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COMMENTARY

Natural selection in orchid mantises' body coloration

Xiao-Jin Pei[1] **and Sheng Li**[1,*]

[1]Guangdong Provincial Key Laboratory of Insect Developmental Biology and Applied Technology, Guangzhou Key Laboratory of Insect Development Regulation and Application Research, Institute of Insect Science and Technology & School of Life Sciences, South China Normal University, Guangzhou 510631, China

*Correspondence: lisheng@scnu.edu.cn

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INTRODUCTION

Alfred Russel Wallace, renowned for co-discovering the theory of natural selection with Charles Darwin, made significant contributions to the biology of animal coloration. In his seminal work "*Darwinism*", Wallace systematically documented numerous natural phenomena to support his theory of natural selection. Among these examples, he highlighted striking color adaptation of the orchid mantis (*Hymenopus coronatus*), interpreting its floral resemblance as a case of aggressive mimicry—a strategy to deceive prey by imitating flowers. However, later observations revealed a more complex ontogenetic body color shift: newly hatched orchid mantis exhibits a black-and-red body color, but it dramatically switches to a flower-like white coloration after their first molt. This programmed body color transition and the resulting stage-specific ecological adaptations require re-examination. Moreover, advances in biotechnology and genomics have opened unprecedented opportunities to investigate the molecular mechanisms and evolutionary drivers underlying programmed body color transition in the orchid mantis. Our previous research has identified a novel pigment transporter,[1] establishing a crucial bridge between classical evolutionary theories and modern molecular biology (Figures 1A-C). In this commentary, we reconcile Wallace's hypotheses with contemporary genetic insights and synthesize the broader implications of these findings for understanding evolutionary adaptations in programmed body color transition.

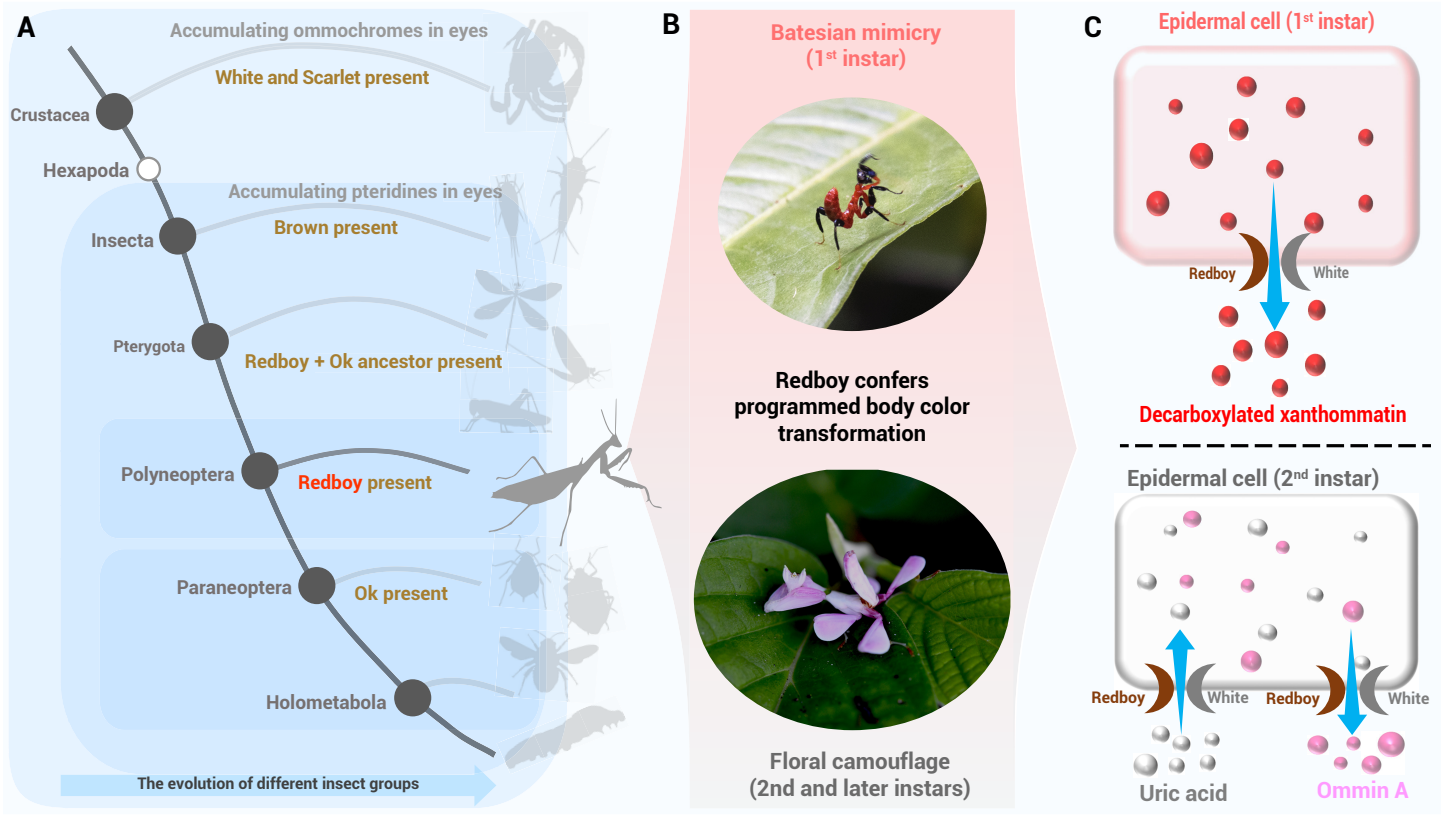

Figure 1. An overview of programmed body color transition in the orchid mantis (A) Origin and evolution of the newly recognized ABCG pigment transporter Redboy. (B) Programmed body color transition and ecological significance at different life stages. (C) The mechanism by which Redboy mediates programmed body color transition in the orchid mantis. The higher instar orchid mantis photograph was kindly provided by Dr. Ren-Bin Zhu from the Xishuangbanna Tropical Botanical Garden.

PROGRAMMED BODY COLOR TRANSITION AND ECOLOGICAL SIGNIFICANCE

Contrary to the popular perception that orchid mantises primarily mimic orchid blossoms to attract prey, their far more complex and dynamic color-adaptive strategy has not been widely recognized. Newly hatched orchid mantises exhibit a striking black-and-red coloration (Figure 1B); this conspicuous coloration serves as an exquisite example of Batesian mimicry, closely resembling local unpalatable stink bug nymphs. This adaptive strategy provides essential protection for vulnerable first-instar nymphs, which lack physical defenses against predators. After the first molt, a remarkable chromatic transition mediated by coordinated molecular and physiological mechanisms occurs, transforming the coloration from black-red to pink-white (Figure 1B). The orchid mantis imitates generalized light-colored flowers rather than the orchid specifically,[2] which serves a dual ecological function: as aggressive camouflage that deceives pollinating insects and as defensive camouflage against avian predators. Wallace originally cited the orchid mantis's remarkable floral coloration as compelling evidence for natural selection. Our study not only corroborates his fundamental premise that these color patterns evolved through adaptive processes, but also extends Wallace's framework by elucidating how developmental programming mediates sequential color-adaptive strategies. Specifically, we demonstrate that the ontogenetic body color transitions (from early-instar Batesian mimicry to late-instar floral camouflage) represent an exquisite evolutionary solution to

stage-specific ecological challenges, emerging from the dynamic interplay between predator-prey interactions and developmental constraints.

The orchid mantis's ontogenetic body color transition reveals a fundamental principle in animal coloration: adaptive body colorations are rarely static, but rather dynamic solutions that address shifting ecological pressures across an organism's life history. Programmed body color transitions constitute a ubiquitous yet understudied adaptive phenomenon across animals, manifesting in diverse forms throughout an organism's life history - from the metamorphic pigment shifts in arthropods to the ontogenetic and age-related changes in avian plumage and mammalian coat coloration. Research on body color change has primarily emphasized phenotypic plasticity and polymorphism, yet these developmental color transitions represent a fundamental—though underexplored—axis of phenotypic adaptation in evolutionary biology. Crucially, these transformations often serve concurrent adaptive functions—including predator avoidance, prey attraction, thermoregulation, and social signaling. Future research exploring how environmental variability, predator-prey coevolution, and developmental constraints interact to shape these programmed body color transitions may represent a key direction in understanding the adaptability of body coloration. Additionally, it holds the potential to bridge diverse fields ranging from ecology to evolutionary developmental biology.

THE MOLECULAR EVOLUTION BEHIND PROGRAMMED BODY COLOR TRANSITION

In an intriguing scientific coincidence, Professor Wei Fuwen's group and our team independently pursued whole-genome sequencing of *H. coronatus* without prior knowledge of each other's investigations. While their work linked ABCG gene family expansion to camouflage in late-instar nymphs,[3] we discovered additional genetic components governing the remarkable programmed body color transition in the orchid mantis.[1] There is a novel ABCG pigment transporter subfamily that specifically presents in Polyneoptera, which we named Redboy drawing inspiration from the crimson-colored "Red Boy" (Honghai'er) of Chinese mythology Journey to the West (Xiyouji) - a fitting analogy given the gene's role in maintaining red pigmentation. This discovery expands our understanding beyond the classical quartet of insect ABCG pigment transporters (White, Scarlet, Brown, Ok). Evolutionary analysis shows White and Scarlet originated in crustaceans, while Brown emerged in the earliest insect groups (e.g., the rock bristletail and silverfish). Redboy and Ok share a palaeopteran ancestor (e.g., mayflies and dragonflies) but diverged: Redboy remained in Polyneoptera (cockroaches, mantids, etc.), while Ok persisted in Paraneoptera (e.g., aphids and stink bugs) and few Holometabola (e.g., bees and moths) groups (Figure 1A). Notably, while White, Scarlet, and Brown are ancient and highly conserved (likely for screening pigment formation in the eyes), the transporters Ok and Redboy appear to have acquired novel functions in body coloration modification during later evolutionary stages. Functional studies confirmed Redboy's crucial role: knockdown of ecdysone-induced *Redboy* expression blocked decarboxylated xanthommatin excretion and uric acid deposition, locking second-instar nymphs in red coloration (Figure 1C). Together, these discoveries provide unprecedented insights into how molecular mechanisms and evolutionary forces interact to create one of the most visually stunning examples of natural selection. Redboy provides a link between Wallace's body coloration theory and contemporary genetic insights.

The programmed body color transition represents a crucial adaptive strategy in organisms, with the evolutionary mechanisms identified in orchid mantises revealing complex interactions between gene family evolution and regulatory network innovation. Our study demonstrates that the subfunctionalization of ABCG transporters, exemplified by the Redboy gene, illustrates how genetic redundancy from gene duplication provides the molecular substrate for phenotypic innovation, while conserved endocrine regulation ensures precise developmental timing of programmed body color transitions: juvenile hormone determines the expression patterns of melanin synthesis genes and ecdysone actives *Redboy* expression around the molting. This conserved regulatory layer, coupled with variable effector modules, appears to represent a fundamental paradigm in programmed body color transition.[1,4] However, many critical questions remain unresolved. For instance, while our work has established this regulatory framework and confirmed that duplication and functional innovation of pigment transporters like Redboy provide evolutionary raw material for programmed body color transitions, the key question of how these pigmentary modules become developmentally integrated into hormonal regulatory networks to achieve such transitions remains largely unanswered. Specifically, the molecular mechanisms—such as cis-regulatory evolution—underlying the hormonal recruitment of specific pigment pathways require further elucidation.

FUTURE PERSPECTIVES

The discovery of Redboy as a key regulator of body color transition in *H. coronatus* opens several promising avenues for future research. First, Redboy has been demonstrated to transport at least three distinct pigments.[1] Resolving the three-dimensional structure of Redboy through cryo-EM or X-ray crystallography could reveal how it binds and transports multiple substrates, providing insights into how this transporter evolved multifunctionality. Second, functional assays in non-mimetic mantis species could test the evolutionary conservation of Redboy's role—does it retain similar pigment transport functions in lineages without dramatic color shifts, or has its role been co-opted specifically for dynamic camouflage? Finally, the petal-like legs of orchid mantises have been demonstrated to serve gliding functions.[5] However, their role in camouflage and the evolutionary origins of this unique morphological adaptation require further investigation to fully understand the mimicry-camouflage system in these organisms.

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AUTHOR CONTRIBUTIONS

Supervision, S.L.; funding acquisition, X.J.P, and S.L., conceptualization, X.J.P, and S.L.; formal analysis, X.J.P.; writing – original draft, X.J.P.; writing – review & editing, X.J.P, and S.L. All authors contributed to the manuscript and approved the final version.

DECLARATION OF INTERESTS

The authors declare no competing interests.