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Developmental Biology and Morphological Evolution in Coleoptera

Yunping Huang, Jia Xuan ✉
Institute of Life Science, Jiyang College of Zhejiang A&F University, Zhuji, 311800, Zhejiang, China
✉ Corresponding email: jia.xuan@jicat.org

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Abstract This study explores the complex relationship between developmental biology and morphological evolution in Coleoptera (beetles). By investigating developmental pathways, allometric growth, modularity, and the role of homeotic genes, it reveals how Coleoptera drive morphological diversification through developmental processes, thereby adapting to different ecological environments. The research aims to enhance the understanding of the origin of existing morphological diversity and provide important insights into evolutionary mechanisms, thus laying a solid theoretical foundation for further exploration of insect morphological evolution.

Keywords Coleoptera; Developmental biology; Morphological evolution; Allometry

1 Introduction

Coleoptera, commonly known as beetles, represent one of the most diverse and ecologically significant orders of insects, with over 360 000 described species across four suborders: Adephaga, Archostemata, Myxophaga, and Polyphaga. This vast diversity is reflected not only in their morphology and behavior but also in their adaptation to a wide range of ecological niches, from aquatic environments to terrestrial habitats (Sheffield et al., 2008). The success of Coleoptera is largely attributed to their evolutionary adaptations, including the development of hardened forewings (elytra) and diverse feeding strategies that range from herbivory to predation (Ferns and Jervis, 2016).

Understanding the developmental biology of Coleoptera is crucial for several reasons. Firstly, it provides insights into the mechanisms that drive their extraordinary morphological diversity, which in turn can reveal broader patterns in evolutionary biology. Developmental biology, particularly through the lens of evolutionary developmental biology (evo-devo), has shown how changes in developmental pathways can lead to significant morphological innovations, such as the diverse wing structures and feeding apparatus seen in beetles (Heffer and Pick, 2013). Additionally, studying the developmental stages of beetles, from larvae to adults, helps in understanding the ecological roles they play at different life stages, which is vital for conservation and pest management strategies (Polilov and Beutel, 2010).

This study explores the developmental biology and morphological evolution of Coleoptera, including comparative analyses of various species within the order to identify key developmental genes and pathways that drive their morphological diversity. By utilizing morphological and molecular data, the research examines the phylogenetic relationships among different beetle families to understand the evolutionary history of these insects, with the aim of gaining a comprehensive understanding of how developmental processes shape the evolution of Coleoptera.

2 Developmental Biology in Coleoptera

2.1 Key stages of coleopteran development

Coleopteran development is a complex process involving several distinct stages, each crucial for the survival and adaptation of the species. The life cycle of beetles typically includes the egg, larval, pupal, and adult stages. Each stage is marked by significant morphological and physiological transformations. For instance, in the hooded beetle *Sericoderus lateralis*, there are three larval stages, each with unique morphological traits that play a critical role in the insect's adaptation to its environment.

These larval stages are characterized by significant changes in body size, organ development, and behavior, which are essential for the beetle's ability to exploit different ecological niches. The transition from one stage to another is regulated by both genetic and environmental factors, ensuring that the insect develops in a manner best suited to its surroundings. In particular, environmental conditions such as temperature and humidity can significantly influence the duration of each developmental stage, thereby affecting the overall life cycle of the beetle. Understanding these stages is crucial for developing effective pest control strategies and for conservation efforts aimed at protecting endangered beetle species (Polilov and Beutel, 2010).

2.2 Genetic and molecular mechanisms

The genetic and molecular mechanisms underlying coleopteran development are complex and involve a multitude of genes that regulate key developmental processes. Studies have shown that mitochondrial genomes play a critical role in the development of various beetle species. For instance, specific genetic sequences in the mitochondrial DNA are conserved across different beetle species, indicating their essential role in maintaining the integrity of developmental processes (Mckenna et al., 2019; Pandit et al., 2019).

Moreover, the expression of certain genes is crucial for the development of morphological traits such as wings and antennae, which are vital for the survival and reproductive success of beetles. Research has also highlighted the phenomenon of phenotypic plasticity, where the same genotype can result in different phenotypes depending on environmental conditions. This adaptability is particularly evident in traits such as wing morphology, where environmental factors such as temperature and food availability can influence gene expression, leading to different developmental outcomes. Understanding these genetic and molecular mechanisms is not only important for comprehending the evolutionary success of beetles but also for identifying potential targets for genetic manipulation in pest control strategies (Wang et al., 2015; Benton et al., 2016).

2.3 Environmental influences on development

Environmental factors play a critical role in shaping the development of Coleoptera, influencing everything from the timing of developmental stages to the expression of specific traits. Temperature is one of the most significant environmental factors affecting coleopteran development. For instance, in the beetle *Zygogramma bicolorata*, different temperature regimes can lead to the emergence of fast or slow developers within a population, demonstrating a clear case of developmental polymorphism. This polymorphism is not only a result of genetic factors but is also heavily influenced by environmental conditions, with higher temperatures generally favoring faster development.

Additionally, environmental factors such as humidity, light, and diet also significantly impact the development of beetles. For example, variations in diet and moisture levels can influence the duration of larval development, with optimal conditions leading to faster development and higher survival rates. These environmental influences are crucial for the adaptability of beetles to different habitats and play a significant role in their evolutionary success. Understanding these factors is essential for developing effective strategies for managing beetle populations, particularly in the context of climate change and habitat destruction (Xu et al., 2020; Afaq et al., 2021).

3 Morphological Evolution in Coleoptera

3.1 Evolutionary adaptations in beetle morphology

Beetles, or Coleoptera, are renowned for their extraordinary morphological diversity, which has enabled them to adapt to a vast array of ecological niches. One of the most remarkable examples of morphological adaptation in beetles is the evolution of their forewings, known as elytra. These hardened structures serve as protective shields for the delicate hindwings and abdomen, allowing beetles to survive in harsh environments. The evolution of elytra represents a significant morphological innovation that has contributed to the evolutionary success of Coleoptera. Research has shown that the molecular mechanisms underlying this adaptation involve the co-option and modification of existing genetic pathways. For instance, a comparative study of wing transcriptomes in beetles revealed that several genes are uniquely expressed in the elytra, including those involved in pigmentation, hardening, and sensory development (Linz et al., 2023).

Additionally, stag beetles exhibit significant morphological adaptations in their mandibles, which are enlarged and used for combat during mating rituals. The development of these structures is regulated by a suite of appendage-patterning genes, with specific genes such as dac playing a crucial role in the size and shape of male mandibles (Gotoh et al., 2017). These examples highlight the intricate genetic and developmental processes that drive morphological evolution in beetles, enabling them to adapt to a wide range of environments and ecological challenges.

3.2 Comparative morphology across coleopteran families

The vast diversity of beetles is reflected in the wide range of morphological traits observed across different Coleopteran families. Comparative studies have revealed that these morphological differences are often linked to adaptations to specific ecological niches. For example, the evolution of aquatic adaptations in fireflies (Lampyridae) has led to significant changes in larval morphology. Aquatic firefly larvae exhibit morphological features such as modified tracheal systems and cuticles adapted to an underwater environment. Transcriptomic analysis has shown that these morphological adaptations are associated with the evolution of genes involved in metabolic efficiency and hypoxia response, which are essential for survival in freshwater habitats (Zhang et al., 2020).

Similarly, comparative studies of stag beetles (Lucanidae) have demonstrated that the evolution of their characteristic large mandibles is closely tied to developmental plasticity, which allows these beetles to develop different morphologies in response to environmental conditions. This plasticity not only contributes to the intraspecific variation seen within populations but also plays a critical role in interspecific diversification (Kawano, 2020). By studying the comparative morphology of beetles across different families, researchers can gain insights into the evolutionary processes that have shaped the incredible diversity of this order, revealing how different lineages have adapted to their unique ecological contexts.

3.3 Role of developmental genes in morphological diversification

The diversification of beetle morphology is deeply rooted in the complex interplay of developmental genes that regulate the growth and differentiation of various body parts. Developmental genes, particularly those involved in the formation of appendages and other key structures, have been shown to play a pivotal role in the evolution of beetle morphology. One of the most well-studied examples is the role of Hox genes, which are critical for determining the identity of body segments and their associated appendages. In beetles, modifications in the expression of Hox genes have been linked to the evolution of novel morphological traits, such as the elongation of mandibles or the development of specialized hindwings (Ravisankar et al., 2016).

Additionally, the evolution of the elytra in beetles has been associated with changes in the expression of wing-patterning genes, which have been co-opted and modified to produce this unique structure. RNA interference (RNAi) studies in species such as *Tribolium castaneum* have identified several genes, including Tc-cactus and members of the odd-skipped family, that are essential for the proper development of elytra and other wing structures (Linz et al., 2015). These findings underscore the importance of developmental genes in driving the morphological innovations that have enabled beetles to diversify and adapt to a wide range of ecological niches.

4 Developmental Pathways and Their Role in Evolution

4.1 Heterochrony and its impact on morphology

Heterochrony, the change in the timing of developmental events, plays a significant role in the morphological evolution of Coleoptera. By altering the onset, rate, or duration of developmental processes, heterochrony can lead to significant morphological changes, often resulting in the evolution of novel traits. For instance, studies on the evolutionary development of pigmentation pathways in Lepidoptera suggest that heterochronic shifts in gene expression timing contribute to the diversification of wing patterns and body coloration. This is seen in the sexually dimorphic development of melanin pathway genes, where females and males exhibit different peak activities at various developmental stages (Kuwalekar et al., 2020).

Similarly, heterochrony is implicated in the evolution of predatory behavior in certain species, where shifts in gene expression timing have led to novel phenotypes that provide adaptive advantages in specific ecological contexts (Ledón-Rettig, 2021). In beetles, such heterochronic shifts can result in the prolongation or truncation of developmental stages, leading to diverse adult morphologies that are key to their adaptive success in varied environments. Thus, heterochrony is a crucial mechanism driving the morphological diversity observed in Coleoptera and other insect orders (Benton et al., 2016; Yuan et al., 2016; Linz et al., 2023).

4.2 Evolutionary role of homeotic genes

Homeotic genes, particularly the Hox genes, are central to the regulation of body plan development in insects and play a pivotal role in the morphological diversification of Coleoptera. These genes determine the identity of body segments and their associated structures, such as limbs and wings, by regulating the expression of downstream genes involved in segment-specific development. In Coleoptera, the evolution of novel structures, such as the elytra (hardened forewings), has been closely linked to modifications in Hox gene expression. For example, the gene Ultrabithorax (Ubx) has been shown to play a critical role in determining the morphology of the third thoracic segment in beetles, including the differentiation of hindwings and the development of elytra (Fu et al., 2020).

Studies using CRISPR/Cas9-mediated mutagenesis in other insects, such as the Asian corn borer, have further demonstrated the impact of disrupting Hox genes like Abd-A and Ubx, leading to severe morphological defects and homeotic transformations (Bi et al., 2022). These findings highlight the evolutionary significance of homeotic genes in shaping the diverse morphologies observed in beetles, making them a key focus in studies of insect evolutionary developmental biology.

4.3 Modularity and morphological innovation in beetles

Modularity refers to the concept that certain traits or structures within an organism develop relatively independently from others, allowing for more flexible evolutionary changes. In beetles, modularity has facilitated the evolution of highly specialized structures, such as the mandibles of stag beetles, which are used in combat and mating rituals. This modular development allows specific traits to evolve rapidly in response to selective pressures without necessarily affecting other parts of the body. For example, the development of beetle mandibles involves the modular expression of appendage-patterning genes, which can be co-opted and modified to produce the exaggerated mandibles seen in some species (Figure 1) (Gotoh et al., 2017).

The concept of modularity is also crucial in understanding how complex traits, such as the elytra, can evolve through the integration of multiple developmental pathways, leading to the innovation of entirely new structures that are critical for survival. The role of modularity in morphological innovation underscores the flexibility of developmental processes in Coleoptera, enabling these insects to adapt to a wide range of ecological niches and contributing to their remarkable evolutionary success.

5 Case Study

5.1 Overview of selected beetle species

The Colorado potato beetle (Leptinotarsa decemlineata), one of the most notorious agricultural pests, has garnered significant attention due to its incredible adaptability and resistance to insecticides. Originally native to North America, this beetle has expanded its range globally, posing a severe threat to potato crops. Its evolutionary success can be attributed to its rapid adaptive responses, driven by genetic diversity and phenotypic plasticity. Recent genomic studies have provided insights into the beetle's ability to quickly evolve resistance to various insecticides, highlighting the role of standing genetic variation in these adaptive processes. The beetle's ability to survive in different climates and on various host plants underscores its status as a "super-pest," making it a prime model for studying evolutionary biology and pest management strategies (Schoville et al., 2017; Cohen et al., 2022).

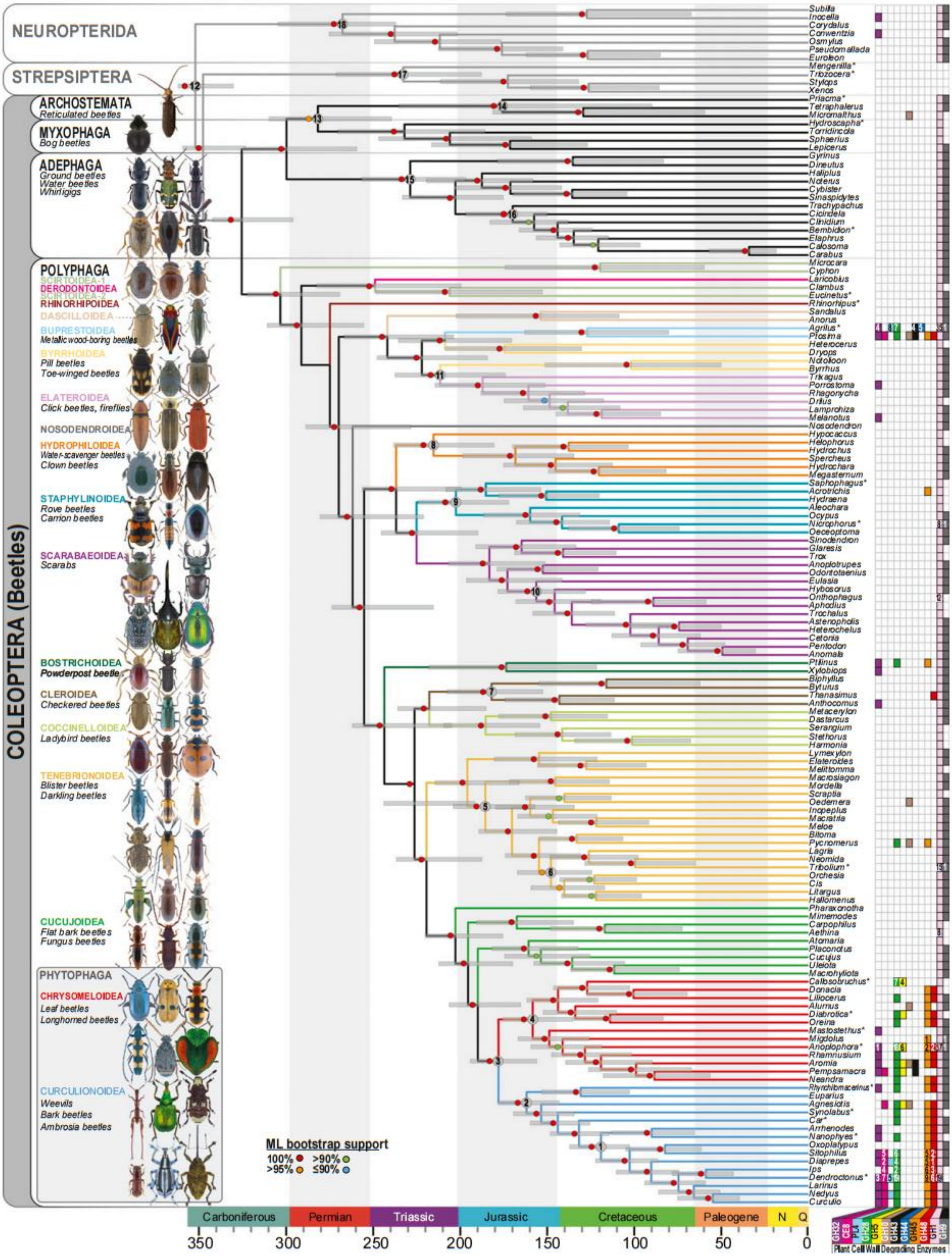

Figure 1 Reconstructed phylogenetic tree of Coleoptera (beetles), including genomic data from 146 beetle species and their close relatives (Adopted from Mckenna et al., 2019)

Image caption: Different superfamilies are color-coded, and the distribution of certain gene families (e.g., GH1, GH9) is shown. These gene families are associated with plant cell wall-degrading enzymes that help beetles break down lignocellulose in plants. The figure also indicates a link between the emergence of these enzyme genes and beetle diversification, particularly in the evolution of herbivorous beetles (Adopted from Mckenna et al., 2019)

Moreover, phylogenomic studies have placed the Colorado potato beetle within a broader evolutionary context, revealing how its diversification aligns with other beetle species. These studies suggest that the beetle's success is partly due to its ability to exploit a wide range of ecological niches, a trait that is common among many beetles. The integration of genetic and environmental data has allowed researchers to better understand the evolutionary pathways that have led to the beetle's current status as a dominant agricultural pest (Figure 1) (Mckenna et al., 2019; Weng et al., 2021).

5.2 Detailed analysis of developmental pathways

The developmental pathways of the Colorado potato beetle are a critical aspect of its adaptability and resilience. These pathways are underpinned by a complex genetic architecture that allows the beetle to thrive under various environmental conditions. The beetle's genome contains a large number of detoxification genes, including cytochrome P450 enzymes, esterases, and glutathione S-transferases, which are crucial for metabolizing and resisting insecticides. These genes are not only numerous but also highly inducible, meaning they can be upregulated in response to chemical exposure, providing a rapid defense mechanism against insecticides (Schoville et al., 2017; Cohen et al., 2022).

Additionally, the beetle's developmental plasticity is supported by its extensive genetic diversity, particularly in genes related to digestion and metabolism. This diversity enables the beetle to adapt to a variety of host plants, a trait that has facilitated its spread across different geographic regions. Furthermore, recent studies have shown that the beetle's developmental pathways are closely linked to its ability to undergo rapid evolutionary changes, with certain pathways being more prone to selection pressures, leading to the evolution of resistant populations (Weng et al., 2021; Linz et al., 2023). The beetle's ability to exploit standing genetic variation and its capacity for rapid evolutionary change make it an excellent model for studying the interplay between genetics, development, and adaptation in insects.

5.3 Morphological adaptations and evolutionary significance

The Colorado potato beetle exhibits several morphological adaptations that have played a crucial role in its evolutionary success. One of the most prominent adaptations is the development of its elytra, the hardened forewings that protect the delicate hindwings and body. This adaptation not only provides physical protection against predators and environmental hazards but also plays a significant role in the beetle's dispersal capabilities, allowing it to colonize new areas rapidly. The evolutionary significance of these adaptations is reflected in the beetle's ability to thrive in a wide range of environments, from temperate regions to areas with more variable climates (Schoville et al., 2017; Asgari et al., 2020).

Moreover, the beetle's robust exoskeleton and efficient digestive system, which includes specialized enzymes for processing a variety of plant materials, have enabled it to exploit diverse ecological niches. This flexibility in diet and habitat choice has been a key factor in the beetle's global spread and its ability to persist in agricultural settings despite intensive pest control efforts. Phylogenetic analyses have further supported the idea that these morphological traits have evolved in response to both natural and anthropogenic selection pressures, highlighting the beetle's capacity for rapid adaptation and evolutionary innovation (Mckenna et al., 2019; Cohen et al., 2022). The Colorado potato beetle thus serves as a prime example of how morphological and genetic adaptations can drive the success of a species in a changing world.

6 Implications of Developmental Biology for Understanding Coleopteran Evolution

6.1 Insights into evolutionary processes

The study of developmental biology in Coleoptera provides crucial insights into the evolutionary processes that have shaped the immense diversity within this order. Developmental pathways, particularly those involving key regulatory genes, play a significant role in the evolution of novel traits. For instance, research on the evolution of wing structures in beetles has revealed how modifications in gene expression during development can lead to the emergence of unique morphological features, such as the elytra, which have been instrumental in the ecological success of beetles (Timmermans et al., 2015; Short, 2018).

These developmental processes are not only important for understanding how current morphological diversity arose but also provide insights into the broader mechanisms of evolutionary change, including the role of genetic variation and the impact of environmental pressures on development (Timmermans et al., 2015; Linz et al., 2023). Additionally, studies on the evolution of neuropeptide signaling in beetles highlight how changes in developmental processes can influence behavior and physiology, further driving evolutionary diversification (Pandit et al., 2019).

6.2 Developmental constraints and evolutionary outcomes

Developmental constraints are limitations imposed by an organism's developmental biology that can restrict the range of potential evolutionary outcomes. In Coleoptera, these constraints are evident in the conservation of certain developmental pathways, despite the vast morphological diversity within the order. For example, studies on mitochondrial genomes and phylogenetic relationships among beetles have shown that despite the evolutionary plasticity in some traits, others are highly conserved due to developmental constraints.

These constraints can lead to evolutionary trade-offs, where certain adaptations are favored over others, shaping the evolutionary trajectory of a species. Understanding these constraints is essential for predicting evolutionary outcomes, as they can limit the directions in which a lineage can evolve. This is particularly relevant in the context of beetle phylogeny, where the balance between conservation and innovation has resulted in a wide array of forms while maintaining core developmental mechanisms (Tammaru et al., 2015; Yuan et al., 2016).

6.3 Future directions for research

Future research in the developmental biology and evolution of Coleoptera should focus on expanding our understanding of the genetic and molecular bases of key developmental processes. This includes the continued exploration of the roles of Hox genes, neuropeptide signaling pathways, and other regulatory networks in driving morphological diversification. Moreover, there is a need to integrate high-throughput genomic technologies, such as transcriptomics and epigenomics, to uncover how gene expression patterns during development influence evolutionary outcomes.

Another promising area of research is the study of developmental plasticity and how environmental factors interact with genetic mechanisms to produce phenotypic variation. Understanding these interactions will be crucial for predicting how beetle species might respond to changing environments, such as those caused by climate change or habitat destruction. Finally, comparative studies across different beetle lineages and other insect orders will help to identify common developmental themes and unique adaptations, providing a more comprehensive picture of insect evolution (Laland et al., 2015; McKenna et al., 2019).

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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