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Editorial overview: Cool, colorful, and complex animal systems

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In a COVID world, we need something to brighten our lives. More than ever, we feel the need for diversity. The need to travel again and experience a Thai forest packed with insect life; be awed by brilliant color whilst diving in the coral reefs off West Papua; or feel a sense of overall beauty whilst hiking though meadows in the Alps. Anything to get us out of the place we live in now. However, if we cannot physically travel, we can at least travel in our minds.

Here we present a smörgåsbord of intellectual delights to provide rescue from the pandemic doldrums. With the help of all our contributors, we have assembled an issue replete with the most recent advances in the genetics and development of our favorite, most colorful, most quirky animal systems.

The review articles in this special edition focus mainly on the genetics and evo-devo of non-model animal organisms. Work on non-models is often difficult and time-consuming, as establishing and breeding viable populations in the lab is often the limiting step. However, new technologies, such as whole-genome sequencing and different RNA-sequencing techniques, are quite suitable to study evo-devo in a wide variety of species, as long as they can be obtained in the wild.

Is this effort really worth it? We believe so, as deep and long-standing questions about the evolution and development of the myriad distinct body plans and hundreds of novel traits will never be addressed by researchers focusing solely on the few standard models, like the house mouse, zebrafish, chicken, frog, nematode, and the common fruit fly.

Model species, however, have provided us with broad knowledge about the function of many genes in organismal development. When those same genes pop-up associated with novel traits in a non-model species, they can provide a rich starting point in the investigation of mechanisms that drove the evolution of those novel animal forms.

As new molecular technologies are rapidly developing, such as CRISPR, the use of non-model organisms becomes more valuable and informative. Comparative evo-devo work, traditionally descriptive, starts to acquire a functional component. The use of these functional tools, however, requires that the investigated species be reared in the lab, and that their embryos can be collected and injected. This requirement can still be a challenge for many systems, but CRISPR experiments are rapidly expanding across non-models.

In the following sections, we introduce the 22 review articles that were assembled for this issue. This collection, we think, is quite suitable for an upper-level undergraduate or graduate course on evo-devo. The newest research from the past two years is highlighted in each article, which is written by experts at the cutting edge of their field. We split the 22 review articles into five general topics: (1) the evolution of distinct cell types, (2) the evo-devo of 3D traits, (3) the evolution of pigmentary and structural colors, (4) the evo-devo of color patterns, and (5) the latest reviews on insect sexual dimorphism and plasticity.

Group 1: cell types

Our start-off topic is the evolution and diversification of various cell types in animals, which is obviously one of the most fundamental questions in developmental biology. In their review article, Kishi and Parker focus the discussion on the evolution of excretory glands in animals. Excretory glands have evolved independently thousands of times in different animal lineages. Therefore, they are ideal for the study of parallel evolution leading to novel cell types. This review also discusses how newly arisen cell types evolve cooperativity among each other to form functional glands. As excretory glands produce a vast array of substances, they are great models to further our understanding of how novel biosynthetic pathways evolve.

Group 2: 3D traits and their development

In this cluster of articles, focusing on traits that stick out of the body, Kittlemann *et al.* review recent work around the gene *shavenbaby/ovo* that controls the number of hair-like projections, the trichomes, found on the body of *Drosophila* larvae. Yes, we know, *Drosophila* is a model system, but examining how the regulation of this gene evolved highlights interesting aspects of pleiotropy and modularity, two favorite themes in evo-devo. Then, Tomoyasu gives us the latest perspective on the origin of the insect wing. The latest work incorporates detailed developmental and functional work on crustacean leg development to indicate that wings might have evolved from modifications of the most proximal segments of crustacean legs, hidden as part of the lateral body wall in more primitive wingless insects. Gotoh *et al.* provide a novel perspective into how beetle horns acquire their unique shapes by focusing on the patterns of epithelial folding and cell movements that take place during the pre-pupal and pupal stages. Jockush and Fisher take a more comparative transcriptomics approach to novelty. By sequencing the transcriptomes of several hemipteran bugs, they discover that novel traits in this group of insects come from different types of genetic novelties: duplicate genes, novel genes, and borrowed genes from other species that crossed horizontally into the genome. The remaining three reviews in this group of articles concern vertebrates. Saxena and Cooper discuss how the use of next-generation sequencing helped move research away from the traditional mouse and chicken models to study limb development in a wide array of vertebrate species. Their review article is followed by a paper by Howenstine *et al.*, who discuss the evo-devo of mammalian forelimb diversity, reaching far beyond the traditional mouse model by covering monotremes, bats, moles and many more mammals. Finally, Chen *et al.* then take a detailed look at the development of integumentary organs in birds, particularly focusing on the fine architecture of bird feathers, which is closely linked to the production of structural colors.

Group 3: pigmentary and structural colors

This cluster focuses on animal colors, and we all need a bit more color in our lives. Popadic reviews recent work on hemipterans as well as other insects, showing that when melanin pathway genes get knocked-down, not all pigmented areas are affected in the same way. They propose that insects start off with a particular background color and that **black** color can be produced by the regional expression of melanin-promoting enzymes, or a lighter color produced by the regional expression of melanin-suppressing enzymes. Okude and Futahashi focus on the molecular mechanisms of producing colors in the order Odonata (dragonflies and damselflies). They particularly focus on **blue** color tones, which have evolved many times independently among these insects, involving a mix of ommochromes and pteridines deposited in different cuticular layers. Tong *et al.* then review the molecular mechanisms that produce the **different colors** of eggs and larvae of lepidopterans. Saranathan and Finet move on to **structural colors** in bird feathers. These are colors that are produced via light interacting with nano-patterned structures on the feathers. They organize all the recent literature of this topic for us. Lloyd and Nadeau do the same for butterfly structural colors. They also review recent genetic work that has begun to implicate genes in the development of the scale nanostructures that give rise to brilliant colors.

Group 4: color patterns

In group 4, we move on to color patterns. Sounds the same? Well, it isn't. This set of papers focuses on developmental mechanisms that set up **where** each color goes at the surface of an animal. And yes, we know, we are biased towards colorful animals. First off, we have Schilthuizen discuss research progress of the beautiful patterns of snail shells. Then, one of us, Werner, and his students review the complex wing color patterns of non-model flies, and how sometimes subtle changes in those patterns are essential for species identification. They reference new species identification guides, notably for drosophilid flies, and also discuss pest control strategies through the manipulation of pigmentation genes. Niimi and Ando follow suit with a review of the recent progress made on elucidating the molecular basis of ladybird beetle color patterns. And one of us, Monteiro, and Beldade review the progress around the genetics and eco-evo-devo of eyespot color patterns in butterflies. Papa *et al.* then review recent studies in the highly diverse *Heliconius* group of butterfly species, focusing on the genetic mechanisms that give each race their specific bright red, black, and yellow color patterns. Parichy gives us an overview of the molecular mechanisms underlying the diversification of fish color patterns, including how their stripes and spots have evolved. Finally, Curantz and Manceau review mathematical models that explain self-establishing patterns in vertebrate species, such as the famous Turing patterns. Self-establishing patterns that are independent of simple morphogen gradients are thought to give rise to a wide variety of morphological characters. The authors explain how pattern self-organization can lead to the formation of periodic patterns, pattern diversity, as well as pattern fidelity.

Group 5: sexual dimorphism and plasticity

In group 5, we have two reviews of two other classic topics in evo-devo: sexual dimorphism and plasticity. Hopkins and Kopp provide a review of the recent literature of the different genetic and physiological mechanisms allowing male and female insects to look different from each other. Reed and van der Burg follow that with a review on the molecular mechanisms that underlie the evolution of phenotypic plasticity in butterfly wing patterns, and they propose new directions of research in this field.

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