

# 昆虫肠道乳酸菌多样性、功能及应用研究进展

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**摘要:** 乳酸菌作为一类重要的益生菌, 在昆虫肠道微生态系统中发挥着关键作用。本文综述了膜翅目(Hymenoptera)、双翅目(Diptera)、鞘翅目(Coleoptera)、半翅目(Hemiptera)、鳞翅目(Lepidoptera)、蜚蠊目(Blattodea)和直翅目(Orthoptera)等重要昆虫类群中肠道乳酸菌的物种组成、生态功能及应用价值。目前已从昆虫肠道中成功鉴定出的乳酸菌包括乳杆菌属(*Lactobacillus*)、乳球菌属(*Lactococcus*)、明串珠菌属(*Leuconostoc*)、片球菌属(*Pediococcus*)、肠球菌属(*Enterococcus*)、双歧杆菌属(*Bifidobacterium*)和魏斯氏菌属(*Weissella*)等。昆虫肠道乳酸菌群落结构受宿主系统发育背景、食性特征、发育阶段、肠道微环境及外界生态因子的综合调控。昆虫肠道乳酸菌不仅可通过分泌胞外酶协助宿主降解难分解的复合物, 还能通过合成细菌素等抗菌物质抑制病原菌、调节宿主免疫应答, 促进宿主生长发育并调控其行为, 参与外源有毒物质的代谢解毒过程, 进而提升昆虫的生存适应能力。此外, 昆虫源乳酸菌在资源昆虫养殖、害虫绿色防控、农业废弃物高值转化与生物制造等方面也展现出应用潜力。综上, 昆虫肠道是发掘与分离新型乳酸菌资源的重要来源。

**关键词:** 昆虫微生物组; 肠道共生菌; 免疫调节; 病原菌拮抗; 益生潜力

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# Research progress in the diversity, functions, and applications of lactic acid bacteria in insect guts

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**Abstract:** As a crucial group of probiotics, lactic acid bacteria (LAB) play a vital role in the gut microbial ecosystem of insects. This article comprehensively reviewed the species composition, ecological functions, and practical values of LAB in the guts of major insect orders, including Hymenoptera, Diptera, Coleoptera, Hemiptera, Lepidoptera, Blattodea, and Orthoptera. To date, multiple LAB genera including *Lactobacillus*, *Lactococcus*, *Leuconostoc*, *Pediococcus*, *Enterococcus*, *Bifidobacterium*, and *Weissella* were successfully identified from insect guts. The community composition of these bacteria was shaped by factors such as host phylogeny, dietary traits, developmental stages, gut microenvironment, and external ecological conditions. The LAB in insect guts not only assist the hosts in degrading recalcitrant complexes by secreting extracellular enzymes but also inhibit pathogens through the synthesis of antimicrobial substances such as bacteriocins. Additionally, they modulate host immune responses, promote growth and development, regulate host behavior, and participate in the metabolic detoxification of xenobiotics, thereby enhancing host survival and adaptability. Furthermore, insect-derived LAB held great potential in the production of resource insects, pest management, agricultural waste utilization, and green manufacturing. In summary, insect guts represent an important reservoir for the discovery and isolation of novel LAB.

**Keywords:** insect microbiota; gut symbionts; immune modulation; antagonism against pathogens; probiotic potential

乳酸菌(lactic acid bacteria, LAB)是一类革兰氏阳性、不产芽孢、兼性厌氧细菌的总称,其核心代谢特征是通过糖类发酵产生大量乳酸。在系统分类学上,绝大多数乳酸菌属于芽孢杆菌门(*Bacillota*)芽孢杆菌纲(*Bacilli*)下的乳杆菌目(*Lactobacillales*)。该目是乳酸菌的核心分类单元,下设乳杆菌科(*Lactobacillaceae*)、肠球菌科(*Enterococcaceae*)、明串珠菌科(*Leuconostocaceae*)、链球菌科(*Streptococcaceae*)

等主要科级单位<sup>[1-2]</sup>。本文涉及的昆虫肠道乳酸菌主要涵盖了该目下的乳杆菌属(*Lactobacillus*)、乳球菌属(*Lactococcus*)、明串珠菌属(*Leuconostoc*)、链球菌属(*Streptococcus*)、漫游球菌属(*Vagococcus*)、片球菌属(*Pediococcus*)、肠球菌属(*Enterococcus*)和魏斯氏菌属(*Weissella*)等<sup>[1]</sup>。此外,放线菌门(*Actinomycetes*)下的双歧杆菌属(*Bifidobacterium*)虽然在亲缘关系上与乳杆菌目较远,但因其具有相似的生理生化特性

和益生功能,学术界通常也将其纳入乳酸菌范畴进行研究<sup>[2]</sup>。乳酸菌在自然界各类生态系统中广泛分布,在动物肠道内扮演着至关重要的角色,展现出调节宿主免疫、维持肠道微生物稳态、促进消化及抵抗病原菌等多重益生效应<sup>[2-3]</sup>。

目前已对人和反刍动物等哺乳动物肠道乳酸菌进行了大量研究<sup>[4-6]</sup>。然而,随着对功能性菌株需求的不断增长,源自传统宿主(如哺乳动物)的乳酸菌资源筛选日趋饱和。同时,现有菌株在应对某些特定应用(如农业、工业发酵)的极端环境(如高温、低温)时功能受限<sup>[7-8]</sup>。因此,发掘具有新颖特性和更强适应性的乳酸菌新资源已成为该领域的研究热点。昆虫作为地球上物种数量、生态习性(栖息环境)和生物量最为多样化和丰富的动物类群<sup>[9]</sup>,提供了一个有待开发的乳酸菌菌种“宝库”。昆虫肠道环境极为多样,其理化特性(如极端 pH)、消化酶和特殊的营养底物,为微生物的生存和演化提供了强大的自然选择压力<sup>[10]</sup>。这种独特的生态位被认为是筛选具有强环境耐受性、特殊底物降解能力或新颖抗菌活性乳酸菌的理想来源。

近年来,针对昆虫肠道乳酸菌的研究已成为一个快速发展的热点。初步研究不仅揭示了其在不同昆虫类群中高度多样化的群落组成,更证实了它们在宿主生理中扮演着多重关键角色<sup>[11]</sup>,在辅助消化代谢<sup>[12-13]</sup>、促进营养物质合成与吸收<sup>[14-15]</sup>、调节宿主免疫防御<sup>[16-17]</sup>以及通过产生抗菌物质抵抗外来病原体<sup>[18-21]</sup>等方面均发挥着重要作用。此外,昆虫源乳酸菌在资源昆虫产业、害虫绿色防控和农业废弃物转化等领域也表现出较大的应用潜力<sup>[14,22-23]</sup>。然而,与脊椎动物相比,昆虫肠道乳酸菌的研究整体上仍处于初步阶段。现有研究通常集中在特定昆虫或菌株上,且学术界对于昆虫肠道乳酸菌的系统分类、功能多样性以及其与宿主互作的普遍机制的系统性认知尚显不足。本文将从昆虫肠道乳酸菌的多样性、生态功能及应用潜力

3个方面对相关研究进展进行系统综述,以期更好地了解该领域的研究现状和发展动向。

## 1 昆虫肠道乳酸菌组成与多样性

在不同昆虫目中乳酸菌的组成和多样性存在差异,其中膜翅目(Hymenoptera)、双翅目(Diptera)和蜚蠊目(Blattodea)表现出较高的物种多样性,在直翅目(Orthoptera)、鞘翅目(Coleoptera)、鳞翅目(Lepidoptera)和半翅目(Hemiptera)的肠道中也发现了丰富的乳酸菌类群(表 1)。

### 1.1 膜翅目

膜翅目昆虫(如蜜蜂、熊蜂和蚂蚁等社会性昆虫)因其复杂的社会结构和重要的生态功能,成为研究昆虫与微生物互作的理想模型。这些昆虫的肠道中定殖着广泛多样的乳酸菌,其中西方蜜蜂(*Apis mellifera*)和东方蜜蜂(*Apis cerana*)的研究最为系统,其肠道优势乳酸菌主要包括片球菌属、乳杆菌属、双歧杆菌属、明串珠菌属、蜜蜂乳杆菌属(*Apilactobacillus*)和果糖乳杆菌属(*Fructobacillus*)等<sup>[15,24-29]</sup>。熊蜂(*Bombus* spp.)肠道菌群具有较高的分类多样性;传统分离培养结合 16S rRNA 基因测序技术已鉴定出多个乳酸菌新分类单元,如熊蜂蜂鸣乳杆菌(*Bombilactobacillus bombi*)、居熊蜂乳杆菌(*Lactobacillus bombicola*)、熊蜂魏斯氏菌(*Weissella bombi*)、蜜胃乳杆菌(*Lactobacillus melliventris*)以及一个新属新种肠道伴生菌(*Convivina intestini*)<sup>[33-35]</sup>。尽管针对蚂蚁(Formicidae)肠道乳酸菌的系统性分离培养研究相对较少,但越来越多的宏基因组学分析揭示了其广泛存在和多样性。对中国南方 21 个地点的红火蚁(*Solenopsis invicta*)肠道菌群分析发现,其组成在不同地理种群间存在显著差异,虽然乳杆菌科是该蚂蚁肠道常见菌科之一,但在属

表1 不同昆虫目中肠道乳酸菌属的分布情况

Table 1 Distribution of intestinal lactic acid bacteria genera in different insect orders

Insect order	Insect family	Insect species	Identified lactic acid bacteria	References	
Hymenoptera	Apidae	<i>Apis mellifera</i>	<i>Apilactobacillus kunkeei</i> , <i>Lactobacillus apis</i> , <i>Lactobacillus helveticus</i> , <i>Limosilactobacillus reuteri</i> , <i>Lactiplantibacillus plantarum</i> , <i>Leuconostoc mesenteroides</i> , <i>Fructobacillus</i> sp., <i>Bifidobacterium</i> sp., <i>Pediococcus</i> sp.	[13,15, 24-28]	
		<i>Apis cerana</i>	<i>Limosilactobacillus reuteri</i> , <i>Lactobacillus helveticus</i> , <i>Lactiplantibacillus plantarum</i> , <i>Lactobacillus apis</i>	[29-32]	
		<i>Bombus</i> spp.	<i>Bombilactobacillus bombi</i> , <i>Lactobacillus bombicola</i> , <i>Weissella bombi</i> , <i>Convivina intestini</i> , <i>Lactobacillus melliventris</i>	[33-35]	
	Formicidae	<i>Solenopsis invicta</i>	<i>Lactobacillus</i> sp., <i>Pediococcus</i> sp.	[36]	
		<i>Eciton burchellii</i>	<i>Weissella</i> sp.	[37]	
		<i>Oecophylla smaragdina</i>	<i>Lactobacillaceae</i>	[38]	
		<i>Cephalotes varians</i>	<i>Lactobacillales</i>	[39]	
		<i>Camponotus floridanus</i>	<i>Lactobacillales</i>	[40]	
	Diptera	Drosophilidae	<i>Drosophila melanogaster</i>	<i>Leuconostoc mesenteroides</i> , <i>Paucilactobacillus vaccinostercus</i> , <i>Lactiplantibacillus plantarum</i> , <i>Weissella paramesenteroides</i> , <i>Lacticaseibacillus rhamnosus</i>	[41-45]
			<i>Phortica okadai</i>	<i>Lactiplantibacillus argentoratensis</i> , <i>Leuconostoc citreum</i> , <i>Levilactobacillus brevis</i>	[46]
Muscidae		<i>Musca domestica</i>	<i>Streptococcus sanguinis</i> , <i>Limosilactobacillus fermentum</i> , <i>Lactiplantibacillus plantarum</i>	[47-48]	
Calliphoridae		<i>Aldrichina grahami</i>	<i>Vagococcus</i> sp., <i>Lactobacillus</i> sp.	[49]	
		<i>Lucilia sericata</i>	<i>Lactobacillus</i> sp., <i>Lactococcus</i> sp., <i>Vagococcus</i> sp.	[50]	
		<i>Lucilia cuprina</i>	<i>Lactobacillus</i> sp., <i>Lactococcus</i> sp., <i>Vagococcus</i> sp.	[50]	
Stratiomyidae		<i>Hermetia illucens</i>	<i>Lactiplantibacillus plantarum</i> , <i>Lactobacillus</i> sp., <i>Weissella</i> sp., <i>Pediococcus</i> sp.	[51-52]	
Culicidae		<i>Culex quinquefasciatus</i>	<i>Vagococcus fluvialis</i>	[53]	
Tephritidae		<i>Bactrocera dorsalis</i>	<i>Lactobacillus</i> sp., <i>Enterococcus casseliflavus</i> , <i>Lactococcus lactis</i>	[54-55]	
		<i>Ceratitis capitata</i>	<i>Lactococcus lactis</i>	[56]	
Coleoptera	Tenebrionidae	<i>Tenebrio molitor</i>	<i>Pediococcus pentosaceus</i> , <i>Enterococcus</i> sp., <i>Lactococcus</i> sp., <i>Weissella</i> sp.	[57-58]	
		<i>Allomyrina dichotoma</i>	<i>Lactococcus allomyrinae</i>	[59]	
	Scarabaeidae	<i>Protaetia brevitarsis seulensis</i>	<i>Lactococcus protaetiae</i>	[60]	
		<i>Batocera lineolata</i>	<i>Enterococcus saccharolyticus</i>	[61]	
		<i>Cybister lewisianus</i>	<i>Vagococcus coleopterorum</i>	[62]	
	Hydrophilidae	<i>Hydrophilus acuminatus</i>	<i>Vagococcus hydrophili</i>	[62]	
	Curculionidae	<i>Rhynchophorus ferrugineus</i>	<i>Lactococcus</i> sp.	[63]	

(待续)

(续表 1)

Insect order	Insect family	Insect species	Identified lactic acid bacteria	References	
Hemiptera	Miridae	<i>Adelphocoris suturalis</i>	<i>Enterococcus faecalis</i> , <i>Lactococcus</i> sp.	[64-65]	
	Alydidae	<i>Riptortus pedestris</i>	<i>Lactococcus lactis</i> , <i>Enterococcus faecalis</i>	[66]	
	Pyrrhocoridae	<i>Pyrrhocoris sibiricus</i>	<i>Enterococcus faecalis</i> , <i>Enterococcus casseliflavus</i>	[67]	
Lepidoptera	Bombycidae	<i>Bombyx mori</i>	<i>Enterococcus mundtii</i> , <i>Weissella</i> sp., <i>Enterococcus</i> sp.	[68-69]	
	Saturniidae	<i>Samia ricini</i>	<i>Enterococcus hirae</i> , <i>Weissella cibaria</i> , <i>Enterococcus</i> sp.	[19]	
	Plutellidae	<i>Plutella xylostella</i>	<i>Enterococcus mundtii</i>	[70]	
	Noctuidae	<i>Spodoptera littoralis</i>	<i>Enterococcus mundtii</i>	[20]	
		<i>Spodoptera litura</i>	<i>Enterococcus mundtii</i>	[71]	
		<i>Spodoptera frugiperda</i>	<i>Weissella</i> sp., <i>Enterococcus</i> sp.	[72-73]	
	Sphingidae	<i>Manduca sexta</i>	<i>Enterococcus</i> sp.	[74]	
	Oecophoridae	<i>Hofmannophila pseudospretella</i>	<i>Lactococcus lactis</i>	[75]	
	Hesperiidae	<i>Aegiale hesperiaris</i>	<i>Lactobacillus</i> sp.	[76]	
	Blattodea	Rhinotermitidae	<i>Coptotermes formosanus</i>	<i>Pilibacter termitis</i> , <i>Lactococcus</i> sp., <i>Weissella</i> sp., <i>Lactobacillus</i> sp.	[14,77-79]
<i>Reticulitermes speratus</i>			<i>Lactococcus reticulitermitis</i>	[80]	
Termitidae		<i>Nasutitermes arborum</i>	<i>Lactococcus lactis</i> , <i>Enterococcus faecalis</i>	[81]	
		<i>Thoracotermes macrothorax</i>	<i>Lactococcus lactis</i> , <i>Enterococcus faecalis</i>	[81]	
		<i>Anoplotermes pacificus</i>	<i>Lactococcus lactis</i> , <i>Enterococcus faecalis</i>	[81]	
		<i>Nasutitermes takasagoensis</i>	<i>Lactococcus termiticola</i>	[82]	
Archotermopsidae		<i>Hodotermopsis sjostedti</i>	<i>Lactococcus insecticola</i> , <i>Lactococcus hodotermopsisidis</i>	[83]	
Blaberidae		<i>Nauphoeta cinerea</i>	<i>Bifidobacterium</i> sp.	[84]	
		<i>Archimandrita tessellata</i>	<i>Bifidobacterium</i> sp.	[84]	
		<i>Blaberus giganteus</i>	<i>Bifidobacterium</i> sp.	[84]	
Cryptocercidae		<i>Cryptocercus kyebangensis</i>	<i>Periweissella cryptocerci</i>	[85]	
Blattidae		<i>Periplaneta americana</i>	<i>Limosilactobacillus fermentum</i> , <i>Enterococcus</i> sp.	[86]	
Orthoptera		Acrididae	<i>Locusta migratoria</i>	<i>Weissella</i> sp., <i>Lactococcus</i> sp.	[87-88]
		Tettigoniidae	<i>Gampsocleis gratiosa</i>	<i>Enterococcus</i> sp.	[89]
			<i>Anabrus simplex</i>	<i>Lactobacillus</i> sp., <i>Pediococcus</i> sp.	[90]
	Pyrgomorphaeidae	<i>Zonocerus variegatus</i>	<i>Streptococcus</i> sp., <i>Lactobacillus</i> sp.	[91]	

的层面上, 包括乳杆菌属和片球菌属在内的多个菌属的相对丰度在不同地区的样本中表现出极大差异<sup>[36]</sup>; 布氏游蚁(*Eciton burchellii*)的肠道内检测到魏斯氏菌属<sup>[37]</sup>; 对马来西亚 12 个不同巢群的黄猄蚁(*Oecophylla smaragdina*)肠道微生物群落的测序表明乳杆菌科是其肠道主导菌科之一, 其丰度受到地理环境的显著影响<sup>[38]</sup>。此外, 在分化龟蚁(*Cephalotes varians*)和佛罗里达弓背蚁(*Camponotus floridanus*)的肠道中也检测到了乳杆菌目菌群的存在<sup>[39-40]</sup>。

## 1.2 双翅目

双翅目昆虫具有高度多样化的肠道微生物群落, 其中乳酸菌是重要类群之一。Gallus 等<sup>[41]</sup>在黑腹果蝇(*Drosophila melanogaster*)肠道中分离鉴定出肠膜状明串珠菌(*Leuconostoc mesenteroides*)、牛粪寡碳乳杆菌(*Paucilactobacillus vaccinostercus*)及植物乳植杆菌(*Lactiplantibacillus plantarum*)等乳酸菌。冈田绕眼果蝇(*Phortica okadai*)的肠道中有阿根廷拉特乳植杆菌(*Lactiplantibacillus argentoratensis*)、柠檬色明串珠菌(*Leuconostoc citreum*)和短发酵剂乳杆菌(*Levilactobacillus brevis*)等乳酸菌定殖<sup>[46]</sup>。Stathopoulou 等<sup>[54]</sup>报道在桔小实蝇(*Bactrocera dorsalis*)成虫的肠道中检测到比幼虫肠道中更高丰度的乳杆菌。家蝇(*Musca domestica*)肠道中血链球菌(*Streptococcus sanguinis*)是其核心菌群的成员之一<sup>[47]</sup>。丝光绿蝇(*Lucilia sericata*)和铜绿蝇(*Lucilia cuprina*)从幼虫到成虫的发育过程中, 尽管经历了完全变态, 但其肠道核心菌群(主要为乳杆菌属、乳球菌属和漫游球菌属)仍能在不同发育阶段保持相对稳定<sup>[50]</sup>。巨尾阿丽蝇(*Aldrichina grahami*)肠道中也发现以漫游球菌属和乳杆菌属为优势菌群<sup>[49]</sup>。黑水虻(*Hermetia illucens*)幼虫肠道中也栖息着乳杆菌属、魏斯氏菌属和片球菌属等乳酸菌<sup>[51]</sup>。在疾病媒介昆虫致倦库蚊(*Culex quinquefasciatus*)中肠内首次分离到河流漫游球菌(*Vagococcus fluvialis*), 该菌株此前主要见于家畜和人类环

境, 表明其具有较强的宿主适应能力<sup>[53]</sup>。

## 1.3 鞘翅目

乳酸菌是鞘翅目昆虫肠道重要定殖菌群, 其群落结构表现出显著的宿主特异性与生态适应性。Li 等<sup>[57]</sup>报道在黄粉虫(*Tenebrio molitor*)肠道内检测到了肠球菌、乳球菌、魏斯氏菌等乳酸菌。金龟甲总科(Scarabaeoidea)昆虫的肠道同样含有丰富的乳酸菌资源, Heo 等<sup>[59-60]</sup>从双叉犀金龟(*Allomyrina dichotoma*)与白星花金龟(*Protaetia brevitaris seulensis*)幼虫肠道中分别鉴定了 2 个新种: 叉犀金龟乳球菌(*Lactococcus allomyrinae*)和星花金龟乳球菌(*Lactococcus protaetiae*)。在重要害虫红棕象甲(*Rhynchophorus ferrugineus*)的幼虫肠道中乳球菌属的相对丰度达到 8.9%<sup>[63]</sup>。同样地, 朱林慧等<sup>[61]</sup>在云斑白条天牛(*Batocera lineolata*)的 4 龄幼虫肠道中分离出解糖肠球菌(*Enterococcus saccharolyticus*)。Hyun 等<sup>[62]</sup>从水生鞘翅目昆虫黄唇真龙虱(*Cybister lewisianus*)和尖突巨水龟虫(*Hydrophilus acuminatus*)肠道中分别发现了 2 个漫游球菌新种: 鞘翅漫游球菌(*Vagococcus coleopterorum*)和水龟虫漫游球菌(*Vagococcus hydrophili*)。

## 1.4 半翅目

半翅目昆虫种类繁多, 其肠道微生物组成也反映了其多样的生态位和食性。基于 16S rRNA 基因测序的群落分析显示, 在 30 种半翅目昆虫的肠道菌群中芽孢杆菌门作为优势菌门之一, 包含丰富的乳酸菌类群, 其中猎蝽科(Reduviidae)昆虫的肠道菌群呈现出肠球菌属绝对主导并伴随多种假单胞菌门(*Pseudomonadota*)细菌的独特模式<sup>[92]</sup>。重要农业害虫黑盲蝽(*Adelphocoris suturalis*)的肠道微生物中同样检测到乳球菌属<sup>[64]</sup>, 而粪肠球菌(*Enterococcus faecalis*)是其肠道主要乳酸菌之一<sup>[65]</sup>。点蜂缘蝽(*Riptortus pedestris*)是一种危害大豆的重要害虫, 其肠道内也发现存在乳酸乳球菌(*Lactococcus lactis*)和粪肠球菌<sup>[66]</sup>。类似地, 地红蝽

(*Pyrrhocoris sibiricus*)的中肠不同解剖部位均检测到与粪肠球菌及铅黄肠球菌(*Enterococcus casseliflavus*)高度同源的乳酸菌<sup>[67]</sup>。

### 1.5 鳞翅目

在鳞翅目昆虫的肠道微生物群落中肠球菌属常作为优势菌群存在。例如,从家蚕(*Bombyx mori*)的高碱性肠道环境中分离获得的蒙氏肠球菌(*Enterococcus mundtii*)展现出高效的乳酸生产能力<sup>[68]</sup>。当家蚕分别取食天然桑叶和人工饲料时,其肠道乳酸菌群落的优势属发生变化,肠球菌属仅在取食桑叶的家蚕肠道中特异性富集,而魏斯氏菌属则在取食人工饲料的家蚕肠道中占据绝对优势地位<sup>[69]</sup>。蓖麻蚕(*Samia ricini*)肠道微生物的分离研究中肠球菌属出现频率最高,同时也分离到了食物魏斯氏菌(*Weissella cibaria*)<sup>[19]</sup>。在小菜蛾(*Plutella xylostella*)、海灰翅夜蛾(*Spodoptera littoralis*)、烟草天蛾(*Manduca sexta*)、斜纹夜蛾(*Spodoptera litura*)及草地贪夜蛾(*Spodoptera frugiperda*)的肠道中,肠球菌属(尤其是蒙氏肠球菌)同样是核心菌属之一<sup>[20,70-71,73-74,93]</sup>。此外,魏斯氏菌属也被报道为草地贪夜蛾肠道的优势类群<sup>[72]</sup>。除肠球菌属外,其他乳酸菌类群也广泛分布于鳞翅目昆虫肠道中。如 *Aegiale hesperiaris* 幼虫肠道中鉴定出3种乳杆菌科细菌<sup>[76]</sup>;在褐家蛾(*Hofmannophila pseudospretella*)幼虫中肠中鉴定出乳酸乳球菌<sup>[75]</sup>。

### 1.6 蜚蠊目

蜚蠊目昆虫包括白蚁和蟑螂,其肠道是研究微生物共生的独特体系。白蚁作为高度社会性昆虫,其肠道乳酸菌研究尤为深入。在食木性象白蚁(*Nasutitermes arborum*)和食土性胸白蚁(*Thoracotermes macrothorax*)及 *Anoplotermes pacificus* 的后肠中,乳酸菌是可培养碳水化合物降解菌群的重要成员,其中多数乳酸菌与粪肠球菌和乳酸乳球菌的亲缘关系较近<sup>[81]</sup>。Zhang 等<sup>[77]</sup>也在台湾乳白蚁(*Coptotermes formosanus*)和

黄球白蚁(*Globitermes sulphureus*)肠道中检测到芽孢杆菌门,该类群主要由乳酸菌和芽孢杆菌科细菌组成。此外,高通量测序也证实,乳球菌属是多种高等和低等白蚁肠道中共有的核心菌属之一<sup>[94]</sup>。宏基因组分析进一步揭示了乳酸菌在白蚁肠道不同区域的分布差异,例如在台湾乳白蚁中魏斯氏菌和乳杆菌主要富集于前肠(相对丰度分别为1.0%和0.8%),而在中、后肠则骤降至0.1%以下<sup>[78]</sup>。白蚁肠道系统已成为发现乳酸菌新种的重要来源,包括散白蚁乳球菌(*Lactococcus reticulitermitis*)、居白蚁乳球菌(*Lactococcus termiticola*)、居昆虫乳球菌(*Lactococcus insecticola*)、原白蚁乳球菌(*Lactococcus hodotermopsidis*)及乳球菌 X1<sup>[14,80,82-83]</sup>。Higashiguchi 等<sup>[79]</sup>还报道了一个从台湾乳白蚁肠道分离的新属新种白蚁重标枪杆菌(*Pilibacter termitis*)。相较于白蚁,蟑螂肠道乳酸菌的研究虽较有限,但也显示出丰富的多样性。Kopečný 等<sup>[84]</sup>报道双歧杆菌属在灰色庭螻(*Nauphoeta cinerea*)、方斑巨螻(*Archimandrita tessellata*)和巨硕螻(*Blaberus giganteus*)肠道中的丰度存在差异(0-34%)。在褐顶隐尾螻(*Cryptocercus kyebangensis*)的肠道中分离出了一株魏斯氏菌属新种隐尾螻近魏斯氏菌(*Periweissella cryptocerci*,之前被称为 *Weissella cryptocerci*)<sup>[85]</sup>。此外,从美洲大螻(*Periplaneta americana*)肠道分离到发酵黏液乳杆菌(*Limosilactobacillus fermentum*,之前被称为 *Lactobacillus fermentum*)及多种肠球菌属菌株<sup>[86]</sup>,证实了蟑螂肠道乳酸菌的多样性特征。

### 1.7 直翅目

直翅目昆虫,包括蝗虫、蟋蟀和螽斯等,其肠道内同样定殖着丰富的乳酸菌群落。系统发育分析显示,芽孢杆菌门是该类群肠道微生物组的优势菌门<sup>[95-96]</sup>。在不同类群中乳酸菌的组成与分布呈现显著差异:在剑尾亚目(*Ensifera*)昆虫中常见乳酸菌属包括乳球菌属、

片球菌属、乳杆菌属和肠球菌属等<sup>[97]</sup>。具体而言, 优雅蝟螽(*Gampsocleis gratiosa*)肠道优势菌群为乳杆菌目, 其中肠球菌属是优势属<sup>[89]</sup>; 摩门蟋蟀(*Anabrus simplex*)前肠以乳杆菌属为主, 而中肠则富集片球菌属<sup>[90]</sup>。此外, 在东亚飞蝗(*Locusta migratoria*)肠道中魏斯氏菌属在中肠和后肠的相对丰度分别达到 41.48% 和 51.62%<sup>[87]</sup>。臭腹腺蝗(*Zonocerus variegatus*)早期若虫肠道以链球菌属和乳杆菌属为优势菌群<sup>[91]</sup>, 而乳球菌属是东亚飞蝗整个生命周期的核心菌属之一<sup>[88]</sup>。

## 2 昆虫肠道乳酸菌的功能

昆虫肠道乳酸菌的功能多样, 主要包括促进消化与代谢、参与抗病与免疫、调控发育与行为以及解毒(表 2)。其中, 乳杆菌属是目前功能研究最为广泛和深入的类群, 其研究几乎涵盖了全部 4 个功能。此外, 肠球菌属、片球菌属和乳植杆菌属等也被发现在抗病与免疫及发育与行为等方面发挥关键作用。同时, 部分菌属可能表现出功能特异性, 如现有研究表明果糖乳杆菌属的功能主要集中于消化与代谢。

表2 昆虫肠道乳酸菌的主要功能类别及其研究概况

Table 2 Main functional categories of intestinal lactic acid bacteria in insects and their research overview

Function	Mechanism	Representative species	Host	References
Digestion & metabolism	Promotion of Firm-5 growth via fructose and lignin metabolism	<i>Fructobacillus</i> sp.	<i>Apis mellifera</i>	[17]
	Degradation of hemicellulose and pectin via GH43/GH3 secretion	<i>Bifidobacterium</i> sp.	<i>Apis mellifera</i>	[13,24]
	Synthesis of biotin and vitamin C	<i>Lactococcus</i> sp.	<i>Coptotermes formosanus</i>	[14]
	Fermentation of sugars from wood chewing in foregut	<i>Weissella</i> sp., <i>Lactobacillus</i> sp.	<i>Coptotermes formosanus</i>	[78]
	Correlation with hemicellulose digestibility	<i>Enterococcus</i> sp.	<i>Oxya chinensis</i> , <i>Pararcyptera microptera meridionalis</i> , <i>Gastrimargus marmoratus</i> , <i>Calliptamus abbreviatus</i>	[98]
Disease resistance & immunity	Suppression of pathogens (e.g., <i>Bacillus cereus</i> ) via organic acids	<i>Enterococcus hirae</i>	<i>Samia ricini</i>	[19]
	Inhibition of gut bacteria via mundtacin KS secretion	<i>Enterococcus mundtii</i>	<i>Spodoptera littoralis</i>	[20]
	Regulation of immune-related gene expression (e.g., antimicrobial peptides) to enhance pathogen resistance	<i>Lactobacillus</i> sp., <i>Bifidobacterium</i> sp.	<i>Apis mellifera</i>	[17]
	Upregulation of vitellogenin and antimicrobial peptide genes (e.g., <i>hymenoptaecin</i> )	<i>Leuconostoc mesenteroides</i>	<i>Apis mellifera</i>	[25]
	Synergistic inhibition of <i>Paenibacillus larvae</i> (AFB pathogen)	<i>Lactobacillus</i> sp., <i>Bifidobacterium</i> sp.	<i>Apis mellifera</i>	[99]
	Inhibition of <i>Paenibacillus larvae</i> and <i>Melissococcus plutonius</i>	<i>Lactiplantibacillus plantarum</i> , <i>Apilactobacillus kunkeei</i>	<i>Apis mellifera</i>	[27]
	Resistance to microsporidia via serine protease and defensin regulation	<i>Pediococcus acidilactici</i>	<i>Apis mellifera</i>	[28]

(待续)

(续表2)

Function	Mechanism	Representative species	Host	References
	Inhibition of <i>Escherichia coli</i> , <i>Salmonella typhimurium</i> , and <i>Shigella flexneri</i>	<i>Limosilactobacillus reuteri</i>	<i>Apis cerana</i>	[29]
	Inhibition of <i>Flavobacterium</i> sp.	<i>Lactobacillus helveticus</i> , <i>Limosilactobacillus reuteri</i>	<i>Apis cerana</i>	[30]
	Interaction with host Toll immune pathway; abundance significantly reduced by chronic bee paralysis virus infection	<i>Lactobacillus apis</i>	<i>Apis cerana</i>	[31]
	Restoration of gut dysbiosis caused by antibiotics	<i>Lactiplantibacillus plantarum</i>	<i>Apis cerana</i>	[32,100]
	Inhibition of pathogens	<i>Limosilactobacillus fermentum</i> , <i>Enterococcus hirae</i>	<i>Periplaneta americana</i>	[86]
	Enhancement of disease resistance via modulation of gut microbiota structure and broad-spectrum antimicrobial activity	<i>Pediococcus pentosaceus</i>	<i>Tenebrio molitor</i>	[58]
	Competitive exclusion of pathogens (e.g., <i>Crithidia bombi</i> )	<i>Lactobacillus</i> sp.	<i>Bombus terrestris</i>	[101]
Development & behavior	Enhancement of larval body weight and reduction of mortality	<i>Enterococcus hirae</i>	<i>Samia ricini</i>	[19]
	Attraction behavior modulation	<i>Lactiplantibacillus argenteratensis</i>	<i>Phortica okadai</i>	[46]
	Support of larval development	<i>Streptococcus sanguinis</i>	<i>Musca domestica</i>	[47]
	Enhancement of larval growth and feed conversion efficiency	<i>Pediococcus pentosaceus</i>	<i>Tenebrio molitor</i>	[58]
	Promotion of larval growth and feed conversion efficiency	<i>Lactobacillus</i> sp., <i>Lactiplantibacillus plantarum</i>	<i>Hermetia illucens</i>	[52]
	Restoration of development under high-sugar diet	<i>Limosilactobacillus fermentum</i> , <i>Lactiplantibacillus plantarum</i>	<i>Musca domestica</i>	[48]
	Regulation of glucose homeostasis via <i>InR</i> downregulation	<i>Lactiplantibacillus plantarum</i>	<i>Drosophila melanogaster</i>	[42]
	Acceleration of development via ecdysone and insulin signaling modulation	<i>Weissella paramesenteroides</i>	<i>Drosophila melanogaster</i>	[43]
	Induction of foraging and oviposition behaviors via volatile compounds	<i>Lactiplantibacillus plantarum</i>	<i>Drosophila melanogaster</i>	[44]
	Improvement of offspring survival via Wnt/mTOR signaling regulation	<i>Lactobacillus melliventris</i>	<i>Bombus terrestris</i>	[35]
	Enhancement of long-term memory via dopamine and cAMP pathways	<i>Lactobacillus apis</i>	<i>Bombus</i> sp.	[102]
Detoxification	Mitigation of pesticide stress via regulation of antioxidant genes (e.g., <i>GPx-like 2</i> , catalase)	<i>Pediococcus acidilactici</i>	<i>Apis mellifera</i>	[28]
	Reduction of pesticide absorption via physical adsorption (e.g., chlorpyrifos)	<i>Lacticaseibacillus rhamnosus</i>	<i>Drosophila melanogaster</i>	[45]
	Detoxification of pesticides (e.g., chlorpyrifos) via binding	<i>Lactobacillus</i> sp.	<i>Apis mellifera</i>	[103]
	Reduction of pesticide cytotoxicity via cell-free supernatant	<i>Pediococcus pentosaceus</i>	<i>Apis mellifera</i>	[104]
	Enhancement of insecticide resistance via CncC pathway activation (P450s/GSTs)	<i>Enterococcus casseliflavus</i> , <i>Lactococcus lactis</i>	<i>Bactrocera dorsalis</i>	[55]

## 2.1 消化与代谢

昆虫肠道乳酸菌在宿主的营养获取中扮演着多元化的关键角色, 不仅可协助分解食物中难以利用的成分(如纤维素和木质素)<sup>[12]</sup>, 还可合成宿主必需的营养素, 并通过关键代谢产物调节宿主生理过程。在西方蜜蜂肠道中果糖乳杆菌属通过代谢糖类和木质素, 不仅为自身供能, 其代谢副产物还可促进蜜蜂肠道中核心菌群 Firm-5 的生长, 从而间接增强宿主的营养吸收和整体健康<sup>[15]</sup>。此外, Zheng 等<sup>[13]</sup>通过对蜜蜂肠道菌群宏基因组及肠道菌基因组的分析发现其肠道内双歧杆菌是半纤维素和果胶的主要分解者之一。对蜜蜂肠道双歧杆菌属的基因组与宏基因组分析进一步揭示其具有一个双重糖基水解酶系统: 一方面, 不同菌株普遍具有糖苷水解酶(glycoside hydrolases, GH) 43、GH3 以降解多种寡糖; 另一方面, 不同的菌株类群又各自拥有独特的糖基水解酶(如 GH77、GH144 等), 共同展现出对复杂碳水化合物环境的高度代谢适应能力<sup>[24]</sup>。对台湾乳白蚁的宏基因组分析表明, 富集于其前肠的魏斯氏菌和乳杆菌被认为主要参与由木材咀嚼产生的糖类发酵<sup>[78]</sup>。Ling 等<sup>[98]</sup>在对 4 种蝗虫的肠道菌群与消化能力进行相关性分析时发现, 肠球菌属的丰度与纤维素的消化率呈显著负相关, 但与半纤维素的消化率呈正相关。部分乳酸菌还具有合成必需营养素的功能。例如, 从台湾乳白蚁肠道分离的乳球菌 X1 菌株能够分泌生物素(维生素 B<sub>7</sub>)和维生素 C, 为食物单一的白蚁提供关键营养补充<sup>[14]</sup>。

## 2.2 抗病与免疫

### 2.2.1 抵抗病原体

乳酸菌作为昆虫抵御病原微生物侵染的重要防线, 主要通过产生抗菌物质和竞争性排斥等多种机制发挥作用。多种昆虫肠道乳酸菌能够分泌广谱的抗菌物质。蜜蜂肠道乳酸菌能产生有机酸(如乳酸、乙酸和甲酸)、过氧化氢、乙

醇、酶类、苯甲酸盐及抗菌肽等多种活性物质, 这些成分共同作用, 对褪色沙雷氏菌(*Serratia marcescens*)、产气克雷伯氏菌(*Klebsiella aerogenes*)和肠沙门氏菌(*Salmonella enterica*)等病原体表现出显著抑制效应<sup>[21]</sup>。在蓖麻蚕肠道中分离筛选出的小肠肠球菌(*Enterococcus hirae*) SX2 对多种病原体如蜡样芽孢杆菌(*Bacillus cereus*)、金黄色葡萄球菌(*Staphylococcus aureus*)和普通变形菌(*Proteus vulgaris*)具有体外抑制活性, 饲喂活菌可显著提高幼虫体重并降低死亡率<sup>[19]</sup>。同样地, 分离自黄粉虫的戊糖片球菌(*Pediococcus pentosaceus*)不仅具有广谱体外抗菌活性, 还可通过定殖肠道并改变菌群结构, 显著增强其幼虫抗病能力<sup>[58]</sup>。细菌素也是乳酸菌抗菌策略的重要一环。在海灰翅夜蛾的肠道中其优势共生菌蒙氏肠球菌通过分泌细菌素 mundticin KS 来有效抑制入侵的细菌, 维持肠道菌群的平衡, 这既保护了宿主, 也增强了该菌自身的竞争优势<sup>[20]</sup>。东方蜜蜂肠道中分离的罗伊特氏黏液乳杆菌(*Limosilactobacillus reuteri*) LP4 在体外对大肠埃希氏菌(*Escherichia coli*)、肠沙门氏菌(*Salmonella typhimurium*)和弗氏志贺氏菌(*Shigella flexneri*)均表现出较强抑制作用<sup>[29]</sup>。美洲大蠊肠道中发酵黏液乳杆菌及多种肠球菌的培养上清液也对多种病原菌有广谱抑制效果, 其中小肠肠球菌的抑菌能力最为显著<sup>[86]</sup>。汪思凡等<sup>[30]</sup>在东方蜜蜂大肚病研究中自患病工蜂肠道分离出 12 株菌株, 并经鉴定确认其中 KMD1 与 LPD2 为黄杆菌属(*Flavobacterium*)致病菌, 而从健康蜜蜂肠道中分离的瑞士乳杆菌(*Lactobacillus helveticus*)和罗伊特氏黏液乳杆菌在体外试验中表现出对上述致病黄杆菌的显著抑制能力。从西方蜜蜂肠道中分离的植物乳植杆菌和昆基氏蜜蜂乳杆菌(*Apilactobacillus kunkeei*)也能够有效抑制美洲幼虫腐臭病(American foul-brood, AFB)的病原菌幼虫类芽孢杆菌(*Paenibacillus larvae*)和欧洲幼虫腐臭病(European foul-brood, EFB)的病原菌冥王星蜜蜂

球菌(*Melissococcus plutonius*)<sup>[27]</sup>。Forsgren 等<sup>[99]</sup>从蜜蜂分离了 11 种乳酸菌(乳杆菌和双歧杆菌属), 单独使用这些乳酸菌对幼虫类芽孢杆菌的抑制效果存在差异, 但混合使用时可实现完全抑制, 幼虫感染试验也进一步证实在饲料中添加该乳酸菌组合能显著降低美洲幼虫腐臭病发病率。此外, Blasco-Lavilla 等<sup>[101]</sup>发现熊蜂感染寄生虫熊蜂短膜虫(*Crithidia bombi*)后, 其肠道乳杆菌属丰度显著增加, 但未伴随抗菌肽等免疫基因表达水平的显著变化。这一现象支持竞争排斥假说, 即乳酸菌可能通过占据生态位和竞争营养物质来抑制病原体定殖。

### 2.2.2 调节免疫应答

乳酸菌除直接抑制病原体外, 还可通过调节昆虫免疫应答增强宿主抗性。Martinson 等<sup>[17]</sup>报道蜜蜂核心肠道菌群的乳杆菌属(主要为 Firm-4 和 Firm-5)和双歧杆菌属能够调控宿主免疫相关基因(如抗菌肽编码基因)的表达, 从而增强宿主对病原体的抵抗力。Peghaire 等<sup>[28]</sup>发现饲喂乳酸片球菌(*Pediococcus acidilactici*)可通过调控丝氨酸蛋白酶 40 (serine protease 40)、防御素(defensin)相关基因的表达, 在不改变肠道菌群结构的情况下共同增强西方蜜蜂对东方蜜蜂微孢子虫(*Nosema ceranae*)感染和农药如噻虫嗪(thiamethoxam)、啮酰菌胺(boscalid)胁迫的复合抗性。Huang 等<sup>[25]</sup>报道肠膜状明串珠菌 TBE-8 菌株能显著上调西方蜜蜂腹部抗菌肽基因表达(*hymenoptaecin* 和 *apidaecin* 分别上调 17 倍和 7 倍), 同时促进营养相关基因的表达, 蜂王浆蛋白 1 (jelly protein 1)和卵黄蛋白原(vitellogenin)分别提高约 1 400 倍和 20 倍, 且该菌能在肠道内稳定定殖至少 5 d, 展现出良好的益生潜力。病毒感染可显著破坏蜜蜂肠道乳酸菌的稳态平衡: 东方蜜蜂感染慢性麻痹病毒后, Toll 免疫通路激活, 抗菌肽基因 *defensin* 和 *hymenoptaecin* 表达显著上调, 但核心菌群蜜蜂乳杆菌(*Lactobacillus apis*)丰度显著降低, 体现了病毒-宿主免疫-肠道微生物三者间复杂的互作关系<sup>[31]</sup>。

此外, 肠道乳酸菌在维持宿主菌群稳态和抵御外界胁迫方面也有关键作用。高丽娇等<sup>[32,100]</sup>报道东方蜜蜂经四环素处理会破坏工蜂肠道乳酸菌群落, 导致中肠壁结构损伤、消化酶(淀粉酶和蛋白酶)活性下降及免疫基因表达抑制, 最终缩短工蜂寿命约 2.4–3.1 d; 而补充植物乳植杆菌可显著改善菌群结构、提升淀粉酶活性和 Toll 通路表达, 延长寿命约 2.4–2.8 d。

## 2.3 发育与行为

### 2.3.1 促进昆虫发育

昆虫肠道乳酸菌可通过提高宿主存活率、增加体重、调控关键内分泌信号通路等多种途径, 对宿主的生长发育产生直接的促进作用。例如, 将从蓖麻蚕分离的小肠肠球菌 SX2 活菌添加到饲料中能够显著提高幼虫的体重并降低死亡率<sup>[19]</sup>。同样地, 禹铭洋等<sup>[52]</sup>报道, 在资源型昆虫黑水虻中添加特定乳酸菌可显著提升其生产性能, 试验筛选出 3 株益生菌乳杆菌 L4、乳杆菌 L7 和植物乳植杆菌 L8, 其中添加植物乳植杆菌 L8 组幼虫的鲜重、饲料转化率和粗蛋白含量较对照组分别提高 9.43%、13.60% 和 17.63%。同样地, 将黄粉虫内源菌戊糖片球菌添加至饲料后, 不仅能使其成功在幼虫肠道内定殖并重塑菌群结构(使乳杆菌目成为优势菌群), 还使试验组幼虫达到收获体重的时间较对照组缩短约 1.5 周, 且健康成虫羽化率由 24% 提升至 56%, 实现翻倍增长<sup>[58]</sup>。此外, Zurek 等<sup>[47]</sup>报道家蝇幼虫的正常发育依赖于特定肠道菌群, 其中来自火鸡垫料的菌群促生长效果显著优于玉米青贮来源, 以血链球菌为代表的乳酸菌表现出最优的发育支持能力。值得注意的是, 乳酸菌还能逆转不良饮食带来的负面影响, 高糖饮食导致家蝇幼虫肠道菌群失调(乳杆菌属丰度下降、魏斯氏菌属过度增殖)并引发发育迟缓, 而补充健康幼虫肠道源的发酵黏液乳杆菌和植物乳植杆菌可恢复菌群平衡并显著改善生长发育<sup>[48]</sup>。在黑腹果蝇中乳酸菌通过调控内分泌和代谢通路精确调节宿主发育, 李玉娟等<sup>[42]</sup>

报道植物乳植杆菌 FY1 可使其促前胸腺激素 (prothoracicotropic hormone, PTH) 基因表达高峰提前并下调胰岛素受体 (insulin receptor, InR) 基因, 从而影响血糖稳态, 并将其从卵至成虫的发育时间从 30 d 缩短至 10.7 d, 并且该菌株还可稳定跨代传递。李恩惠等<sup>[43]</sup>进一步发现黑腹果蝇肠道中副肠膜状魏斯氏菌 (*Weissella paramesenteroides*) 通过双重调控机制促进宿主生长发育: 一方面上调蜕皮激素 (ecdysone) 信号通路关键基因 (*dib*、*E74B* 和 *PTTH*) 表达, 另一方面协同调节胰岛素信号通路 (上调 *DILP2/DILP3*、下调 *InR*), 从而显著缩短发育期并提高生长速率。

### 2.3.2 调控昆虫行为

昆虫肠道乳酸菌通过“菌-肠-脑”的协同调控, 可显著影响昆虫的繁殖、觅食等行为, 但其效应呈现菌株特异性与环境依赖性。王露等<sup>[44]</sup>发现植物乳植杆菌对黑腹果蝇的觅食与产卵行为均具有显著引诱作用, 并且由 2-3 种微生物组成的混合菌群比单一微生物表现出更强的引诱力, 表明黑腹果蝇在觅食和产卵选择中可能更倾向于微生物多样性较高的生境。熊蜂肠道蜜胃乳杆菌可以通过复杂的酪氨酸代谢通路, 对宿主的 Wnt/哺乳动物雷帕霉素靶蛋白 (mammalian target of rapamycin, mTOR) 信号通路进行双重调控, 将其后代存活率提升至 2.5 倍, 并提高工蜂的访花效率 10%, 直接证实了益生菌对宿主繁殖与行为的调控作用<sup>[35]</sup>。陈蓉<sup>[102]</sup>进一步发现熊蜂肠道共生菌蜜蜂乳杆菌通过“菌-肠-脑”影响认知功能; 该菌通过降低肠道谷氨酰胺水平, 进而激活脑部多巴胺受体表达、促进多巴胺合成并最终上调 cAMP 信号通路, 显著增强长期记忆能力, 为微生物干预认知功能提供了新依据。此外, 冈田绕眼果蝇肠道的阿根廷拉特乳植杆菌和柠檬色明串珠菌可影响其摄食行为, 其中阿根廷拉特乳植杆菌对宿主表现出显著吸引力<sup>[46]</sup>。

## 2.4 解毒

### 2.4.1 代谢或结合有毒化合物

在昆虫应对化学胁迫的适应机制中, 肠道乳酸菌发挥着关键的解毒功能, 可通过多种机制协助宿主抵御植物次生代谢物及农药的毒性效应<sup>[105]</sup>。在果蝇中鼠李糖乳酪杆菌 (*Lactocaseibacillus rhamnosus*) GG 通过其细胞壁直接吸附毒死蜱 (chlorpyrifos), 而非代谢该农药, 这种物理隔离作用降低了毒素在宿主体内的生物可利用浓度, 无菌果蝇模型研究证实, 定殖该菌可显著提高宿主存活率, 展现出明确的保护效果<sup>[45]</sup>。Leska 等<sup>[103]</sup>报道, 西方蜜蜂源乳酸菌的活菌细胞可高效结合毒死蜱、蝇毒磷 (coumaphos) 和吡虫啉 (imidacloprid), 最高结合率达 64%, 显著减轻这些农药对昆虫及哺乳动物细胞的细胞毒性和遗传毒性。此外, 乳酸菌代谢产物 (即无细胞上清液) 同样具有保护功能, 如戊糖片球菌 14/1 菌株的无细胞上清液能够将蝇毒磷对 Caco-2 细胞的毒性降低 19.32%, 这表明乳酸菌可能通过分泌胞外物质来中和或缓解杀虫剂的危害<sup>[104]</sup>。

### 2.4.2 调控宿主自身的解毒基因网络

共生微生物可通过调控宿主的解毒基因表达, 进而增强昆虫对杀虫剂的抗性, 这一机制在多种昆虫中得到验证。桔小实蝇的肠道乳酸菌如铅黄肠球菌和乳酸乳球菌通过激活 CncC 信号通路 (昆虫中与哺乳动物 Nrf2 同源的核心抗氧化通路), 上调细胞色素 P450 (cytochrome P450, CYP) 和谷胱甘肽-S-转移酶 (glutathione S-transferase, GST) 等关键解毒酶活性, 从而显著增强其对  $\beta$ -氯氰菊酯 ( $\beta$ -cypermethrin) 的抗性<sup>[55]</sup>。类似地, 片球菌属菌株可缓解噻虫啉和啶酰菌胺对蜜蜂的毒性, 不仅可降低其死亡率, 还能调控谷胱甘肽过氧化物酶样 2 (GPx-like 2) 及过氧化氢酶等相关解毒基因的表达水平, 以减轻农药引发的生理紊乱<sup>[28]</sup>。

## 3 昆虫肠道乳酸菌的应用

### 3.1 资源昆虫

在资源昆虫产业化应用中昆虫乳酸菌展现出多重应用价值,既可作为益生菌保障资源昆虫(如蜜蜂)种群健康、促进宿主(如黑水虻)生长,也能作为昆虫饲料的组成部分间接改善下游养殖动物的健康状况。在益生菌开发方面,昆虫肠道是重要菌种资源库。例如蓖麻蚕源小肠肠球菌 SX2 能显著促进宿主生长并提高存活率,开发这类益生菌可改善蓖麻蚕的经济性状,并为蚕丝产业提供抗生素之外的生态友好型管理方案<sup>[19]</sup>。多种市售的食用昆虫(如黄粉虫、家蟋蟀)原料中含有较高的微生物载量,包括多种乳酸菌<sup>[23]</sup>。Garofalo 等<sup>[106]</sup>在市售食用昆虫产品(如东亚飞蝗和黄粉虫)中检测到可能具有产胞外多糖等发酵潜力的魏斯氏菌属等微生物。在动物饲料领域,昆虫蛋白替代传统鱼粉已成为研究热点,如在金头鲷(*Sparus aurata*)饲喂试验中发现,当用黄粉虫粉高比例替代鱼粉时,鱼的生长性能与肠道内混淆魏斯氏菌(*Weissella confusa*)等共生菌的丰度呈显著正相关<sup>[107]</sup>。这表明昆虫饲料不仅提供了蛋白质,其携带的共生乳酸菌也可能作为“益生菌”进入鱼类肠道,调节其肠道菌群,从而进一步促进了鱼类的生长和发育。这些发现为昆虫资源的综合开发利用提供了新的思路。

### 3.2 害虫防治

昆虫肠道乳酸菌在害虫绿色防控中展现出多方面的应用潜力。一些乳酸菌代谢产物可用于增强诱捕效率,如将酒酒球菌(*Oenococcus oeni*)接种至诱捕剂 Droskidrink<sup>®</sup>后,其发酵产生的挥发性物质显著提高了对斑翅果蝇(*Drosophila suzukii*)的诱捕效率,体现了乳酸菌在害虫监测中的价值<sup>[108]</sup>。Daisley 等<sup>[45]</sup>报道果蝇肠道源植物乳植杆菌会将毒死蜱优先代谢为毒性更强的氧毒死蜱(chlorpyrifos-oxon, CPO),而非低毒产物三氯吡啶酚(3,5,6-trichloro-2-pyridinol, TCP),

并在无菌果蝇试验中证实,定殖该菌会显著降低宿主在毒死蜱暴露后的存活率。在不育昆虫技术(sterile insect technique, SIT)中补充含乳酸乳球菌的益生菌群可显著改善地中海实蝇(*Ceratitis capitata*)不育雄虫的生理状态,提高成虫羽化率、飞行能力及交配竞争力,从而提升 SIT 项目的整体效率<sup>[56]</sup>。在田间应用中某些乳酸菌制剂可与化学杀虫剂协同使用,并表现出显著增效作用。例如, Jayaveni 等<sup>[109]</sup>也发现乳酸菌制剂与氯虫苯甲酰胺(chlorantraniliprole)联用小菜蛾的抑制效果显著优于单一处理,同时单独喷施乳酸菌的植株能吸引瓢虫等天敌昆虫,揭示了乳酸菌通过调节天敌行为实现间接生物防治的潜力。这些发现为开发基于乳酸菌的绿色综合防控策略提供了重要科学依据。

### 3.3 农业废弃物高值转化与生物制造

昆虫肠道乳酸菌在农业废弃物资源化利用中展现出显著价值,尤其在提升资源昆虫转化效率及推动生物制造方面具有独特优势。以黑水虻为代表的高效有机废弃物转化体系中,乳酸菌发挥着关键的催化作用,研究证实,利用其进行农业废弃物的厌氧发酵预处理可显著提升饲料营养价值,进而促进幼虫生长并缩短发育周期<sup>[11]</sup>。在生物制造领域,昆虫肠道源乳酸菌表现出卓越的合成能力。例如,从台湾乳白蚁肠道分离的乳球菌 X1 菌株,可在无需复杂氮源条件下高效转化多种糖类(包括纤维素水解产生的葡萄糖和木糖)为乳酸,产率高达 99.9%<sup>[14]</sup>。这些研究表明,昆虫源乳酸菌不仅可优化农业废弃物的昆虫转化过程,还能推动高值生物基化学品的绿色制造,具有重要的应用潜力和开发前景。

## 4 总结与展望

昆虫肠道乳酸菌的研究揭示了其在宿主适应性及功能多样性方面的重要作用。不同昆虫

目(如膜翅目、鞘翅目等)的肠道乳酸菌群落表现出显著的宿主特异性与生态适应性分化。这些微生物通过参与营养代谢(如木质纤维素降解)、免疫调节(如抗菌肽诱导)以及解毒过程(如农药代谢)等关键生理活动,与宿主形成紧密的共生关系。在应用层面,昆虫源乳酸菌展现出广泛的潜力,包括生物防治、推进可持续农业、废弃物资源化利用;在工程菌剂开发、食用昆虫生产等领域也具有应用前景。然而,与脊椎动物相比,昆虫肠道乳酸菌研究仍处于初步阶段,尤其在菌种系统分类、功能多样性及宿主互作机制等方面尚存诸多未解问题。此外,该领域仍面临不可培养菌株占比较高与应用转化效率低等挑战。

为应对上述挑战并推动该领域发展,未来研究应着重在以下方向进行深化:(1)综合利用多组学技术与无菌昆虫模型,深入解析乳酸菌的定殖机制、代谢互作及信号传递途径;(2)深入比较昆虫源乳酸菌与已知的人和反刍动物等哺乳动物源乳酸菌的组成差异,明确其系统发育关系;(3)开发基于昆虫肠道仿生环境的培养策略,提高苛刻菌株的可培养性,拓展可培养乳酸菌种资源;(4)构建从基础研究到产业应用的全链条研发体系,涵盖标准菌种库建设、工程菌剂开发与生物安全评估。总之,通过多学科交叉与技术创新,昆虫肠道乳酸菌研究有望为农业、食品提供新型微生物解决方案,并为推动绿色生物技术的发展提供理论依据与实践支撑。同时,应同步建立完善的生物安全监管框架,规范其开发与应用,保障其可持续性与环境相容性。

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曾泰儒:撰写文章,数据收集与监管;杨欣亚:撰写文章,验证;张健龙:撰写文章,监督管理;刘秋旭:提供资源;王偲:提出概念,监督管理,获取基金。

## 作者利益冲突公开声明

作者声明不存在任何可能会影响本文所报告工作的已知经济利益或个人关系。

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