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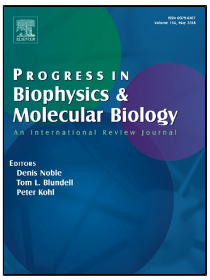

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Wing Morphogenesis in Lepidoptera

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Abstract

The wings of Lepidoptera develop from imaginal disks tat are made up of a simple two-layered epithelium whose structure is always congruent with the final adult wing. It is therefore possible to map every point on the imaginal disk to a location on the adult wing throughout the period of growth and morphogenesis. The wings of different species of Lepidoptera differ greatly in both size and shape, yet it is possible to fate-map homologous locations on the developing wing disks and explicitly monitor the growth, size, and shape, of the wing, or any of its regions, throughout the entire ontogeny of the wing. The wing achieves its final form through spatially patterned cell divisions, oriented cell divisions, physical constraints on directional growth by an actin network between the wing veins, and by patterned cell death. Each of these factors contributes differently to morphogenesis and to the development of species-specific differences in wing shape. The final shape of the wing is sculpted out of the much larger imaginal disk by a pattern for programmed cell death that removes all cells distal to the bordering lacuna, and is responsible for the detailed outline of the wing.

Introduction

Size and shape are the most characteristic attributes of species. Yet, the developmental mechanisms that regulate the final sizes and shapes of body and appendages are for the most part unknown. Although the genetic and molecular mechanisms that control growth are becoming well-understood, we still lack much fundamental knowledge about how these play out at the organ and organismal level to control the final size and shape of tissues and organs. The mechanisms that control body size and the proportional sizes and shapes of body parts continue to be among the great puzzles in Biology, as are the ways in which these mechanisms change during evolution to generate the diversity of sizes and shapes we see among species.

The wings of Lepidoptera offer a particularly attractive and tractable system in which to investigate the morphogenesis and evolution of an epithelial structure. Species of Lepidoptera differ greatly in the size and shape of their wings (Figure 1), but all have the same venation pattern, consisting of a standard set of homologous veins that correspond to the Comstock-Needham groundplan [1-3].

The wing veins form a reliable coordinate system that allows one to identify homologous points on the wing surface across species. The venation system is established very early in wing development, so that it is also possible to map homologous locations on the wing throughout development. This makes the wing a particularly suitable system in which to study the interplay between development and evolution in morphogenesis because it is possible to ascribe