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Animal pigment pattern: An integrative model system for studying the development, evolution, and regeneration of form

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Pigment patterns have long fascinated biologists of all sorts. Evolutionary biologists and behavioral ecologists have focused on pigment pattern as one of the most obvious traits of many animals, and one that has important functions ranging from camouflage to mate choice. Likewise, developmental biologists and geneticists have used pigment pattern as a tractable system for uncovering genes and cell behaviors underlying form within a species and differences in form among species.

This issue highlights some of the many ways in which pigment pattern can be studied, integrating approaches from both basic, organismal biology to more applied, biomedical research. Together, the reviews highlight the extraordinary versatility of pigment pattern as a system with great potential for studies across levels of biological organization.

In the first review, Wittkopp & Beldade discuss breakthroughs in understanding the pigment patterns of insects. While industrial melanism is one of the more famous examples of evolution in natural populations, pigment pattern development and evolution now have been dissected across a range of species. These patterns have been especially useful because of their tremendous diversity, because they form *in situ*, without the added complication of cell migration, and because it has been possible to exploit the power of *Drosophila* genetics in studying closely related species. Although a frequently cited reason for studying pigment pattern is its independence from other traits, in the sense that pigment mutants are often viable in the laboratory, Wittkopp & Beldade document extensive evidence for pleiotropic effects of “pigment” genes on behavior, immunity, and other traits. Such covariance is important because it implies that pigment patterns may evolve through direct selection on the patterns themselves, and also as correlated responses to selection on other traits.

The second review, by Mills & Patterson, introduces vertebrate pigment patterns. Whereas the vast majority of studies have focused on just one type of pigment (melanin) produced by one type of cell (the melanocyte of mammals), these authors remind us that many types of pigments and pigment cells exist in nature and, together, they generate an extraordinary array of pattern variation. This review takes a “top down” approach by asking what we

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know about particular pattern types and colors, highlighting both recent progress and how much remains to be discovered.

Anyone who has visited a zoo or aquarium, or has observed animals in nature, cannot help being struck by the diversity of animal color patterns. As intriguing as this variation has been to empirical biologists, it has been equally inspirational for theoretical biologists. Mathematical approaches to studying pigment pattern development have coexisted alongside genetic and cellular approaches for many years, with remarkably little interaction between the two. The third review, by Kondo & Shirota, seeks to rectify this situation. These authors show how a classic, theoretical description of pattern formation—as a reaction–diffusion system—can explain many types of patterns. Perhaps more importantly, they also show how such a system can be probed using modern, empirical approaches of genetics and cell biology. One can envision how a combination of mathematical theory and experiments at the bench may ultimately provide explanations for both general features of pigment pattern development and evolution, as well as the particular characteristics of any given pattern.

The next review, by Kelsh et al. documents recent progress in elucidating the mechanisms of pigment cell morphogenesis. Pigment cells of vertebrates are derived from the neural crest, and this paper discusses some of the many factors that contribute to the dispersal of pigment cell precursors from their origin above the neural tube, as well as their subsequent migration, proliferation, and survival. As Kelsh et al. point out, pigment cell morphogenesis has been studied in several model organisms. For the non-specialist (and even sometimes the specialist), it can be difficult to discern which features of morphogenesis are common among species and which are likely to be unique. This paper helps matters by explicitly comparing events and mechanisms across species ranging from zebrafish to mouse, and across stages ranging from embryo to adult. In so doing, Kelsh et al. provide a valuable framework in which to recognize areas we now understand well, and those deserving of more attention in the future.

The most-studied pigment cell by far is the melanocyte of endotherms, or its presumed homologue, the melanophore of ectotherms. Cooper & Raible discuss what is known about the specification and differentiation of these melanin-containing cells. One of the important themes to emerge from this body of work is that genetic pathways often have reiterated roles during pigment cell development, being required at multiple steps of specification or differentiation. Cooper & Raible discuss the developmental and evolutionary implications of such reiterative mechanisms, and also identify several outstanding questions that remain to be addressed in melanocyte and melanophore biology.

The last two reviews, by Robinson & Fisher and O’Reilly-Pol & Johnson address a particularly exciting, still-emerging subfield focusing on melanocyte (or melanophore) stem cells. Robinson & Fisher discuss what is known about the specification and niche of such stem cells in mammals, including critical signaling pathways and interactions with keratinocytes. They further emphasize the implications of melanocyte stem cell biology for the relatively benign (and eminently “treatable”) graying of hair as we age, as well as the malignant (and much less treatable) transformation of normal cells to an oncogenic phenotype in melanoma. By contrast, O’Reilly-Pol & Johnson present what has been learned

about such stem cells through manipulative experiments in zebrafish, particularly in the context of pigment pattern regeneration. This system promises to be valuable for allowing the identification of novel genes and pathways having both basic and biomedical significance.

Together, this collection of reviews highlights the breadth and depth of research into pigment pattern development. The papers also highlight many areas for future research. As such they should be an excellent, and inspirational, guide for graduate students, postdocs, and established investigators.