figure 2　Division modes of dimorphic prosthecate bacteria. A: Asymmetric binary fission; B: Budding fission.

合成后不久，细胞通过从 PopZ 微区释放 *oriC* 开始染色体复制，自此细胞进入合成阶段(简称 S 相)。在 S 相，柄细胞逐渐伸长成为预分裂的细胞。染色体的复制和分离触发了在新极形成一个新的 PopZ 微区，使得新复制的染色体的 *oriC* 锚定在新的 PopZ 微区。与 PopZ 微区相关的蛋白之一是染色体分隔蛋白 ParB，位于细胞两极的 ParB 使得细胞分裂调控因子 MipZ 在两极的浓度最高，在中心浓度最低。MipZ 作为一种关键的细胞分裂蛋白 FtsZ 的负调控因子，将 FtsZ 限制在细胞中心，以确保细胞分裂。一旦完成染色体复制，细胞便进入合成后阶段(简称 G2 相)。预分裂的细胞中心形成隔膜，在新的子细胞的旧极合成新的鞭毛。隔膜将母细胞与新的子细胞分离，产生新的子代，并且鞭毛旋转被激活，旋转产生的动力有助于分离子代[34-35]。

2.2　出芽分裂：以罗马海神生丝单胞菌为例

罗马海神生丝单胞菌的出芽分裂同样遵循 G1 相、S 相、G2 相的阶段特异性调控，但在母-子代细胞连接方式、遗传物质传递路径等核心特征上，与弧形柄杆菌的非对称二分裂存在显著差异[36]。如图 2B 所示，罗马海神生丝单胞菌在 G1 相游动细胞鞭毛脱落，旧极合

成固着器，新极伸出柄，这与弧形柄杆菌的旧极生柄不同。进入 S 相后，染色体开始复制，柄细胞伸长成为预分裂的细胞，柄的末端膨大，形成一个芽体。新复制的染色体通过柄内部的通道被特异性运输至芽体内，其 *oriC* 最终锚定在新的子细胞旧极的 PopZ 微区。在 G2 相，预分裂的细胞芽体底部形成隔膜，在新的子细胞旧极上合成新的鞭毛，隔膜将母细胞与新的子细胞分离，产生新的子代。值得注意的是，在这种模式下，柄成为了连接母细胞与子细胞的桥梁，是细胞质和遗传物质传输的重要通道[37]。

2.3 生活史的核心调控网络

DPB 的生活史之所以能精确运行，依赖于多个层级的严格调控。在弧形柄杆菌中有 4 个关键转录调控因子(DnaA、CtrA、GcrA 和 CcrM)直接调节众多基因的表达，并且每个主调控因子也会影响另一个主调控因子的表达，形成异相振荡。这种自我维持的异相振荡使得每个主调控因子在细胞周期的离散时期最活跃，确保了整个细胞周期中基因表达的时间序列调节[5]。此外，第二信使环二鸟苷酸(c-di-GMP)在此过程中扮演了关键的“代谢计时器”角色。其在细胞内的浓度随细胞周期发生规律性振荡：在游动细胞中维持低水平，在向柄细胞转化时急剧升高并达到峰值，进而促进固着器形成并触发染色体复制[38]。这是首次在细菌细胞周期中发现代谢物丰度的周期性变化，揭示了代谢信号与发育程序的深度整合。

3 二态性柄细菌的生存策略

在营养物质普遍匮乏且竞争激烈的自然环境中，二态性柄细菌进化出了一套协同高效的多层次生存策略。这些策略贯穿于从种群扩散、界面定植到营养摄取的各个层面，共同构成了其强大的生态竞争优势。

3.1 风险对冲：二态性生活史提供的适应性优势

二态性生活史本身是 DPB 在进化上最成功的“风险对冲”策略。它通过在定居(柄细胞)与扩散(游动细胞)之间维持动态平衡来应对环境的不确定性[39]。当局部位点资源耗尽或环境恶化时，种群可通过增加游动细胞的产生比例将子代投资于对新栖息地的探索，从而有效规避竞争、分散风险。反之，在资源充足的地点则通过柄细胞的持续分裂来巩固和扩大种群[40]。此外，柄细胞与始终处于“幼年”状态的游动细胞在衰老速率上存在差异，这种“非对称老龄化”确保了种群中始终保有具有高增殖潜力的个体，为种群的长期存续提供了保障。

3.2 界面定植：占据有利生态位

界面定植是许多细菌生存的关键策略，它可以提高细胞对营养物质的吸收和环境胁迫的耐受性[41]。对于 DPB 而言，主动选择并占据有利生态位同样是其核心适应策略之一。它们尤为擅长在液-固、气-液等界面定植并形成生物膜[42-43]。这些界面通常是营养物质和氧气相对富集的区域，为 DPB 这类普遍好氧且异养的微生物提供了显著的生存优势。同时，DPB 对生物表面也表现出特定的亲和性，尤其易与藻类形成密切的附生关系[3]。例如，研究发现当三角褐指藻(*Phaeodactylum tricornutum*) CCMP2561 或莱茵衣藻(*Chlamydomonas reinhardtii*) UVM4 与嗜碱糖柄杆菌(*Glycocaulis alkaliphilus*) 6B-8^T 共培养时大量嗜碱糖柄杆菌细胞附着在藻类细胞表面或裂解的藻类细胞附近(图 3)。这种定植策略使其能够便捷地利用藻类分泌或裂解释放的可溶性有机物，同时，藻类光合作用产生的氧气也可能为 DPB 创造了适宜的微好氧环境[18]。除藻类外，DPB 也常定殖于植物根系，通过代谢根系分泌物与宿主相互作用[44]。有研究从西瓜植株中分离到一株 DPB 新种——黄色柄杆菌(*Caulobacter flavus*) RHGG3^T，并证实该

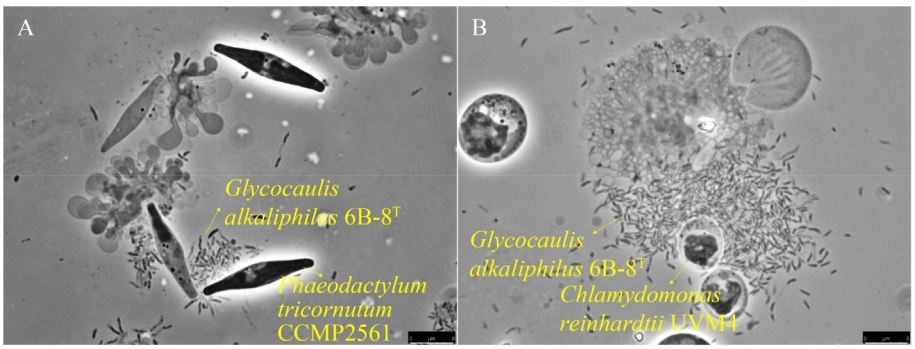

图3　相差显微镜下藻类与二态性柄细菌的共培养结果

Figure 3　Coculture results of algae and dimorphic prosthecate bacteria under phase-contrast microscopy. A: *Phaeodactylum tricornutum* CCMP2561 and *Glycocaulis alkaliphilus* 6B-8^T; B: *Chlamydomonas reinhardtii* UVM4 and *Glycocaulis alkaliphilus* 6B-8^T. Experimental methods: Seed cultures of *P. tricornutum* CCMP2561 and *C. reinhardtii* UVM4 in the logarithmic growth phase were individually inoculated into their respective suitable fresh liquid media for cultivation. Meanwhile, the bacterial culture of *G. alkaliphilus* 6B-8^T in the logarithmic growth phase was collected; The bacterial cells were harvested by centrifugation, and the supernatant was discarded. The bacterial cells were then individually inoculated into the above two algal culture systems and co-cultured under optimal conditions. After a certain period of co-cultivation, the morphological characteristics of the algae and dimorphic prosthecate bacteria were observed using a phase-contrast microscope.

菌株能显著促进西瓜植株茎秆与根系的生物量积累[45]。基因组数据也支撑了这一生态关联：目前已完成测序和注释的柄杆菌属基因组中超过一半来源于植物微生物组，印证了其与植物的广泛互作[46]。此外，在动物体表或体内微生物群落(如人体[47]、山羊[48]、海绵[23]等的表皮或肠道)中也常检测到 DPB 的存在。它们可能作为附生或共生菌参与宿主的有机物降解与氮循环过程。综上所述，界面定植不仅是 DPB 获取营养的重要手段，更是其优化局部微环境、参与复杂生态系统互作的关键适应性策略。

DPB 的界面定植主要依赖于其极强的黏附性，而这一特性是借助其柄末端的固着器实现[49]。研究证实，弧形柄杆菌的固着器是目前已知黏附力最强的生物材料之一，其吸附强度最高可达 70 N/mm^2[50]，通过冷冻电镜可以观察到其微观形态(图 4A)[51]。这种堪称“超强生物胶水”的结构，确保了细胞在流动水体等动态环境中能够被牢牢锚定。固着器的功能远不止于单个细胞的附着，它还能介导细胞间的相互黏附，使多个细胞聚集形成被称为“玫瑰花簇(rosette)”的多细胞结构，利用扫描电镜即可观察到这一典型形态(图 4B)[52]。这种聚集行为能使原本固着的细胞群体产生协同运动，从而实现种群在表面的主动扩散，以寻找更优的微环境[52]。

3.3　营养天线：柄介导的营养获取

DPB 会形成细长的柄，不同于鞭毛或菌毛，柄是细胞身体的延伸，具有细胞外膜、肽聚糖层和细胞内膜，有些柄也含有细胞质。尽管柄的生理功能尚不完全清楚，但目前普遍认为柄是一种“营养天线”[53-55]。柄的长度并非固定不变，而是能积极响应环境信号。研究发现，在富营养条件下弧形柄杆菌柄的长度约 1 μm，但是在磷酸盐饥饿条件下，弧形柄杆菌的柄会急剧伸长，长度可达 30 μm，相当于细胞身体的 15 倍[56-57]。早期人们认为在磷酸盐饥饿过程中柄伸长会通过增加细胞的表面积与体积的比值来增强磷酸盐的吸收，并提出 2 种假说以解释

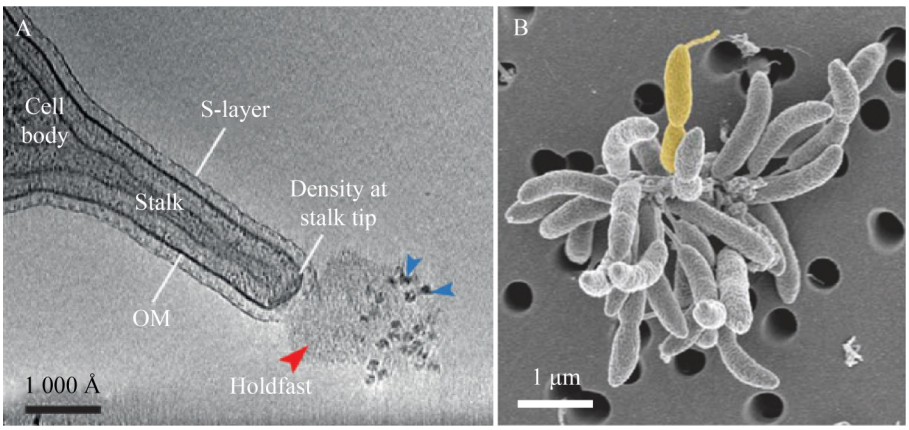

图4 弧形柄杆菌固着器及玫瑰花簇的微观形态

Figure 4 Microscopic morphology of the holdfast and rosette cluster in *Caulobacter vibrioides*. A: Cryo-electron tomography structure of the holdfast in *C. vibrioides*[51]; B: Scanning electron microscopy morphology of the rosette cluster in *C. vibrioides*[52].

柄在磷吸收中的作用[58]。第 1 种假说，周质扩散模型认为在柄的外膜上存在的特异性磷酸盐受体可将磷酸盐转运至柄的周质，随后与高度亲和的周质磷酸盐结合蛋白(PstS)结合将磷酸盐传递至细胞身体的周质，通过 2 个内膜通道蛋白(PstA 和 PstC)将磷酸盐转运至细胞身体内；第 2 种假说，柄中心扩散模型认为当磷酸盐与 PstS 结合后会通过柄内膜上的 PstA 和 PstC 将磷酸盐先转运至柄的中心，再与细胞质转运 ATP 酶(PstB)结合将磷酸盐传递至细胞身体内[59]。然而，近期研究对 2 种假说提出了挑战，研究发现在弧形柄杆菌柄的内部存在隔断蛋白(Stp 复合物)，它将细胞身体和柄分区，使进入柄的磷酸盐并不能转运到细胞身体内(图 5A)[60]。然而，上述研究结果对其他出芽分裂的 DPB 而言可能并不成立，如罗马海神生丝单胞菌中并不存在隔断蛋白，而且其柄是用于连通母细胞和子细胞传递细胞质的桥梁，柄的内部允许物质的扩散(图 5B)[61]。因此，物质进入柄后其命运如何在不同的 DPB 中可能不同。也有学者提出另一种关于磷酸盐饥饿期间柄伸长的假说：DPB 经常定植在表面，而表面定植的一个劣势是环境中的营养通量有限。当柄伸长时会推动细胞身体远离表面，获得表面上方的营养物质。据估计柄从 1 μm 伸长到 10 μm 营养流通可增加约 10%，这为 DPB 提供了相对于其他表面定植生物的竞争优势[53]。此外，对于好氧的 DPB 而言，柄还可能通过降低细胞的沉降速率帮助其悬浮于含氧量更高的水层，避免沉入缺氧区，从而维持有氧呼吸[62]。

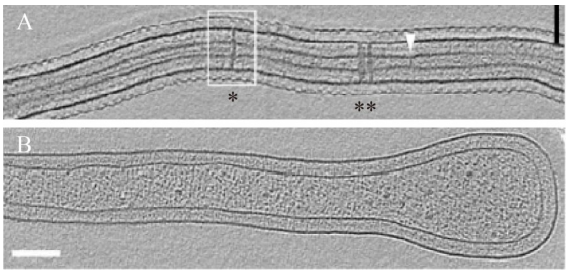

图5 冷冻电镜下二态性柄细菌柄的内部结构

Figure 5 Internal structure of the stalk of dimorphic prosthecate bacteria under cryo-electron microscopy. A: *Caulobacter vibrioides* (Asterisks denote cross-bands. Arrowheads point at unidentified structures spanning the stalk core. Scale bars, 100 nm)[60]; B: *Hyphomonas neptunium* (Scale bars, 100 nm)[61].

4 二态性柄细菌的生态功能与生物技术应用

DPB 是一类能够耐受长期营养匮乏的微生物，广泛分布于各类生态环境中，并以其独特的代谢方式参与地球生物圈的物质循环[63]。它们常附着在动植物残体及藻类表面，这表明其在有机碎屑的分解与转化过程中承担着特定功能，能够将复杂的有机聚合物转化为可被利用的溶解性物质，从而促进营养物质的再循环[3]。值得关注的是，近期一项基于基因组学的研究表明，光养相关基因在柄杆菌目中广泛存在，约 10% 的物种具备编码光合作用系统的潜力[64]。这一发现可能改变人们对 DPB 传统上作为寡营养异养菌的认知，将 DPB 的生态角色从有机物质的分解者拓展到初级生产者，丰富人们对 DPB 生态功能多样性的理解。

除参与自然界的物质循环外，DPB 还具有降解多种有机污染物的能力，包括芳香烃、二甲基亚砜、二甲基硫醚、氯代甲烷和各种醇类[65-66]，显示出其在环境修复中的应用前景。尤其在污水处理方面，生丝微菌属(*Hyphomicrobium*)的多个菌株表现出卓越的性能，如脱氮生丝微菌 (*Hyphomicrobium denitrificans*) ATCC 51888、札氏生丝微菌(*Hyphomicrobium zavarzinii*) ZV622 和食硝酸盐生丝微菌 (*Hyphomicrobium nitrativorans*) NL23，它们能够以甲醇为碳源进行反硝化脱氮，为废水处理的工艺优化提供了重要的微生物资源[67-68]。此外，DPB 在合成生物学与材料科学中也展现出重要潜力。其柄部末端分泌的固着器具备极强的生物黏附性，被视为一种环境友好的“生物胶水”。科学家正在通过调控细菌基因制备具有不同附着力的胶水，为今后生产用于不同工况(如海运、给排水管、手术黏合等)的特种粘合剂提供借鉴与参考[69-70]。同时，弧形柄杆菌的表面层由单一蛋白规则排列而成，这种高度有序的 S 层结构为蛋白质工程提供了理想的展示平台[5]。该 S 层蛋白的表达量极高，占细胞总蛋白的相当比例，且易于进行遗传操作和功能修饰[71]。这一特性使其在生物催化、疫苗研发及环境生物监测等多项生物技术领域中展现出广阔的应用前景，为新型生物制剂的开发提供了创新性的技术路线。

5 挑战与展望

尽管对二态性柄细菌的研究已取得显著进展，但其生命活动中诸多核心环节仍亟待深入探索。本文基于现有研究基础提出以下关键挑战与未来研究方向，以期为该领域的持续发展提供参考。

目前，人们对 DPB 二态性生活史的进化动因与路径仍知之甚少。这一复杂生命策略为何及如何在原核生物中出现是进化生物学领域一个极具价值的研究课题。未来研究需要整合比较基因组学、系统发育分析和实验进化生物学等多种手段，通过对更多代表性物种进行全基因组解析与功能比较，揭示关键发育调控网络的进化历程。同时，探究其与真核生物及其他具有简单分化行为的原核生物在发育策略上的同源性，将有助于理解生命史上细胞分化的早期演化轨迹。

作为 DPB 的标志性结构，柄与固着器的合成机制、精细结构及其多功能性仍是当前研究的薄弱环节。虽然已提出多种关于柄功能的假说，但大多缺乏直接的实验证据支持。未来需要运用冷冻电镜断层扫描、原子力显微镜等前沿技术，在近原子分辨率水平解析其三维结构，阐明其组装动力学过程。同时，结合遗传操作与生物化学手段，解析固着器超强黏附的分子基础，并揭示柄在信号感知、物质运输及能量代谢中的潜在新功能。

DPB 在自然环境中并非孤立存在，其与藻类、动植物及其他微生物形成的复杂互作网络是当前研究的盲区。传统纯培养研究难以揭示其在原位环境中的真实生态功能。未来应大力发展原位观测与单细胞技术，结合合成微生物

群落等简化模型，精确解析 DPB 与不同生物界面互作的分子对话机制。重点阐明其定植特异性、群体感应及代谢物交换等过程的调控网络，从而深入理解 DPB 在微生态系统中的功能角色与调控机制。

综上所述，二态性柄细菌研究正处在从现象描述向机制解析深化的重要阶段。通过多学科交叉的研究策略与技术创新，有望在未来突破现有认知边界，不仅全面揭示这类独特微生物的生命规律，也为理解细菌发育生物学与生态进化提供新的模式菌株。

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