昆虫翅多型的分子调控机制研究进展*

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摘 要 生物如何适应复杂的环境变化是生物学研究的重要科学问题。其中，昆虫在长期的进化过程中形成了翅多型现象以适应复杂的环境，由此通过调控翅型的转换，对不同的环境条件做出响应，从而优化资源分配以平衡迁移或繁殖的需求，但目前对其分子调控机制仍不十分清楚。本文基于国内外最新研究进展，结合作者自己的研究，系统地综述了昆虫体内参与翅型转换调控的多种途径的研究进展，包括胰岛素信号通路、蜕皮激素信号通路、保幼激素信号通路、JNK 信号通路、生物胺信号通路和病毒基因水平转移，指出了未来发展的方向。这些研究成果不仅对于进一步阐明昆虫翅多型的分子机制具有指导意义，也为开发以翅型调控为主要内容的害虫综合治理技术提供参考。

关键词 翅多型；分子调控机制；信号通路；小 RNA，基因水平转移

Molecular regulatory mechanism of wing polymorphism in insects

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Abstract How organisms adapt to a changing environment is an important question in biology. Wing polymorphism allows insects to respond rapidly to environmental cues and balance their energy allocation between dispersal and reproduction. However, the molecular mechanism underlying this process is largely unknown. In this review, we discuss current knowledge regarding the mechanisms regulating wing polymorphism at the molecular level, including the insulin/insulin-like growth factor signaling pathway, ecdysone signaling pathway, JH signaling pathway, JNK signaling pathway, biogenic amine signaling pathway, as well as the lateral transfer of virus genes. These results not only shed light on how such pathways regulate the switching between different wing types, but also provides new perspectives for developing novel insect management strategies.

Key words wing polyphenism; molecular regulatory mechanism; signaling pathway, micro RNA; lateral gene transfer

翅多型现象是昆虫适应环境的重要策略，即可产生有翅和无翅（或长翅和短翅）等不同形态的个体（Harrison，1980；Roff，1986；Zera and Denno，1997；Braendle *et al.*，2006）。其中，有翅抑或长翅个体具有完全发育的翅和飞行肌因此适合长距离迁飞，可从不适合的栖息地转移到适合的栖息地；相反，无翅或短翅个体则不具有飞行能力，但是在其他生活史特征（如繁殖能力）方面胜过长翅个体。由此通过调控翅型的转换，昆虫可对不同的环境条件做出响应，从而优化资源分配以平衡迁移或繁殖的需求（Zera and Denno，1997；Zera and Brisson，2012）。

大部分昆虫的翅多型现象在发育中的特定时期受环境因素诱导决定，属于非遗传多型性中的一种。已有报道表明，多种环境因素胁迫如种群密度、寄主植物的营养、温度、物种间相互作

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用、光周期等（Kisimoto，1956，1965；Watanabe，1967；Mochida，1975；Iwanaga *et al.*，1987; Zera and Denno，1997；Müller *et al.*，2001；Braendle *et al.*，2006）都能够影响昆虫的翅型转换。在翅型转换的关键时期，昆虫首先感受到环境条件，并将其转换成细胞间信号以引导特定组织（如翅芽与飞行肌）向适应这一环境条件的形态发育（Xu and Zhang，2017；Lin and Lavine，2018；Zhang *et al.*，2019）。尽管学界已经对影响昆虫翅多型的环境因素较为明确，但是昆虫体内信号传递的分子机制目前尚不清楚。本文重点介绍昆虫调控翅型转换分子机制的研究进展，以期对昆虫翅多型研究起到参考与推动作用。

1　调控昆虫翅多型的主要信号通路

1.1　胰岛素信号通路

胰岛素信号通路（Insulin/insulin-like growth factor（IGF）signalling（IIS） pathway）作为后生动物中一种非常保守的营养相关信号转导通路，不仅控制组织和器官的生长发育，而且参与了生物表型可塑性的调控过程，如雄性犀牛甲虫的角的大小（Brogiolo *et al.*，2001；Britton *et al.*，2002；Emlen *et al.*，2012；Hietakangas and Cohen，2009）。已有科学证据表明，寄主植物的发育阶段和营养状况是影响褐飞虱 *Nilaparvata lugens* 的翅型转换的重要因素（王希仁和张灿东，1981；Padgham，1983）；褐飞虱脑部分泌的 ILP3（Insulin-like peptide 3）可激活胰岛素受体 InR1（Insulin receptor 1）并通过 PI3K（Phosphatidylinositol-3-OH kinase）–Akt（Protein kinase B）的逐级磷酸化过程抑制翅芽中 FOXO（Forkhead transcription factor subgroup O）的活性，从而发育成长翅型个体；而 InR2（Insulin receptor 2）则能够直接与 InR1 结合来抑制 InR1-PI3K-Akt 信号通路并导致翅芽中转录因子 FOXO 从细胞质进入到细胞核中激活其下游基因表达，最终发育成短翅型个体（Xu *et al.*，2015；Lin *et al.*，2016a）。这些结果显示，褐飞虱幼虫的胰岛素受体（InR1 和 InR2）作为分子开关控制的胰岛素信号通路是昆虫本代内翅型转换的重要分子调控途径（Xu *et al.*，2015）。

最近的一系列研究结果也证实，多种环境因素都会通过胰岛素信号通路影响褐飞虱翅型比例。如寄主植物水稻中较高的葡萄糖含量可导致胰岛素分泌增加从而激活胰岛素信号通路并最终抑制下游的转录因子 FOXO，从而产生长翅型雌性褐飞虱；而当寄主植物中葡萄糖水平较低时，胰岛素分泌较少，FOXO 处于激活状态，从而产生短翅型雌性褐飞虱（Lin *et al.*，2018）。褐飞虱幼虫身体受伤后由长翅型向短翅型个体的转变过程也受胰岛素信号通路控制（Lin *et al.*，2016b）。有趣的是，雌性褐飞虱成虫的性别决定基因 *Transformer-2*（*tra-2*）可通过调控子代胰岛素信号通路来控制子代的翅型转换（Zhuo *et al.*，2017）。

与褐飞虱类似，蚜虫种群中的有翅蚜比例也与寄主植物的营养状况和发育阶段具有明显的相关性（Sutherland，1969；Vereschagina and Shaposhnikov，1998）。Guo 等（2016）研究发现豌豆蚜 *Acyrthosiphon pisum* 有翅型和无翅型三龄幼虫之间胰岛素信号通路相关基因表达水平存在显著差异，RNAi 干扰 irp5 （Insulin-related peptide 5）表达可使无翅蚜出现体重下降、蛋白水平升高、碳水化合物含量增加和卵巢变小等类似有翅蚜的特征。该结果暗示胰岛素信号通路也可能参与了蚜虫本代内翅型转换的调控过程，但是目前仍然缺乏直接的实验证据。

1.2　蜕皮激素信号通路

蜕皮激素是昆虫中广泛存在的一种类固醇激素，不仅控制昆虫蜕皮与变态（Nijhout，1998；Yamanaka *et al.*，2013），也参与了昆虫表型可塑性的调控过程（Nijhout，1999；Monteiro *et al.*，2015）。Brisson 研究组依不同密度处理后的孤雌豌豆蚜母代组织的转录组分析，表明蜕皮激素信号通路可能参与了豌豆蚜跨代翅多型的分子调控（Vellichirammal *et al.*，2016）。进一步的研究发现，给母代孤雌豌豆蚜注射蜕皮激素或其类似物可显著增加子代的有翅蚜比例；相反，使用

RNAi 技术降低蜕皮激素受体基因的表达水平则可降低子代的有翅蚜比例（Vellichirammal *et al.*，2017）。显然，蜕皮激素信号通路在豌豆蚜跨代翅型转换中发挥重要的调控功能。

1.3 保幼激素信号通路

早在 20 世纪就有学者提出保幼激素参与了昆虫翅多型的调控，随后多位学者从不同角度对这一假设进行了验证。其中，保幼激素信号通路在褐飞虱翅型转换中的功能较为明确。如使用保幼激素或其激动剂处理褐飞虱幼虫可显著增加短翅型个体的比例（Iwanaga and Tojo，1986；Ayoade *et al.*，1999；Bertuso *et al.*，2002），而使用保幼激素抑制剂（Precocene II）则可诱导产生更高比例的长翅型个体（Ayoade *et al.*，1996a，1996b）。RNAi 抑制保幼激素环氧化物水解酶（Juvenile hormone epoxide hydrolase）的表达可诱导较高比例短翅型雌性褐飞虱的产生（Zhao *et al.*，2017）。但保幼激素信号通路在蟋蟀和蚜虫翅多型中的调控功能则存在较大争议。例如，使用 JH-III 处理蟋蟀 *Gryllus rubens* 幼虫可显著降低其长翅型个体的比例（Zera and Tiebel，1988）。生物化学实验结果显示，长翅型蟋蟀幼虫血淋巴中保幼激素酯酶（JH esterase）的活性也显著高于短翅型个体（Zera and Tiebel，1989；Zera and Holtmier，1992；Fairbairn and Yadlowski，1997）。然而，长翅型和短翅型蟋蟀在翅发育关键时期的保幼激素滴度却没有显著差异（Zera *et al.*，1989；Zeng and Zhu，2015）。类似地，以 JH-I 处理甜菜蚜 *Aphis fabae* 一龄幼虫能改变其翅型的发育方向，使原本应该发育成长翅型的蚜虫发育成无翅型个体（Hardie，1980）。但 Schwartzberg 等（2008）的实验结果发现孤雌豌豆蚜母代血淋巴中 JH-III 的含量与其子代有翅蚜比例没有具有明显的相关性。因此，保幼激素信号通路在不同种类昆虫的翅多型调控中的功能可能具有较大差异。

1.4 Micro RNA（miRNA）介导的信号通路互作

miRNA 是多种生物学事件的重要调控分子（Bartel，2009）。最新的研究结果表明，miRNA 也参与了褐飞虱翅多型的分子调控过程（Ye *et al.*，2019）。在该研究中，Ye 等（2019）发现褐飞虱 miR-34 能够通过与 InR1 的 3′UTR 区结合来抑制 InR1 表达。注射激动剂 agomir-34 可诱导长翅型褐飞虱发育成短翅型褐飞虱，而同时注射抑制剂 antagomir-34 和 dsInR2（InR2 dsRNA）则可诱导产生较高比例的长翅型褐飞虱。此外，miR-34 的启动子区存在顺式作用元件 Broad Complex（Br-C），提示蜕皮激素也可能参与了褐飞虱翅多型的调控。而且，以蜕皮激素处理褐飞虱可降低 miR-34 的表达水平；以保幼激素处理则可增加 miR-34 的表达，并诱导更高比例的短翅型个体产生。RNAi 干扰胰岛素信号通路上的关键基因可改变保幼激素水平和 miR-34 的丰度。这些结果清楚表明，miRNA 介导了保幼激素、蜕皮激素和胰岛素三种信号通路之间的互作，从而形成了褐飞虱翅型转换的正向循环调控途径（Ye *et al.*，2019）。

2 其他参与昆虫翅多型调控的途径

2.1 Jun-N-terminal Kinase（JNK）信号通路

JNK 信号通路是生物界非常保守的信号转导途径，不仅参与多种生理过程（如细胞凋亡、细胞增殖、DNA 修复等），而且可响应多种环境胁迫（如温度胁迫、紫外线照射等）（Ip and Davis，1998；Davis，2000）。Lin 等（2016c）通过对褐飞虱幼虫注射 JNK dsRNA 干扰 JNK 基因表达或使用 JNK 抑制剂 CC-401 处理显著增加了短翅型雌性个体的比例，说明 JNK 信号通路参与了褐飞虱翅型转换的调控。但有关褐飞虱 JNK 下游的靶标基因尚未被鉴定出来，其作用机制仍不清楚。

2.2 生物胺信号通路

生物胺是由中枢神经系统合成的一类控制神经活动的小分子化合物，在多种生物过程中发挥功能，如心血管系统平衡、生物节律、情绪状态、内分泌、性别行为、体温调节和学习与记忆等（Roeder，1994；Monastirioti，1999；Blenau and Baumann，2001）。昆虫的生物胺信号通路是

表型可塑性的重要调控途径。如蝗虫具有种群密度依赖的散居型和群居型相互转变现象，其体内多巴胺和五羟色胺水平的变化是决定其两型转变的关键因素（Anstey *et al.*，2009；Ma *et al.*，2011；Alessi *et al.*，2014）。此外，生物胺信号通路还可被多种环境压力激活，帮助昆虫适应复杂的环境条件（Iba *et al.*，1995；Hirashima *et al.*，2000；Chen *et al.*，2008；Wada-Katsumata *et al.*，2011），提示生物胺信号通路有可能参与了昆虫翅多型的分子调控。Vellichirammal 等（2016）的 HPLC 分析结果也显示，拥挤处理的孤雌豌豆蚜（诱导产生高比例有翅蚜）母代组织中多巴胺、五羟色胺和章鱼胺水平显著低于单头处理（诱导产生低比例有翅蚜）。Wang 等（2016）发现 RNAi 干扰酪胺-β羟化酶（Tyramine β-hydroxylase，TβH）会降低产生有翅蚜子代的母代孤雌蚜（Winged-offspring producers，WOP）的数量，说明章鱼胺信号通路可能参与了豌豆蚜翅多型的调控；但 RNAi 抑制 TβH 表达不会影响 WOP 子代的有翅蚜比例。可见，生物胺信号通路在昆虫翅多型调控中的功能仍不明确。

2.3　病毒基因水平转移

不同生物间的基因水平转移（Lateral gene transfers）是生物界常见的自然现象（Dunning Hotopp *et al.*，2007；Aswad and Katzourakis，2012；Husnik and McCutcheon，2018）。最新的研究显示，从病毒到昆虫的基因水平转移也介导了昆虫翅多型的分子调控（Parker and Brisson，2019）。如 Parker 和 Brisson（2019）发现豌豆蚜基因组中存在两个含有“parvovirus nonstructural protein NS1 superfamily”保守结构域的基因 Apns-1 和 Apns-2，它们是在长期进化中由浓核病毒（Densovirus）的基因水平转移形成。且 Apns-1 和 Apns-2 在高诱导能力豌豆蚜品系和低诱导能力品系之间的表达水平存在显著差异，RNAi 抑制这两个基因的表达水平可显著降低孤雌豌豆蚜子代的有翅蚜比例。该结果不仅揭示了基因水平转移在昆虫翅多型中发挥了重要的调控功能，而且提示昆虫翅型转换的分子调控机制非常复杂。

3　结论与展望

翅多型（或翅二型）现象是昆虫在扩散和繁殖能力之间分配能量的重要策略，也是害虫暴发成灾的重要原因。昆虫翅多型现象可分为本代和跨代两种类型，其中褐飞虱和豌豆蚜就是这 2 种类型的代表。目前，以褐飞虱为研究对象的本代内翅型转换的分子调控机制研究进展相对较快，而对豌豆蚜跨代翅型转换的分子调控过程了解则较为有限。譬如，豌豆蚜中有关蜕皮激素信号通路和病毒基因水平转移调控孤雌跨代翅多型的具体分子机理仍不清楚；在褐飞虱翅多型中发挥核心作用的胰岛素信号通路如何调控豌豆蚜的跨代翅型转换也尚未被揭示。此外，也有报道指出 Notch 信号通路、Wingless/Wnt 信号通路、内共生菌 *Buchnera* 等也可能在蚜虫翅多型调控中发挥作用（Ishikawa *et al.*，2012；Zhang *et al.*，2015），但是至今仍然缺少有力的实验证据。总体来说，尽管近年来昆虫翅多型调控分子机理的研究进展较快，但已有证据也说明其内在机制非常复杂。因此，未来采取新的研究技术和新的研究角度不仅有利于深入阐明昆虫翅型转换调控的分子机制，而且对于以调控昆虫翅型为主要内容的害虫综合治理具有重要价值。

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