

## A Thing of Beauty

The mesmerizing patterns and brilliant colors found throughout the animal kingdom have long captivated scientists. Research in species as diverse as birds, fish, and insects now addresses the fundamental question of how these remarkable displays are achieved, offering insights on co-opting already existing mechanisms and unexpected lessons for their evolution.



Distinct pigment patterns in a Silver Laced Wyandotte chicken. Image courtesy of D. and P. Akers.

### Cells of a Feather Flock Together

A unique feature of birds is their varied and colorful plumage, replete with striking patterns. By coupling a careful mapping of distinct feather features such as pigment color, distribution, and their temporal variation with a cellular and molecular analysis of melanocytes, Cheng-Ming Chuong and colleagues provide a roadmap for studying feather patterning in chickens. Notably, feather patterns arise through a combinatorial modulation of the presence, arrangement, and differentiation of melanocytes rather than through specific genetically encoded traits. One example of the power of such simple integrative changes is the striped plumage of Barred Plymouth Rock chickens. In these birds, a previously identified defect in the *CDKN2A/B* tumor suppressor locus leads to a premature differentiation of melanocytes and a fluctuating loss of melanocyte progenitors, which, when coupled with the growth of feathers, creates the alternating black and white chevron-shaped pattern. In another example, the authors explored the temporal control of pigment patterning in Taiwan Country chickens, whose feathers display different colors from the distal tip to the proximal end. They find that temporal regulation of melanocyte progenitor activity during the creation of the distinct parts of a feather accounts for the color transitions. A third modulator, conferring laced-edge feathers to Silver Laced Wyandotte chickens turns out to be the pulp

adjacent to melanocytes, expressing a pigment modifier. Therefore, co-opting simple cellular functions affecting the topology of the melanocyte progenitor niche is an effective mechanism for creating complex patterns that ultimately impact animal behavior. Lin, S.J., et al. (2013). *Science* 340, 1442.

### How the (Zebra)fish Got Its Stripes

Cells conferring iridescence are at the focus of two recent papers investigating stripe formation in zebrafish. Pigment patterns in fish have important functions in mate choice, shoaling, and avoiding predators and have been used to study the mechanisms underlying morphological development and evolution. Several pigment cells contribute to the striped patterns decorating the flanks of zebrafish: black melanophores, yellow or orange xanthophores, and iridescent iridophores. Dark stripes of melanophores alternate with light stripes of xanthophores, whereas iridophores convey a luminescent appearance overall. The mechanisms of stripe formation have been under scrutiny, and previous studies have shown the importance of interactions between melanophores and xanthophores. However, the contribution of iridophores to pattern development has not been known. David Parichy's and Christiane Nüsslein-Volhard's groups now show that iridophores do more than convey a shiny look; their presence is necessary for organizing both melanophores and xanthophores. Both papers provide evidence that normal stripe formation cannot occur in the absence of iridophores and show that iridophores both promote and inhibit melanophore and xanthophore development over different spatial scales. Parichy and colleagues also go a step further in identifying molecular mechanisms underlying stripe formation. They show that a highly conserved zinc finger protein, Basonuclin-2 (*Bnc2*), acting in the tissue environment to promote the development of all three pigment cell classes, does so in part by regulating expression of the growth factors Kit ligand a (*Kitlga*) and Colony stimulating factor-1 (*Csf1*), required by melanophores and xanthophores, respectively. They also demonstrate that once *Bnc2*-dependent iridophores appear, iridophores themselves express *Csf1* and thereby specify where xanthophores will develop. These findings demonstrate novel pigment cell autonomous interactions in pattern formation as well as the importance of nonautonomous spatial cues in designating where stripes will form.



Wild-type and *Bnc2* mutant zebrafish. Image courtesy of L. Patterson and D. Parichy.

Patterson, L.B., et al. (2013). *PLoS Genetics*. Published online May 30, 2013. <http://dx.doi.org/10.1371/journal.pgen.1003561>.

Frohnhofer, H.G., et al. (2013). *Development* 140, 2997–3007.



Wing pigmentation pattern diversity among *Drosophila* species. Image courtesy of B. Prud'homme and N. Gompel.

## These Mechanisms Are Spot On

In the insect world, diverse pigmentation patterns on the wings and cuticles have evolved in response to the pressures of predation, geographical adaptation, and mate preference. Seeking to understand the mechanisms of diversification among species has been a longstanding quest. In a recent report, Benjamin Prud'homme, Nicolas Gompel, and colleagues powerfully employ the tools of genetics to study the basis of spot formation on *Drosophila* wings. They examined the expression pattern of a pigment gene *yellow*, which confers some of the characteristic wing markings, and sought to identify the transcription factor regulating its distribution. They find that Distalless (Dll), a transcription factor with an essential, well-characterized role in wing formation, fulfills this role. After its function in wing formation is over, Dll switches its expression pattern to specifically drive the placement of the pigment markings. Strikingly, Dll expression diverges among species of flies to drive the differential placement of pigment spots on the wing. This work illustrates how a gene with an essential function and the ability to control multiple downstream targets can be co-opted to modify traits among different species.

In addition to the formation of markings, some species also have to contend with their maintenance. In the case of caterpillars, markings on their cuticles need to be restored after each molt. The molecular pathways involved in this periodic upkeep are the focus of the work by Haruhiko Fujiwara and colleagues. Analysis of a silkworm mutant caterpillar with twin-spots on the dorsal side of multiple sequential segments reveals that a *cis*-regulatory change in Wnt1 expression in the epidermis is responsible for spot patterning. Moreover, periodic upregulation of Wnt1 within the spot marking area is associated with the presence of a molting hormone. Transgenic expression of ectopic Wnt1 induces additional pigmentation, providing further evidence that Wnt1 expression may confer the diversity of spot patterns found in the insect world. Indeed, this mechanism of spot formation maintenance is conserved among other lepidopteran species.

Arnout, L., et al. (2013). *Science* 339, 1423.

Yamaguchi, J., et al. (2013) *Nat. Commun.* Published online May 14, 2013. <http://dx.doi.org/10.1038/ncomms2778>.



Sequential orange spots in a caterpillar of swallowtail butterfly, *Papilio machaon*. Image courtesy of H. Fujiwara.

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