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Editorial overview: Development and regulation: The diverse traits that have facilitated the successful radiation of insects

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Insects are the most abundant and diverse group of organisms on earth. Insects have conquered almost every corner of the world (except for the marine environment) through a diverse array of adaptive strategies at morphological, physiological, and behavioral levels. In addition, competition among insects (including inter-, intra-, and sexual competition) have further promoted the evolution of diverse traits. Examples of diverse traits can be found in their appendages (antennae, mouthparts, legs, flight appendages and more), which have been evolutionarily modified quite extensively both within, and across species in adaptation to various selective pressures. The diverse colors and textures of insect cuticles are also the result of adaptations used for mimicry, defense, sexual competition, and physiological processes. In addition, the evolution of novel structures, such as beetle horns, has helped insects explore new adaptive strategies. The evolution of eusocialism is another fascinating example of the diverse traits found in insects, which has been achieved by the combination of morphological, physiological, and behavioral evolution.

Although the diverse traits found in insects have fascinated scientists for centuries, until recently, the molecular and developmental underpinnings of these traits have been inaccessible in most species due to the lack of genetic and genomic tools applicable to many insects. However, advances in molecular biology techniques have begun to liberate scientists from this limitation. Twenty years since the first report of RNA interference (RNAi) in an animal species, RNAi-based gene knockdown techniques have now become established approaches in many insects. More recently, the application of CRISPR/Cas9 genome editing technologies in insects has caused quite a stir in the insect community, and many scientists are currently rushing to apply this technique to their insects. Furthermore, as the cost of next generation sequencing continues to drop, comprehensive transcriptomic and genomic analyses can now be performed in various insects, making gene network analyses possible even in non-model species. Leveraging these technical advances, some researchers have begun to explore diverse traits in various insect species.

There is no argument that the fruit fly (*Drosophila melanogaster*) is the most advanced insect model system, and studies in *D. melanogaster* have established our understanding of insect biology at all levels, including genetic,

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cellular, developmental, behavioral, and physiological processes. Application of some genetic and genomic tools in other insects has made these species genetically amenable model systems, however, that does not mean that there is not still much to be learned from *Drosophila* studies. On the contrary, studies in *D. melanogaster* continue to be at the forefront of genetic and developmental studies, spearheading new fields in insect biology.

In this issue, we highlight both *Drosophila* studies that explore detailed developmental mechanisms and studies in non-traditional model insects that investigate diverse traits. *Drosophila* research allows for the elucidation of the intricate genetic and developmental mechanisms responsible for the production of complex morphological traits, while studies outside of *Drosophila* will take us deeper into the molecular mechanisms underlying the evolution and development of many intriguing traits found in various species.

For the articles that feature *Drosophila* studies, first, Tajiri highlights recent reports investigating how pre-existing cuticles and the material property of the newly formed cuticles influence the body shape during ecdysis and metamorphosis. The cuticle of insects plays a pivotal role in maintaining the shape and integrity of insect bodies. Recent studies in *D. melanogaster* have revealed a surprising, novel function of the insect cuticle, where the cuticle is involved in 'determining' the shape of insects (instead of the traditional view where the cuticle shape is the outcome of prior patterning events). This cuticle-driven regulation of morphology provides another step that can be modified during morphological evolution, and thus will inspire investigation of the importance of cuticles in the evolution of diverse morphological traits in other insects.

Next, Kojima reviews our current understanding of the leg formation mechanism, with a particular focus on the tarsus (the most distal leg component). Ventral appendages of insects (including legs) display a dazzling array of diversity in their shape and size. The molecular and development basis for the formation of ventral appendages has been studied quite extensively in *D. melanogaster*, establishing the 'leg gene regulatory network'. The tarsal segments are quite diverged among insects as they have adapted to their specific habitats and life styles. Therefore, the detailed genetic interactions learned from *Drosophila* studies summarized in this article will be used as a paradigm to explore the molecular basis underlying the diversity of tarsal structures.

Two articles in this issue highlight studies that use *D. melanogaster* as a starting point to explore morphological diversity. Rebeiz and Williams provide a comprehensive overview of research that investigates the changes in *cis*-regulatory mechanisms that have facilitated the evolution of pigmentation patterns among *Drosophila* species. With the available genomic resources, the *Drosophila* species group offers powerful opportunities to explore detailed molecular mechanisms underlying a diversity of traits. Pigmentation patterns vary significantly among the *Drosophila* species, and also frequently between males and females. Therefore, investigation into the evolution of pigmentation patterns allows for the pinpointing of the changes in their genomes that are responsible for the phenotypic changes resulting from natural and sexual selection.

Insect wings present one of the chief examples of morphological diversity. The evolutionary modifications on the wing occur not only between species, but also between the two pairs of wings in the same species (*i.e.*, forewing