

昆虫凝集素的免疫功能研究*

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摘要 昆虫主要依赖先天免疫来应对病原体的感染, 而模式识别受体 (Pattern recognition receptors, PRRs) 对病原体的识别是激活免疫反应的基础。凝集素 (Lectin) 家族广泛存在于动物和植物中, 通过糖识别结构域结合特定的糖类、糖蛋白或糖脂, 在昆虫免疫中充当重要的模式识别受体。昆虫的凝集素主要包括 C-型凝集素 (C-type lectin) 和半乳糖凝集素 (Galectin), 在先天免疫系统中承担着多种功能。本文概述了昆虫凝集素的分类、结构及其进化特征, 重点总结了 C-型凝集素和半乳糖凝集素在昆虫先天免疫系统中的作用, 也简要介绍了凝集素在发育中的功能。本文为后续研究昆虫与微生物的免疫互作, 以及靶向免疫系统改良微生物源农药提供参考。

关键词 C-型凝集素; 半乳糖凝集素; 先天免疫; 模式识别蛋白; 病原微生物

Advances on the role of insect lectins in innate immunity

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Abstract Insects primarily rely on innate immunity to defend against pathogens, and the recognition of pathogens by pattern recognition receptors (PRRs) to trigger immune responses. Lectins are widely present in animals and plants, and they bind to specific carbohydrates, glycoproteins, or glycolipids through their carbohydrate recognition domains (CRDs), thereby serving as crucial PRRs in insect immunity. Insect lectins mainly include C-type lectins and galectins which play multiple functions in the innate immune system. This review outlines the classification, structure, and evolutionary characteristics of insect lectins, with a focus on the functions of C-type lectins and galectins in the insect innate immune system, and briefly introduces the functions of insect lectins on growth. It is hoped that this review will inspire studies of host-pathogen interactions, and contribute to the improvement of microbial biopesticides targeting the immune system.

Key words C-type lectins; galectins; innate immunity; pattern recognition receptors; pathogens

昆虫作为地球上种类最多、分布最广的生物类群, 在其生活过程中面临各种病原微生物, 如细菌、病毒、真菌、寄生虫等。在漫长的进化历程中, 为了抵抗病原体的侵染或与之协同共生, 昆虫逐渐形成了一套精细的免疫系统。宿主对外源微生物的识别依赖于模式识别受体 (Pattern recognition receptors, PRRs), 其中凝集素是昆

虫一类重要的模式识别受体, 参与多种免疫应答过程。本文介绍了昆虫凝集素 (Lectins) 的分类与数目 (表 1)、结构及其进化特征, 重点总结了 C-型凝集素 (C-type lectins, CTLs) 和半乳糖凝集素 (Galectins, GALEs) 在昆虫先天免疫系统中的作用 (表 2, 图 1)。此外, 本文也简要介绍了凝集素在昆虫发育中的功能。

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表 1 昆虫凝集素基因数目汇总
Table 1 The number of insect C-type lectin and galectin genes

物种 Species	目 Order	CTL 基因 数量	CTL 分类 Classification of CTL			GALE 基因 数量	参考文献 References
		CTL genes number	CTL-S	IML	CTL-X	GALE genes number	
家蚕 <i>Bombyx mori</i>	鳞翅目 Lepidoptera	23	11	7	5	3	Rao <i>et al.</i> , 2015b
棉铃虫 <i>Helicoverpa armigera</i>	鳞翅目 Lepidoptera	39	11	23	5	10	Lu <i>et al.</i> , 2020b
草地贪夜蛾 <i>Spodoptera frugiperda</i>	鳞翅目 Lepidoptera	—	—	9	—	11	Liu <i>et al.</i> , 2025
斜纹夜蛾 <i>Spodoptera litura</i>	鳞翅目 Lepidoptera	36	14	17	5	13	Lu <i>et al.</i> , 2020b
甜菜夜蛾 <i>Spodoptera exigua</i>	鳞翅目 Lepidoptera	33	19	8	6	—	Bao <i>et al.</i> , 2024
烟草天蛾 <i>Manduca sexta</i>	鳞翅目 Lepidoptera	34	9	19	6	5	Rao <i>et al.</i> , 2015a
小菜蛾 <i>Plutella xylostella</i>	鳞翅目 Lepidoptera	7	—	—	—	—	Yu <i>et al.</i> , 2017
亚洲玉米螟 <i>Ostrinia furnacalis</i>	鳞翅目 Lepidoptera	36	21	15	0	4	Song <i>et al.</i> , 2020
赤拟谷盗 <i>Tribolium castaneum</i>	鞘翅目 Coleoptera	16	10	1	6	2	Zou <i>et al.</i> , 2007
西方蜜蜂 <i>Apis mellifera</i>	膜翅目 Hymenoptera	12	8	0	4	2	Evans <i>et al.</i> , 2006
中华蜜蜂 <i>Apis cerana</i>	膜翅目 Hymenoptera	—	—	—	—	1	Zhong <i>et al.</i> , 2025
黑腹果蝇 <i>Drosophila melanogaster</i>	双翅目 Diptera	42	38	0	4	5	Lu <i>et al.</i> , 2020b
白纹伊蚊 <i>Aedes albopictus</i>	双翅目 Diptera	39	29	1	9	—	Gao <i>et al.</i> , 2024
埃及伊蚊 <i>Aedes aegypti</i>	双翅目 Diptera	39	—	—	—	9	Lu <i>et al.</i> , 2020b
冈比亚按蚊 <i>Anopheles gambiae</i>	双翅目 Diptera	25	—	—	—	8	Holt <i>et al.</i> , 2002
致倦库蚊 <i>Culex quinquefasciatus</i>	双翅目 Diptera	55	—	—	—	15	Arensburger <i>et al.</i> , 2010
桔小实蝇 <i>Bactrocera dorsalis</i>	双翅目 Diptera	42	36	0	6	—	Zhao <i>et al.</i> , 2025
褐飞虱 <i>Nilaparvata lugens</i>	半翅目 Hemiptera	9	—	—	—	2	Zhong <i>et al.</i> , 2025

—: 未检测。—: Undetected.

凝集素 Lectins	微生物 Microbes	免疫功能 ^b Role in immunity
C-型凝集素 C-type lectin CTL-S  IML  CTL-X 	细菌 Bacteria 	凝集多种细菌，促进血细胞的包裹和黑化作用 Agglutinate various bacteria, promote hemocytic encapsulation and melanization 正调控 Positive regulation 激活MAPK信号通路，降低晶体蛋白的毒性 Activate the MAPK signaling pathway, reduce the toxicity of Crystal proteins (Cry) 激活Toll信号通路，诱导抗菌肽表达 Activate the Toll signaling pathway, induce the expression of antimicrobial peptides
		负调控 Negative regulation 结合苏云金芽孢杆菌，促进其感染昆虫 Bind to <i>Bacillus thuringiensis</i> to promote its infection of insects
	真菌 Fungi 	结合球孢白僵菌，激活Toll、JAK/STAT信号通路 Bind to <i>Beauveria bassiana</i> , activate the Toll and JAK/STAT signaling pathways 正调控 Positive regulation 结合微孢子虫，促进血细胞的包裹和黑化作用 Bind to <i>Nosema bombycis</i> , promote hemocytic encapsulation and melanization 结合莱氏绿僵菌，抑制其感染昆虫 Bind to <i>Metarhizium rileyi</i> to inhibit its infection of insects
		结合家蚕核型多角体病毒，抑制病毒的增殖 Bind to <i>Bombyx mori</i> nucleopolyhedrovirus (BmNPV) and inhibit its replication
半乳糖凝集素 Galectin 1 CRD  2 CRDs  3 CRDs ^a 	病毒 Virus 	正调控 Positive regulation 结合家蚕核型多角体病毒，抑制病毒的增殖 Bind to <i>Bombyx mori</i> nucleopolyhedrovirus (BmNPV) and inhibit its replication 负调控 Negative regulation 促进登革病毒、西尼罗病毒和日本脑炎病毒等病毒感染细胞 Promote cell infection by viruses such as Dengue virus (DENV), West Nile virus (WNV) and Japanese encephalitis virus (JEV)
	寄生虫 Parasite 	正调控 Positive regulation 凝集疟原虫，促进蚊子吸血 Agglutinate <i>Plasmodium</i> and promote blood-sucking in mosquitoes 负调控 Negative regulation 结合利什曼虫，协助其在肠道定殖 Bind to <i>Leishmania</i> and facilitate its colonization in the intestine 抑制黑化反应，维持线虫与昆虫媒介之间的免疫平衡 Inhibit melanization, balance immunity between nematodes and insect vectors

a: 拥有3个CRD的半乳糖凝集素的功能未知。

a: The function of galectins with three CRDs is unknown.

b: 图中功能来源于不同的凝集素成员，非全体凝集素共同拥有。

b: The functions shown in this figure are derived from different lectins rather than being universal features across the entire lectin family.

图1 昆虫凝集素免疫功能汇总图

Fig. 1 Overview of lectin-mediated immune responses in insects

1 昆虫先天免疫系统

昆虫缺乏后天免疫系统，但在长期进化过程中形成了精细的先天免疫系统，用于抵御病原微生物的入侵。当病原体突破昆虫表皮或肠道黏膜等物理化学屏障后，昆虫的模式识别受体（PRRs）特异性识别病原微生物表面的病原相关分子模式（Pathogen associated molecular patterns, PAMPs），激活先天免疫系统以清除病原物（Lu *et al.*, 2020a）。脂肪体、肠道和血

细胞是昆虫重要的免疫组织，而昆虫的先天免疫系统是由体液免疫（Humoral immunity）和细胞免疫（Cellular immunity）两部分构成（Lavigne and Strand, 2002; Lemaitre and Hoffmann, 2007）。体液免疫主要通过激活Toll、免疫缺失（Immune deficiency, IMD）、JAK/STAT（Janus kinase-signal transducers and activators of transcription）等信号通路上调抗菌肽（Antimicrobial peptide, AMP）、活性氧（Reactive oxygen species, ROS）和溶菌酶等免疫效应因子的表达，或通过酚氧化酶

表 2 昆虫凝集素在免疫中的功能
Table 2 Functions of insect C-type lectins and galectins in innate immunity

物种 Species	凝集素 Lectin	CRD 数量 CRD number	功能 Functions	参考文献 References
家蚕 <i>Bombyx mori</i>	BmCTL4	1	抑制枯草芽孢杆菌和金黄色葡萄球菌的生长 Inhibits the growth of <i>Bacillus subtilis</i> and <i>Staphylococcus aureus</i>	Shahzad <i>et al.</i> , 2017
家蚕 <i>Bombyx mori</i>	BmCTL5	1	凝集大肠杆菌和金黄色葡萄球菌, 结合球孢白僵菌, 结合整合素的 β 2- β 5 亚基, 激活 JAK/STAT 信号通路和抗菌肽, 促进吞噬作用和黑化反应 Agglutinates <i>Escherichia coli</i> and <i>Staphylococcus aureus</i> , binds to <i>Beauveria bassiana</i> , interacts with integrin β 2- β 5 subunits, activates the JAK/STAT pathway and AMPs, promotes phagocytosis and melanization	Zhan <i>et al.</i> , 2017; Geng <i>et al.</i> , 2021
家蚕 <i>Bombyx mori</i>	BmCTL-S6	1	结合枯草芽孢杆菌肽聚糖和大肠杆菌脂多糖, 促进血细胞的包裹和黑化 Binds to peptidoglycan of <i>Bacillus subtilis</i> and lipopolysaccharide of <i>Escherichia coli</i> , promotes hemocytic encapsulation and melanization	Shen <i>et al.</i> , 2021
家蚕 <i>Bombyx mori</i>	BmCTL10	2	结合整合素 β 3 和 β 4 亚基, 结合血细胞, 促进结节、吞噬和包裹, 上调抗菌肽和一氧化氮酶 Interacts with integrin β 3 and β 4 subunits, binds to hemocytes, promotes nodulation, phagocytosis and encapsulation, induces AMPs and nitric oxide synthase	Liu <i>et al.</i> , 2022
家蚕 <i>Bombyx mori</i>	BmIML2	2	通过促进细胞凋亡抑制家蚕核型多角体病毒的增殖 Inhibits the proliferation of <i>Bombyx mori</i> nucleopolyhedrovirus (BmNPV) by promoting cell apoptosis	Mei <i>et al.</i> , 2022
棉铃虫 <i>Helicoverpa armigera</i>	HaCTL1	2	促进血细胞的包裹和吞噬以抵抗线虫 Promotes hemocytic encapsulation and phagocytosis to defense nematode infection	Chai <i>et al.</i> , 2008
棉铃虫 <i>Helicoverpa armigera</i>	HaCTL3	1	结合寄生虫以抵抗感染, 与整合素 β 亚基互作, 促进血细胞包裹和黑化 Binds to parasites to defense infection, interacts with integrin β subunits, promotes hemocytic encapsulation and melanization	Wang <i>et al.</i> , 2017
棉铃虫 <i>Helicoverpa armigera</i>	HaCTL6	2	调节抗菌肽、溶菌酶的表达, 调控血淋巴菌群稳态 Regulates the expression of AMPs and lysozymes, and regulates microbiota homeostasis in hemolymph	Zhao <i>et al.</i> , 2025
棉铃虫 <i>Helicoverpa armigera</i>	HaCTL7	2	凝集大肠杆菌和金黄色葡萄球菌等细菌, 结合血细胞, 促进包裹和黑化反应 Agglutinates bacteria such as <i>Escherichia coli</i> and <i>Staphylococcus aureus</i> , binds to hemocytes, and promotes encapsulation and melanization	Wang <i>et al.</i> , 2014
棉铃虫 <i>Helicoverpa armigera</i>	HaCTL11	2	凝集莱氏绿僵菌, 抵抗莱氏绿僵菌感染 Agglutinates <i>Metarhizium rileyi</i> to defense infection	Wang <i>et al.</i> , 2023a

续表 2 (Table 2 continued)

物种 Species	凝集素 Lectin	CRD 数量 CRD number	功能 Functions	参考文献 References
棉铃虫 <i>Helicoverpa armigera</i>	HaCTL14	2	凝集球孢白僵菌，促进血细胞的吞噬，调控丝氨酸蛋白酶及其抑制剂，激活黑化反应 Agglutinates <i>Beauveria bassiana</i> , promotes phagocytosis, regulates serine protease and their inhibitor to activate melanization	Cheng <i>et al.</i> , 2018
棉铃虫 <i>Helicoverpa armigera</i>	CD209	1	抑制肠道中条件致病菌植物乳杆菌的扩增 Inhibits the proliferation of <i>Lactobacillus plantarum</i> in the midgut	Xiong <i>et al.</i> , 2024
甜菜夜蛾 <i>Spodoptera exigua</i>	SeCTL-S15	1	抵抗苏云金芽孢杆菌感染 Defenses infections by <i>Bacillus thuringiensis</i>	Bao <i>et al.</i> , 2024
草地贪夜蛾 <i>Spodoptera frugiperda</i>	SfIML1	2	结合并凝集大肠杆菌和金黄色葡萄球菌，促进血细胞的凝集和结节，结合球孢白僵菌以抵抗其感染 Binds and agglutinates <i>Escherichia coli</i> and <i>Staphylococcus aureus</i> , promotes hemocytic agglutination and nodulation, binds to <i>Beauveria bassiana</i> to defense infection	Liu <i>et al.</i> , 2025
小菜蛾 <i>Plutella xylostella</i>	PxCTL5	1	凝集大肠杆菌和苏云金芽孢杆菌 Agglutinates <i>Escherichia coli</i> and <i>Bacillus thuringiensis</i>	Yu <i>et al.</i> , 2017
烟草天蛾 <i>Manduca sexta</i>	MsIML1	2	促进包裹作用和酚氧化酶原的激活 Promotes encapsulation and the activation of prophenoloxidase	Yu and Kanost, 2001
烟草天蛾 <i>Manduca sexta</i>	MsIML2	2	促进包裹、黑化和吞噬作用以及酚氧化酶原的激活 Promotes encapsulation, melanization, and phagocytosis, and the activation of prophenoloxidase	Shi and Yu, 2012
烟草天蛾 <i>Manduca sexta</i>	MsIML3	2	促进血细胞对葡聚糖凝珠的包裹 Promotes the encapsulation of Sephadex beads by hemocytes	Yu <i>et al.</i> , 2005
烟草天蛾 <i>Manduca sexta</i>	MsIML4	2	凝集大肠杆菌、金黄色葡萄球菌和酵母，促进血细胞的包裹和黑化反应 Agglutinates <i>Escherichia coli</i> , <i>Staphylococcus aureus</i> and yeast, and promotes encapsulation and melanization	Yu <i>et al.</i> , 2006
亚洲玉米螟 <i>Ostrinia funacalis</i>	OfIML10	2	结合粒细胞和浆细胞等血细胞，促进血细胞对葡聚糖凝珠的包裹 Sephadex beads Binds to hemocytes such as granulocytes and plasmacytes, promotes their encapsulation of	Song <i>et al.</i> , 2020
黑腹果蝇 <i>Drosophila melanogaster</i>	DmCTL1	1	结合大肠杆菌 Binds to <i>Escherichia coli</i>	Haq <i>et al.</i> , 1996
黑腹果蝇 <i>Drosophila melanogaster</i>	DmCTL2, 3	1	凝集大肠杆菌，结合血细胞，促进包裹和黑化反应 Agglutinates <i>Escherichia coli</i> , binds to hemocytes, and promotes encapsulation and melanization	Ao <i>et al.</i> , 2007
白纹伊蚊 <i>Aedes albopictus</i>	CTL1	1	凝集金黄色葡萄球菌和白色念珠菌、促进血细胞凝集 Agglutinates <i>Staphylococcus aureus</i> and <i>Candida albicans</i> , and promotes hemocytic agglutination	Cheng <i>et al.</i> , 2014

续表 2 (Table 2 continued)

物种 Species	凝集素 Lectin	CRD 数量 CRD number	功能 Functions	参考文献 References
白纹伊蚊 <i>Aedes albopictus</i>	CTL-S12, S17, S19	1	促进登革病毒感染白纹伊蚊细胞 Promote dengue virus (DENV) infection in <i>Aedes albopictus</i> cells	Gao <i>et al.</i> , 2024
埃及伊蚊 <i>Aedes aegypti</i>	mosGCTL1	1	促进西尼罗病毒感染中肠上皮细胞 Promotes west Nile virus (WNV) infection in the midgut epithelial cells	Cheng <i>et al.</i> , 2010
埃及伊蚊 <i>Aedes aegypti</i>	mosGCTL3	1	促进登革病毒感染蚊子 Promotes dengue virus (DENV) infection in mosquitoes	Gao <i>et al.</i> , 2024
埃及伊蚊 <i>Aedes aegypti</i>	mosGCTL7	1	促进日本脑炎病毒感染中肠上皮细胞 Promotes Japanese encephalitis virus (JEV) infection in the midgut epithelial cells	Liu <i>et al.</i> , 2017
埃及伊蚊 <i>Aedes aegypti</i>	CTL16	1	激活 IMD、JAK/STAT 信号通路, 限制登革病毒扩增 Activates the IMD and JAK/STAT signaling pathways to limit replication of dengue virus (DENV)	Chang <i>et al.</i> , 2024
冈比亚按蚊 <i>Anopheles gambiae</i>	AgCTL4, CTLMMA2	1	AgCTL4 与 AgCTLMMA2 形成异二聚体, 抵抗大肠杆菌, 负调控黑化反应 AgCTL4 interacts with AgCTLMMA2, defense <i>Escherichia coli</i> , inhibit melanization	Bishnoi <i>et al.</i> , 2019
冈比亚按蚊 <i>Anopheles gambiae</i>	AgCTL10	1	凝集疟原虫, 促进蚊子吸血 Agglutinates <i>Plasmodium</i> and promotes blood-feeding in mosquitoes	Krairojananan <i>et al.</i> , 2012
骚扰阿蚊 <i>Armigeres subalbatus</i>	AsCTLGA5	1	抵抗大肠杆菌感染 Defenses <i>Escherichia coli</i> infection	Shi <i>et al.</i> , 2014
桔小实蝇 <i>Bactrocera dorsalis</i>	BdCTL-S12	1	结合并抵抗抗球孢白僵菌、雷氏普罗威登斯菌和粪肠球菌感染 Binds and defenses infections by <i>Beauveria bassiana</i> , <i>Providencia rettgeri</i> and <i>Enterococcus faecalis</i>	Zhao <i>et al.</i> , 2025
赤拟谷盗 <i>Tribolium castaneum</i>	TcCTL2, 4, 9, 14, 15	1	凝集大肠杆菌、铜绿假单胞菌和苏云金芽孢杆菌等细菌, 促进 DIF、Relish 和抗菌肽的表达, 此外 TcCTL2、4、9 促进黑化反应, TcCTL2 促进血细胞包裹、吞噬 Agglutinate bacteria such as <i>Escherichia coli</i> , <i>Pseudomonas aeruginosa</i> , and <i>Bacillus thuringiensis</i> ; induces the expression of DIF, Relish and AMPs; TcCTL2, 4, 9 also promote melanization; TcCTL2 also promotes encapsulation and phagocytosis	Wang <i>et al.</i> , 2023b, 2024; Zhang <i>et al.</i> , 2023a, 2024; Li <i>et al.</i> , 2025
赤拟谷盗 <i>Tribolium castaneum</i>	TcCTL12, 6, 13	1	凝集大肠杆菌、铜绿假单胞菌和苏云金芽孢杆菌等细菌, TcCTL6; 13 还能诱导抗菌肽表达 Agglutinate bacteria such as <i>Escherichia coli</i> , <i>Pseudomonas aeruginosa</i> , and <i>Bacillus thuringiensis</i> , TcCTL6, 13 also induce the expression of AMPs	Bi <i>et al.</i> , 2019; Zhang <i>et al.</i> , 2022; Ning <i>et al.</i> , 2024
赤拟谷盗 <i>Tribolium castaneum</i>	TcCTL3	2	抵抗大肠杆菌和金黄色葡萄球菌感染昆虫, 介导肽聚糖或脂多糖诱导的抗菌肽和转录因子表达 Defenses <i>Escherichia coli</i> and <i>Staphylococcus aureus</i> , induces the expression of AMPs and transcription factors under peptidoglycan or lipopolysaccharide stimulation	Bi <i>et al.</i> , 2020

续表 2 (Table 2 continued)

物种 Species	凝集素 Lectin	CRD 数量 CRD number	功能 Functions	参考文献 References
赤拟谷盗 <i>Tribolium castaneum</i>	TcCTL16	1	凝集大肠杆菌、铜绿假单胞菌和金黄色葡萄球菌等细菌, 沉默 <i>TcCTL16</i> 导致抗菌肽和 <i>Relish</i> 的表达量增多, 从而抵御大肠杆菌和金黄色葡萄球菌感染昆虫 Agglutinates <i>Escherichia coli</i> , <i>Pseudomonas aeruginosa</i> and <i>Staphylococcus aureus</i> , silencing <i>TcCTL16</i> led to induced expression of AMPs and <i>Relish</i> , and increased survival rate when infected with <i>E. coli</i> and <i>S. aureus</i>	Bi et al., 2023
赤拟谷盗 <i>Tribolium castaneum</i>	TcCTL1	1	介导肽聚糖或脂多糖诱导的抗菌肽表达 Induces the expression of antimicrobial peptides in response to peptidoglycan or lipopolysaccharide	Zhang et al., 2023b
赤拟谷盗 <i>Tribolium castaneum</i>	TcCTL17	1	结合肽聚糖和脂多糖, 凝集细菌并抑制其扩增 结合到肽聚糖和 lipopolysaccharide, agglutinates bacteria to inhibit replication	Chen et al., 2025
红棕象甲 <i>Rhynchophorus ferrugineus</i>	RfCTL27	1	识别大肠杆菌, 诱导抗菌肽表达 Recognizes <i>Escherichia coli</i> and induces the expression of AMPs	Gong et al., 2024
家蚕 <i>Bombyx mori</i>	BmGALE4	2	凝集大肠杆菌和金黄色葡萄球菌 Agglutinates <i>Escherichia coli</i> and <i>Staphylococcus aureus</i>	Rao et al., 2016
斜纹夜蛾 <i>Spodoptera litura</i>	SIGALE4	1	抵抗莱氏绿僵菌感染昆虫, 促进苏云金芽孢杆菌感染昆虫 Defenses <i>Metarhizium rileyi</i> infection, but promotes <i>Bacillus thuringiensis</i> infection in insects	Zhong et al., 2025
斜纹夜蛾 <i>Spodoptera litura</i>	SIGALE7	1	抵抗苏云金芽孢杆菌感染昆虫 Defenses <i>Bacillus thuringiensis</i> infection in insects	Zhong et al., 2025
埃及伊蚊 <i>Aedes aegypti</i>	AaGALE6, 14	1	竞争性结合 Cry11Aa 的受体, 从而降低 Cry11Aa 的毒性 Bind to the receptor of Cry11Aa and reduce the toxicity of Cry11Aa	Zhang et al., 2018; Hu et al., 2020
沙蝇 <i>Phlebotomus papatasi</i>	GALE	2	协助寄生虫逃避宿主免疫 Assists parasites in evading host immunity	Kamhawi et al., 2004
中华蜜蜂 <i>Apis cerana</i>	AcGALE4	1	结合中蜂囊状幼虫病毒, 与病毒衣壳蛋白 VP3 互作 Binds to Chinese sacbrood virus (CSBV) and interacts with the CSBV capsid protein VP3	Fei et al., 2018
石蚕蛾 <i>Stenopsyche kodaikanalensis</i>	GALE	—	促进血细胞凝集反应 Promotes hemocytic agglutination	Sreeramulu et al., 2018
松墨天牛 <i>Monochamus alternatus</i>	GALE	—	抑制黑化反应 Inhibits melanization	Zhang et al., 2021
香蕉假茎象鼻虫 <i>Odoiporus longicollis</i>	GALE	2	凝集并抑制大肠杆菌、铜绿假单胞菌和金黄色葡萄球菌生长 Agglutinates and inhibits the growth of <i>Escherichia coli</i> , <i>Pseudomonas aeruginosa</i> and <i>Staphylococcus aureus</i>	Tamilarasan et al., 2021

—: 未检测。—: Undetected.

(Phenoloxidase, PO)催化酚类物质转化为醌类物质,并促进黑色素的形成来消灭病原体(Lemaitre and Hoffmann, 2007)。细胞免疫主要由血细胞介导,通过吞噬(Phagocytosis)、包裹(Encapsulation)、结节(Nodulation)、黑化(Melanization)等过程清除病原体(Lavine and Strand, 2002)。鳞翅目昆虫中,原血细胞(Prohemocyte)是最基本的血细胞,具备分化为其他类型血细胞的能力,而浆细胞(Plasmatocyte)、粒细胞(Granulocyte)和类绦色细胞(Oenocytoid)是免疫应答过程最重要的血细胞(Lavine and Strand, 2002)。浆细胞和粒细胞具有强黏附活性,被募集到感染部位后,通过吞噬和包裹杀死病原体;类绦色细胞合成酚氧化酶原(Prophenoloxidase, proPO)并将proPO 释放到血淋巴,最终促进黑化反应(Jiravanichpaisal *et al.*, 2006)。此外,昆虫血细胞还会与病原体形成微聚集体,这些微聚集体会积聚形成结节,随后被有活性的酚氧化酶合成的黑色素包被并清除(Ling and Yu, 2006)。

模式识别受体(PRRs)对病原体的病原相关分子模式(PAMPs)的识别是一个宿主判别“自我”和“非我”的过程。病原微生物(包括细菌、真菌、病毒、寄生虫以及其他各类致病微生物)表面存在异于宿主的特定组分,常见的PAMPs包括细菌细胞壁中的肽聚糖(Peptidoglycan, PGN)、革兰氏阴性菌的脂多糖(Lipopolysaccharide, LPS)、革兰氏阳性菌的磷壁质酸(Lipoteichoic acid, LTA),以及真菌细胞壁的 β -1, 3-葡聚糖(β -1, 3-glucan)等(Lu *et al.*, 2020a)。昆虫体内不同的PRRs,分别识别不同的PAMPs。目前已明确在昆虫中鉴定出的PRRs主要包括肽聚糖识别蛋白(Peptidoglycan-recognition proteins, PGRPs)、革兰氏阴性结合蛋白(Gram-negative binding proteins, GNBPs)、凝集素(Lectins)、清道夫受体(Scavenger receptors, SRs)、以及硫酯蛋白(Thioester-containing proteins, TEPs)等(Lin *et al.*, 2020; Lu *et al.*, 2020b)。昆虫的PRRs可以单独识别PAMPs,也可以形成复合物

识别PAMPs,例如肽聚糖识别蛋白(PGRPs)与革兰氏阴性结合蛋白(GNBPs)可协同激活酚氧化酶原系统,增强昆虫免疫防御(Gobert *et al.*, 2003)。此外,昆虫的PRRs还能调节昆虫的生长发育过程(Pace *et al.*, 2002; Lin *et al.*, 2020)。

2 昆虫凝集素

凝集素含有碳水化合物识别结构域(Carbohydrate recognition domain, CRD),通过CRD识别多种糖缀合物(包括糖蛋白、蛋白聚糖和糖脂等)(Dambuzza and Brown, 2015)。凝集素广泛存在于动植物和微生物中,参与多个关键的生理过程,如免疫调节、细胞内信号转导、细胞识别与黏附等(Sharon and Lis, 2004)。昆虫凝集素通常含有1-3个CRDs,主要涵盖C-型凝集素和半乳糖凝集素(Xia *et al.*, 2018; Zhong *et al.*, 2025)。昆虫凝集素存在于多种组织,如血细胞、脂肪体、肠道、肌肉和体壁等,其中脂肪体和血细胞是合成凝集素的主要场所(Shi *et al.*, 2014; Song *et al.*, 2020; Zhong *et al.*, 2025)。昆虫凝集素参与细胞与分子、细胞与细胞间的识别,是先天免疫系统中一类重要的模式识别受体(Vasta *et al.*, 1999; Xia *et al.*, 2018)。

2.1 昆虫C-型凝集素

2.1.1 昆虫C-型凝集素的结构与进化特征

2.1.1.1 昆虫CTLs的结构与分类 C-型凝集素广泛存在于动物和植物中,因其对糖类的识别和结合依赖于 Ca^{2+} 而得名(Dambuzza and Brown, 2015)。CTLs通常含有信号肽(Signal peptide, SP)、其核心结构区域含一个或多个CRDs(Gao *et al.*, 2024)。根据含有CRD的数目,可将CTLs分为3个亚家族:CTL-S(仅含有一个CRD)、IML(Immulectin,含两个串联的CRDs)和CTL-X(除了CRD外还含有其他功能域)(Xia *et al.*, 2018)。由于部分CTLs具有跨膜结构域,因此CTLs又被划分为膜结合型和游离型两种类型,大部分昆虫的CTLs属于游离型(Xia *et al.*, 2018)。

CTL的CRD三维结构呈现典型的 β -三明治

拓扑构型,由 6 条反向平行 β 链 ($\beta 1$ - $\beta 6$) 构成双层 β -折叠片基底,其中 $\beta 2$ - $\beta 3$ - $\beta 4$ 和 $\beta 1$ - $\beta 5$ - $\beta 6$ 分别形成 2 个反向平行的 β 片层,通过疏水相互作用堆叠形成稳定的三明治结构,通过 α -螺旋结构域和可变环区 (Hypervariable loops) 连接 β 片层,维持结构刚性,并由保守的二硫键网络(通常包含 2-3 对二硫键: Cys1-Cys2、Cys3-Cys6 和 Cys4-Cys5) 增加结构稳定性 (Dambuzza and Brown, 2015)。对 7 种昆虫 CRD 保守残基分析显示, CTL-X 存在 3 组保守的二硫键, Cys3-Cys6 存在于所有的 CRDs 中, IML 的氨基端 CRD 都含有 Cys4-Cys5, IML 的羧基端 CRD 都含有 Cys1-Cys2 (Lu *et al.*, 2020b)。

根据氨基酸基序的差异, CRDs 可分成不同的亚型,其偏好结合的糖类也不同。M 型 CRD 含谷氨酸-脯氨酸-天冬酰胺 (EPN) 基序,通常与 Ca^{2+} 配位形成金属结合位点,能够特异性识别甘露糖型配体(如甘露糖、N-乙酰葡萄糖胺、L-岩藻糖和葡萄糖等); L 型 CRD 含谷氨酰胺-脯氨酸-天冬氨酸 (QPD) 基序,则通过构象互补机制选择性地结合半乳糖型碳水化合物,包括半乳糖及其 N-乙酰化衍生物 (GalNAc); 而 E 型 CRD 则通过谷氨酸-脯氨酸-苏氨酸 (EPT) 基序,偏好结合硫酸化糖(如硫酸半乳糖) (Drickamer, 1992; Zelensky and Gready, 2005)。绝大多数 IMLs 的 CRD 包含至少一个 EPN 或 QPD 基序,有些 IML 氨基端 CRD 含 EPN 基序,羧基端 CRD 含 QPD 基序 (Drickamer, 1992; Lu *et al.*, 2020b)。CTL-X 中的 CRD 通常不含 EPN 或 QPD 元件 (Lu *et al.*, 2020b)。CTLs 一般需要 Ca^{2+} 稳定 CRD 构象、增强结合碳水化合物的活性。有研究发现部分昆虫 CTLs 进化出 Ca^{2+} 非依赖性的结合模式,即不依赖 Ca^{2+} 也能结合病原微生物,但需要 Ca^{2+} 发挥凝集活性 (Yu and Ma, 2006), 说明 Ca^{2+} 有助于这些昆虫 CTLs 形成多聚体。

2.1.1.2 昆虫 CTLs 数量与进化特征 在无脊椎动物中, CTLs 基因数量差异显著,线虫和软体动物有 100-300 个 (Peas *et al.*, 2016), 昆虫仅有 4-55 个 (Lu *et al.*, 2020b)。CTLs 家族成员在不同目,乃至相同目的不同昆虫中数量有别。

膜翅目的西方蜜蜂 *Apis mellifera* 仅有 12 个 CTLs (Evans *et al.*, 2006), 鞘翅目的赤拟谷盗 *Tribolium castaneum* 有 17 个 CTLs (Zou *et al.*, 2007; Wang *et al.*, 2023b)。鳞翅目不同物种的 CTL 数量差异较大 (表 1): 小菜蛾 *Plutella xylostella* 仅有 7 个 CTLs (Yu *et al.*, 2017), 棉铃虫 *Helicoverpa armigera* 则含 39 个 CTLs (Lu *et al.*, 2020b)。双翅目昆虫的 CTLs 数量整体较多,除了冈比亚按蚊 *Anopheles gambiae* 只有 25 个 CTLs 外 (Holt *et al.*, 2002), 其他双翅目昆虫含有 39-55 个 CTLs (Nene *et al.*, 2007; Waterhouse *et al.*, 2007; Lu *et al.*, 2020b) (表 1)。不同于其他类群,膜翅目昆虫中承担传粉功能的类群,其凝集素基因在进化上具有保守性。以传粉榕小蜂和非传粉榕小蜂为例,二者在 C-型凝集素和半乳糖凝集素的基因数量上均无显著差异,进化树分析显示这两类榕小蜂在凝集素基因的进化上基本呈现出对应关系 (Hou *et al.*, 2021)。除 CTLs 基因数目的差异, CTLs 亚型分布也存在显著差异。昆虫通常含有 4-6 个 CTL-X 基因,这些基因在进化上非常保守 (Lu *et al.*, 2020b)。绝大多数 IMLs 存在于鳞翅目昆虫中,数量横跨 7 (家蚕 *Bombyx mori*) 到 23 (棉铃虫) 个 (表 1) (Lu *et al.*, 2020b)。CTL-S 存在于所有的昆虫,在双翅目中含量最多,例如双翅目的黑腹果蝇 *Drosophila melanogaster* 含有 38 个 CTL-S 基因 (Lu *et al.*, 2020b), 而白纹伊蚊 *Aedes albopictus* 拥有 29 个 (Gao *et al.*, 2024)。

进化树分析显示, CTL-S 在不同昆虫中各自含有 1-2 个直系同源基因,部分 CTL-S 在双翅目昆虫中存在扩增现象 (Waterhouse *et al.*, 2007; Adelman and Myles, 2018; Lu *et al.*, 2020b)。IML 存在于鳞翅目中,可能由单 CRD 基因串联复制演化而来,且数量不一,存在不同程度的扩增 (Lu *et al.*, 2020b)。IML 的 2 个 CRD 在进化树上可各自归成 1 个分支,其保守基序和功能也存在差异 (Wang *et al.*, 2014; Lu *et al.*, 2020b)。不同类型的 CTL 基因在进化上面临不同的选择压力。鳞翅目昆虫的部分 IML 和双翅目昆虫的

部分 CTL-S 在基因组上串联重复排列, 在进化树中也成簇分布 (Rao *et al.*, 2015a; Lu *et al.*, 2020b)。这些基因的非同义替换率和同义替换率 (dN/dS) 显著高于其他 CTLs, 说明这些基因经历了更强的选择分化 (Lu *et al.*, 2020b)。CTL-X 在昆虫中高度保守, 且多为单系同源基因 (Lu *et al.*, 2020b)。

2.1.2 昆虫 C-型凝集素的功能

2.1.2.1 CTL-S 亚家族 CTL-S 亚家族只含有 1 个 CRD 结构域, 肽链通常含 200-350 个氨基酸, 部分 CTL-S 成员的多肽链羧基端含有跨膜结构域, 能够形成膜结合型受体 (Zou *et al.*, 2007)。昆虫 CTL-S 成员在多个组织中均有表达, 例如骚扰阿蚊 *Armigeres subalbatus* 的 AsCTLMA15、AsCTLGA5 和 AsCTL15 主要在血细胞表达, AsCTL16 在脂肪体表达, 而 AsCTLMA11 在血细胞和脂肪体中均有表达, AsCTLMA11 和 AsCTL16 在成年雌蚊中高表达 (Shi *et al.*, 2014)。有些 CTL-S 在卵巢发育、胚胎发生等发育过程中高表达 (Zhang *et al.*, 2023a)。

昆虫受病原体入侵后, CTL-S 能够与细菌、真菌、病毒或者线虫等病原微生物表面的糖蛋白结合, 充当模式识别受体; 也能通过促进血细胞包裹、黑化、吞噬作用等手段调节细胞免疫 (Ao *et al.*, 2007; Xia *et al.*, 2018; Zhong *et al.*, 2025)。鳞翅目棉铃虫 HaCTL3 的表达受蜕皮激素 20E 的调控, HaCTL3 能结合血细胞表面的 Ha β -integrin 整合素, 促进血细胞的包裹; HaCTL3 蛋白还能促进血细胞的黑化, 以及结合寄生线虫, 参与抵抗线虫的感染 (Wang *et al.*, 2017)。家蚕 BmCTL5 (即 BmCTL-S3) 能结合细菌、细菌细胞壁成分 LPS、球孢白僵菌 *Beauveria bassiana* 以及血细胞, BmCTL5 蛋白能结合整合素的 $\beta 2$ - $\beta 5$ 亚基, 促进血细胞吞噬, 从而清除血淋巴中的细菌 (Zhan *et al.*, 2016; Sun *et al.*, 2023)。BmCTL-S6 在脂肪体和血细胞的表达受大肠杆菌 *Escherichia coli* 和藤黄微球菌 *Micrococcus luteus* 的诱导, 能结合 LPS 和 PGN, 参与血细胞的包裹和黑化过程 (Shen *et al.*, 2021)。BmCTL4 (即 BmCTL-S2) 能结

合多种细菌组分, 抑制枯草芽孢杆菌 *Bacillus subtilis* 和金黄色葡萄球菌 *Staphylococcus aureus* 的生长 (Shahzad *et al.*, 2017)。小菜蛾 PxCTL5 在幼虫表皮表达, 受大肠杆菌和苏云金芽孢杆菌 *Bacillus thuringiensis*, Bt 侵染后表达量增加, 且对这两种细菌都具有凝集活性 (Yu *et al.*, 2017)。双翅目中, 黑腹果蝇 DmCTL1 能够结合革兰氏阴性大肠杆菌 (Haq *et al.*, 1996; Ao *et al.*, 2007); 而 DmCTL2 和 DmCTL3 除了凝集大肠杆菌外, 还促进血细胞的包裹和黑化 (Tanji *et al.*, 2006; Ao *et al.*, 2007)。白纹伊蚊 AalbCTL1 在雌性蚊子唾液腺表达, 具有凝血活性, 还能够凝集白色念珠菌 *Candida albicans* 和金黄色葡萄球菌, 然而对大肠杆菌没有凝集活性 (Cheng *et al.*, 2014)。骚扰阿蚊 AsCTLGA5 能够凝集细菌, 抵抗大肠杆菌的感染 (Shi *et al.*, 2014)。冈比亚按蚊 AgCTL4 和 AgCTLMA2 以二硫键连接的异二聚体形式分泌至蚊子的血淋巴中, 参与清除蚊子体内的大肠杆菌, 然而对革兰氏阳性菌感染不起作用 (Schnitger *et al.*, 2009; Bishnoi *et al.*, 2019; Simões *et al.*, 2022)。AgCTL10 通过凝集病原微生物 (如疟原虫), 限制其穿透围食膜进入中肠上皮, 间接影响蚊虫的营养吸收与吸血量 (Krairojananan *et al.*, 2012)。鞘翅目赤拟谷盗 TcCTL2 重组蛋白可以促进血细胞介导的包裹、吞噬和黑化 (Wang *et al.*, 2024); 而 TcCTL1、TcCTL4、TcCTL6、TcCTL9、TcCTL13 和 TcCTL14 重组蛋白在 Ca^{2+} 依赖下可以凝集细菌 (Bi *et al.*, 2019; Zhang *et al.*, 2023b, 2024; Ning *et al.*, 2024; Li *et al.*, 2025)。

CTL-S 也参与免疫信号通路和抗菌肽等体液免疫的调控。家蚕 BmCTL5 蛋白能激活血细胞中的免疫基因, 如抗菌肽、JAK/STAT 信号通路基因 (Sun *et al.*, 2023); BmCTL5 结合球孢白僵菌后, 能激活 JAK/STAT 信号通路和黑化反应以抵抗真菌感染 (Geng *et al.*, 2021)。埃及伊蚊 *Aedes aegypti* CTL16 能限制登革病毒 (Dengue virus, DENV) 在体内的扩增, CTL16 敲除后导致 IMD、JAK/STAT 信号通路基因下调 (Chang *et al.*, 2024)。赤拟谷盗 TcCTL2、

TcCTL4、TcCTL6、TcCTL9、TcCTL13 和 TcCTL14 能够同时调节体液免疫和细胞免疫, 通过 Toll 和 IMD 信号通路诱导转录因子、抗菌肽以及酚氧化酶原的表达水平 (Bi *et al.*, 2019; Zhang *et al.*, 2023a, 2024; Ning *et al.*, 2024; Wang *et al.*, 2024; Li *et al.*, 2025)。红棕象甲 *Rhynchophorus ferrugineus* 的 RfCTL27 可以识别革兰氏阴性菌, 上调抗菌肽基因的表达 (Gong *et al.*, 2024)。此外, 亚洲玉米螟 *Ostrinia furnacalis* 喂食 Bt 毒素蛋白 Cry1F 后多个 OfCTLs 的表达量不同程度上调, 这些 OfCTLs 可能通过调控 MAPK 信号通路协助幼虫抵抗 Cry1F 毒素 (Prabu *et al.*, 2022)。

2.1.2.2 IML 亚家族 IMLs 通常存在于鳞翅目昆虫中, 包含 2 个通过柔性铰链区相连的 CRDs, 2 个 CRDs 可以协同 (同源) 或独立 (异源) 结合配体 (Yu *et al.*, 2006; Wang *et al.*, 2014)。同源结合即 2 个 CRDs 结合同类糖链, 例如烟草天蛾 MsIML4 的 2 个 CRDs 均结合细菌脂多糖, 增强对细菌的亲合力 (Yu *et al.*, 2006)。异源结合即 2 个 CRDs 结合的底物不同, 通常扮演不同的功能。棉铃虫 HaCTL7 的羧基端 CRD2 能够凝集细菌, 通过结合粒细胞和类绛色细胞等血细胞促进包裹和黑化, 而氨基端 CRD1 不具备这些功能 (Wang *et al.*, 2014)。值得注意的是, 鞘翅目赤拟谷盗的 TcCTL3 也属于 IML 亚型, 主要通过 CRD1 凝集多种革兰氏阳性菌和革兰氏阴性菌, 并且通过促进抗菌肽的表达抵御微生物感染 (Bi *et al.*, 2020)。

昆虫 IMLs 主要由脂肪体、血细胞分泌, 对多种病原微生物具有结合活性, 能促进包裹、吞噬、黑化、抗菌肽产生等细胞和体液免疫反应 (Xia *et al.*, 2018)。IMLs 的早期研究集中在烟草天蛾 *Manduca sexta* 中: MsIML1、MsIML2、MsIML3 和 MsIML4 都在脂肪体中表达, 能促进血细胞的包裹作用 (Yu and Kanost, 2001, 2003; Yu *et al.*, 2005; Ling *et al.*, 2008); MsIML2 和 MsIML4 能促进黑化; MsIML1、MsIML2 和 MsIML4 能激活血淋巴酚氧化酶原; 而 MsIML2 和 MsIML4 的结合活性不依赖 Ca^{2+} (Yu *et al.*,

2006; Shi and Yu, 2012)。后续在其他昆虫中的研究发现, 草地贪夜蛾 *Spodoptera frugiperda* 的 SfIML-1 能结合多种 PAMPs: PGN、LPS、昆布多糖、酵母聚糖和凝胶多糖, 也能结合大肠杆菌、金黄色葡萄球菌和球孢白僵菌, 促进大肠杆菌和金黄色葡萄球菌的凝集; SfIML-1 能结合到血细胞表面, 促进血细胞聚集和结节。SfIML-1 基因在球孢白僵菌感染后表达量显著增加, RNA 干扰 (RNA interference, RNAi) 沉默 SfIML1 基因导致感染真菌的草地贪夜蛾幼虫死亡率增加, 而注射重组 SfIML1 蛋白则显著提高幼虫存活率 (Liu *et al.*, 2025)。棉铃虫 HaCTL1 在血细胞表达, 通过促进血细胞的包裹和吞噬作用来抵御寄生线虫 (Chai *et al.*, 2008; Wang *et al.*, 2021); HaCTL14 能结合并凝集球孢白僵菌, 促进血细胞对真菌的吞噬, 还能通过调控丝氨酸蛋白酶 (Serine protease, SPs) 和丝氨酸蛋白酶抑制剂 (Serpine) 的表达, 激活黑化反应相关信号通路 (Cheng *et al.*, 2018)。亚洲玉米螟 OfIML10 由脂肪体分泌, 对葡聚糖凝胶珠具有凝集活性, 且 OfIML10 能够与粒细胞和浆细胞表面结合, 从而增强血细胞的包裹能力 (Song *et al.*, 2020)。家蚕 BmCTL10 在脂肪体和表皮表达, 大肠杆菌、金黄色葡萄球菌、白僵菌和 20E 能诱导 BmCTL10 的表达; BmCTL10 蛋白能结合血细胞和多种 PMAPs, 促进血细胞的结节、吞噬和包裹; BmCTL10 蛋白也能上调血细胞中免疫相关的抗菌肽和一氧化氮酶的表达, BmCTL10 能结合整合素的 $\beta 3$ 、 $\beta 4$ 亚基, 可能介导了对细胞免疫和体液免疫的调节 (Liu *et al.*, 2022)。家蚕幼虫感染微孢子虫 *Nosema bombycis* 后 BmCTL11 的表达持续增加, 可能参与抵抗微孢子虫的侵袭 (Ma *et al.*, 2013)。此外, BmIML2 通过促进细胞凋亡显著抑制了家蚕核型多角体病毒 (*Bombyx mori* nucleopolyhedrovirus, BmNPV) 的增殖 (Mei *et al.*, 2022)。

2.1.2.3 CTL-X 亚家族 CTL-X 成员除了 CRD 结构域外还含有其他功能域, CTL-X 中经常含有补体控制蛋白结构域 CCP (Complement control protein domain), 但其他功能域在不同

昆虫类别中存在差异, 如胞外域 CUB (Complement C1r/C1s, Uegf, BMP1 domain)、上皮生长因子域 EGF (Epidermal growth factor domain)、免疫球蛋白结构域 Ig (Immunoglobulin domain)、类胰蛋白酶丝氨酸蛋白酶域 Tryp_SPc 等 (Xia *et al.*, 2018)。CTL-X 的 CRD 能结合外源微生物来源的糖基参与免疫反应, 也能结合自身内的糖基介导信号传递等过程, CTL-X 的其他功能域能够协同 CRD 参与昆虫发育 (Zhang and Ward, 2009; Xia *et al.*, 2018)。

CTL-X 亚家族参与免疫的研究很少, 赤拟谷盗 TcCTL12 和 TcCTL15 重组蛋白在 Ca^{2+} 协助下对多种革兰氏阳性菌和革兰氏阴性菌都具有凝集活性, TcCTL15 还可以诱导抗菌肽基因的表达 (Zhang *et al.*, 2022; Wang *et al.*, 2023b); TcCTL17 能结合 LPS 和 PGN, 凝集和抑制细菌的扩增 (Chen *et al.*, 2025); TcCTL16 主要在血淋巴表达, 感染 TcCTL16 导致抗菌肽和 Relish 的表达量增加, 从而抵御金黄色葡萄球菌和大肠杆菌的侵染 (Bi *et al.*, 2023)。此外, 更多报道显示 CTL-X 成员参与昆虫发育, 如果蝇中不可膨胀蛋白 UninflaTable、皱缩蛋白 furrowed 和接触蛋白 contactin 分别参与胚胎气管成熟、眼睛和刚毛的发育、隔膜连接和细胞旁屏障的组建 (Faivre-Sarrailh *et al.*, 2004; Chin and Mlodzik, 2013; Sun *et al.*, 2017)。

2.1.2.4 昆虫 CTLs 在免疫系统中的双重角色

肠道菌群与宿主免疫的关系复杂, 近年来的研究显示, 昆虫 CTLs 在肠道菌群稳态中发挥重要功能。棉铃虫 CD209 (CTL-S) 能抑制肠道中条件致病菌 *Lactobacillus plantarum* 的繁殖, RNAi 干扰降低 CD209 的表达导致肠道和血淋巴中 *L. plantarum* 的载量增加, 从而延迟变态发育 (Xiong *et al.*, 2024)。棉铃虫 HaCTL6 通过上调溶菌酶的表达, 限制血淋巴中细菌的过度繁殖, 以维持血淋巴微生物的稳态 (Zhao *et al.*, 2025)。相反, 埃及伊蚊肠道中 mosGCTLs 能够特异性地包裹在肠道细菌的表面, 有效地抵消宿主肠道内抗菌肽的杀菌活性, 促进多种细菌在肠道内定殖 (Osta *et al.*, 2004)。RNAi 沉默淡色

库蚊 *Culex pipiens pallens* 中 mosGCTL 的同源基因后, 其肠道共生细菌的存活受到损害, 表明 mosGCTL 及其同源基因都能维持肠道共生细菌的生存 (Pang *et al.*, 2016)。

CTLs 种类多样, 除了参与免疫防御外, 也能被部分病毒和寄生虫利用, 用于逃避免疫反应。西尼罗河病毒 (West Nile virus, WNV) 感染埃及伊蚊时, 其包膜蛋白能特异性结合 mosGCTL1, 而后被膜蛋白 mosPTP-1 捕获, 从而增强 WNV 病毒与中肠上皮细胞的黏附, 促进病毒感染 (Cheng *et al.*, 2010)。日本脑炎病毒 (Japanese Encephalitis virus, JEV) 能特异性结合 mosGCTL7, 激活下游 PI3K/Akt 信号通路以抑制宿主的抗病毒反应 (Liu *et al.*, 2017)。登革病毒表面包膜蛋白以及病毒粒子能结合埃及伊蚊 mosGCTL-3、白纹伊蚊 AalbCTL-S12、AalbCTL-S17 和 AalbCTL-S19, 促进登革病毒感染昆虫细胞, 表明登革病毒通过利用 CTLs 促进对病媒的感染 (Liu *et al.*, 2014; Gao *et al.*, 2024)。

2.2 昆虫半乳糖凝集素

2.2.1 昆虫半乳糖凝集素的结构与进化特征

半乳糖凝集素 (Galectins, GALEs) 携带游离的半胱氨酸残基, 因此最初被称为 S 型凝集素 (Barondes *et al.*, 1994)。GALEs 不含信号肽或跨膜结构域, 在细胞质合成后, 能够进入细胞核或留在细胞质, 也可以通过非经典的方式 (如胞吐作用) 分泌到细胞外, 从而停留在细胞外基质或通过与膜表面的糖缀合物结合锚定在细胞外膜上 (Vasta, 2012; Vasta *et al.*, 2017)。GALEs 在各物种间进化保守, 其 CRD 对 β -半乳糖苷有特殊的亲和力, 大部分 GALEs 发挥功能时不需要依赖 Ca^{2+} 的协助 (Li *et al.*, 2020)。

根据 CRD 的数目和结构, 哺乳动物 GALEs 被分为 3 类: 原型半乳糖凝集素 (Proto-type GALE), 含 1 个 CRD, 天然状态下通过氨基端非 CRD 区域的非共价结合形成同源二聚体或四聚体; 嵌合型半乳糖凝集素 (Chimera-type GALE), 除了具有单个 CRD 外, 在氨基末端

还富含脯氨酸、甘氨酸和酪氨酸等氨基酸残基, 可通过其形成三聚体或者五聚体发挥功能 (Lakshminarayan *et al.*, 2014; Kim and Chun, 2020); 串联重复型半乳糖凝集素 (Tandem-repeat GALE), 含有 2 个不同的 CRDs, 中间由 5-50 个氨基酸的肽链连接 (Troncoso *et al.*, 2012; Cummings *et al.*, 2022)。昆虫 GALEs 含有 1 个、2 个或 3 个串联排列的 CRD, 但是还没有比较清晰的分类 (Zhong *et al.*, 2025)。含有单个 CRD 的原型 GALEs 在昆虫纲中分布最广, 与哺乳动物原型 GALEs 中的 GALE1 和 GALE2 同源性较高, 目前尚不清楚昆虫中含 3 个 CRDs 的 GALEs 与脊椎动物的串联重复型 GALEs 之间的进化关系 (Pace and Baum, 2002)。

全基因组分析显示, GALEs 数目在昆虫物种间存在显著差异。膜翅目、半翅目和鞘翅目昆虫的 GALEs 数量相对较少, 如褐飞虱 *Nilaparvata lugens*、赤拟谷盗和西方蜜蜂分别含有 2 个 GALEs, 七星瓢虫 *Coccinella septempunctata* 和东方蜜蜂 *Apis cerana* 分别含有 1 个 GALE。双翅目昆虫的 GALEs 数量较多, 如黑腹果蝇含有 5 个 GALEs, 白纹伊蚊和埃及伊蚊分别含有 7 和 9 个 GALEs。鳞翅目昆虫的 GALEs 数量最多, 如棉铃虫、草地贪夜蛾和斜纹夜蛾 *Spodoptera litura* 分别含有 10、11 和 13 个 GALEs (Zhong *et al.*, 2025), 可能与它们需要应对复杂多样的病原微生物侵袭有关。

2.2.2 昆虫半乳糖凝集素的功能 哺乳动物的 GALEs 参与调控细胞自噬、细胞迁移、细胞内物质运输、细胞信号转导、免疫反应、癌细胞增殖与扩散、细胞增殖与凋亡等多种生物学功能 (Li *et al.*, 2020; Cummings *et al.*, 2022)。对昆虫 GALEs 的研究少且零散, 其主要功能是参与先天免疫反应和变态发育 (Pace *et al.*, 2002; Rao *et al.*, 2016)。昆虫 GALEs 在昆虫多个发育阶段以及多个部位均有表达, 例如黑腹果蝇 *Dmgal* 在胚胎时期的幼虫躯体、内脏肌肉组织以及中枢神经系统表达, 在果蝇幼虫的薄层细胞、浆细胞和晶细胞等血细胞中也有表达 (Pace *et al.*, 2002); 家蚕 *BmGALE4* 在受精卵发育时

期表达水平持续升高 (Rao *et al.*, 2016); 中华蜜蜂 *Apis cerana* *AcGALE1* 在头部、胸部和表皮中表达 (Wang *et al.*, 2019)。这些结果暗示昆虫 GALEs 可能参与多种生物学过程。

昆虫 GALEs 参与对病原体的识别、凝集和吞噬过程。家蚕 *BmGALE4* 能加速病原细菌的凝集, 但不具有抗菌活性 (Rao *et al.*, 2016)。香蕉假茎象鼻虫 *Odoiporus longicollis* GALE 对耻垢分枝杆菌 *Mycobacterium smegmatis* 具有凝集活性, 对短小芽孢杆菌 *Bacillus pumilus* 具有抗菌活性, 并显著抑制小鼠 Neuro 2a 细胞的增殖 (Tamilarasan *et al.*, 2021)。毛翅目石蚕蛾 *Stenopsyche kodaikanalensis* 和膜翅目中华蜜蜂的 GALE 具有促进血细胞凝集和抗病毒的作用 (Fei *et al.*, 2018; Sreeramulu *et al.*, 2018)。斜纹夜蛾 *SIGALE4* 和 *SIGALE7* 均能结合苏云金芽孢杆菌和莱氏绿僵菌 *Metarhizium rileyi*, 添加 *SIGALE4* 蛋白能增加幼虫对莱氏绿僵菌的抗性, 但是添加 *SIGALE4* 蛋白的幼虫反而对苏云金芽孢杆菌更敏感; 添加 *SIGALE7* 能增加幼虫对苏云金芽孢杆菌的抗性, 但是不影响幼虫抵抗莱氏绿僵菌的侵染 (Zhong *et al.*, 2025)。

昆虫 GALEs 也能被病原菌用于逃避免疫反应或者负调控免疫反应 (Vasta *et al.*, 2017)。寄生虫利什曼虫 *Leishmania major* 表皮 LPS 的 Gal(β 1-3) 侧链能结合宿主沙蝇 *Phlebotomus papatasi* 的 PpGALE, 从而促进利什曼虫黏附于昆虫中肠上皮细胞, 增强其存活率 (Kamhawi *et al.*, 2004)。松墨天牛 *Monochamus alternatus* 是植物病原菌松材线虫 *Bursaphelenchus xylophilus* 的媒介昆虫, 感染松材线虫的松墨天牛中 *MaGALE2* 的表达量增加, RNAi 干扰松墨天牛 *MaGALE2* 导致酚氧化酶活性增加以及松材线虫感染量减少, 表明 *MaGALE2* 能抑制黑化, 维持线虫与其媒介昆虫之间的免疫平衡 (Zhang *et al.*, 2021)。

此外, GALEs 也参与调控苏云金芽孢杆菌毒素的活性。埃及伊蚊的 *AaGALE6* 能竞争性结合 Cry11Aa 的受体 ALP1 和 APN2, 而 *AaGALE14* 能竞争性结合 ALP1, 从而降低 Cry11Aa 对蚊虫

的毒性 (Zhang *et al.*, 2018; Hu *et al.*, 2020)。秀丽隐杆线虫 *Caenorhabditis elegans* GALE8 能竞争性结合棉铃虫中肠的糖脂 (Glycolipid), 从而减少 Cry1Ac 对受体糖脂的结合, 降低 Cry1Ac 对棉铃虫的毒性 (Ma *et al.*, 2012)。

3 昆虫凝集素在植物保护中的应用

微生物源农药是害虫绿色防治的重要工具, 常见的微生物源农药包括: 苏云金芽孢杆菌及其毒素蛋白、绿僵菌/白僵菌、杆状病毒等 (Wend *et al.*, 2024)。基于凝集素在免疫系统中的双重功能, 开发 RNAi 制剂或抑制剂用于抑制抵抗生防菌的凝集素, 添加有助于生防菌免疫逃逸的凝集素, 有望增强微生物源农药的毒力。

甜菜夜蛾 *SeCTL-S15* (CTL-S) 在 Bt 和 Cry 毒素处理后的表达量增加, RNAi 干扰 *SeCTL-S15* 的表达导致幼虫对 Bt 更敏感 (Bao *et al.*, 2024)。棉铃虫 *HaCTL14* 能结合并凝集球孢白僵菌, 促进血细胞对真菌的吞噬、激活黑化反应通路; RNAi 处理降低棉铃虫 *HaCTL14* (IML) 的表达, 导致棉铃虫对球孢白僵菌更加敏感 (Cheng *et al.*, 2018)。*HaCTL11* 则能结合莱氏绿僵菌, RNAi 降低 *HaCTL11* 的表达导致棉铃虫对莱氏绿僵菌更加敏感 (Wang *et al.*, 2023a)。RNAi 沉默草地贪夜蛾 *SfIML1* 基因导致感染真菌的草地贪夜蛾幼虫死亡率增加, 而注射重组 *SfIML1* 蛋白则显著提高幼虫存活率 (Liu *et al.*, 2025)。RNAi 降低桔小实蝇 *Bactrocera dorsalis* *BdCTL-S4*、*S12* 或 *S31* 的表达量, 能提高球孢白僵菌感染桔小实蝇的致死率 (Zhao *et al.*, 2025)。可见, 靶向凝集素的 RNAi 制剂以削弱宿主防御, 可增强微生物农药的毒力。

埃及伊蚊的 AaGALE6 和 AaGALE14 能竞争性结合 Cry11Aa 的受体, 从而降低 Cry11Aa 对蚊虫的毒性 (Zhang *et al.*, 2018; Hu *et al.*, 2020)。秀丽隐杆线虫 GALE8 能竞争性结合棉铃虫中肠 Cry1Ac 的受体糖脂, 降低 Cry1Ac 对棉铃虫的毒性 (Ma *et al.*, 2012)。斜纹夜蛾 *SiGALE7* 能结合苏云金芽孢杆菌, 添加 *SiGALE7* 蛋白降低了 Bt 毒素对幼虫的毒力 (Zhong *et al.*, 2025)。后

续有望开发抑制特定 GALEs (如 AaGALE6、AaGALE14) 的小肽或 RNAi 制剂, 用于增强 Cry 毒素的活性。此外, 斜纹夜蛾 *SiGALE4* 能结合苏云金芽孢杆菌, 添加 *SiGALE4* 蛋白的幼虫对苏云金芽孢杆菌更敏感 (Zhong *et al.*, 2025)。可见, 添加有助于生防菌免疫逃逸的凝集素, 能增强微生物源农药的毒力。

4 总结与展望

昆虫作为地球上种类最多和数量最大的动物类群, 其生存环境多样化, 面临的微生物种类繁多。为了应对微生物的感染, 昆虫进化出一套精细的先天免疫系统。凝集素在识别“自我”与“非我”等方面扮演着核心角色, 能作为模式识别受体通过识别异源微生物激活宿主的免疫反应 (Xia *et al.*, 2018)。随着多种昆虫基因组测序的完成, 大量凝集素被相继鉴定, 这些凝集素在昆虫中的生理功能还有待进一步阐明。凝集素作为细胞表面受体, 能够识别广泛的配体, 包括糖链、蛋白质和脂类等 (Dambuzza and Brown, 2015)。昆虫凝集素的配体鉴定困难重重, 近年来糖生物学的快速发展有望能推动凝集素配体的鉴定及其生物学功能的揭示。昆虫缺乏后天免疫中的抗原-抗体识别体系 (Lemaitre and Hoffmann, 2007), 不同类别的凝集素在昆虫体内是否能特异性识别不同的病原微生物仍有待探究。哺乳动物的凝集素参与细胞间的黏附、识别、吞噬和信号转导等, 在免疫防御以及免疫监视中发挥重要作用 (Dambuzza and Brown, 2015)。昆虫凝集素是否具有类似的抗原提呈功能, 其与免疫信号通路的关联也有待研究。

昆虫与人类的生活紧密交织, 既包含农业生产中的害虫, 又有蜜蜂、家蚕等经济昆虫, 也是生态平衡的重要一环。昆虫凝集素参与抵御病原微生物, 但是有些病原微生物也会利用凝集素逃避免疫反应 (Kamhawi *et al.*, 2004; Xia *et al.*, 2018), 可见凝集素在昆虫-病原体的“战役”中扮演重要角色。研究昆虫凝集素, 不仅能解析昆虫-病原体的互作机制, 也能为改造微生物农药提供靶向分子, 助力绿色害虫防治。

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