DEVELOPMENTAL DYNAMICS 244:1181–1183, 2015
DOI: 10.1002/DVDY.24346

Preface to the Special Issue on Evolution and Morphological Diversity

Kimberly L. Cooper[1] and Michael D. Shapiro[2]

[1]Division of Biological Sciences, University of California San Diego, La Jolla, California
[2]Department of Biology, University of Utah, Salt Lake City, Utah

A century ago developmental biology was primarily comparative embryology, the beginnings of "evo devo". Today, anyone interested in an unusual organism can find anatomical studies and developmental staging series dating to the 19th and early 20th century, but often not more recent than the 1940s. The advent of molecular developmental genetics led to a funneling of focus down to a few model organisms based on ease of acquisition and husbandry, simple genetics, and a standard toolkit to study and manipulate developmental processes. Thus there was one plant, one worm, one fly, one fish, one bird, and one mammal. Despite once thriving as important embryological models at Woods Hole and elsewhere, marine invertebrates were woefully underrepresented in mainstream developmental genetics, and non-avian reptiles were left right out.

Similarly, developmental biology once played a prominent role in evolutionary biology. For example, 19th century embryologists recognized the importance of conserved developmental traits as clues to shared ancestry among species. Indeed in *The Origin of Species*, Charles Darwin pondered the fact of "embryos of different species within the same class, generally, but not universally, resembling each other" (Darwin, 1859, Chapter 13, p.442). However, with the rise of statistical population genetics in the mid-20th century and a focus on the proximate and ultimate causes of natural selection, there was no longer a clear place for developmental mechanisms in the new Modern Synthesis.

Nevertheless, many researchers continued to pursue an understanding of the developmental mechanisms that distinguish species from one another, but on the edges of the fold of evolution. Bold ideas about simple developmental mechanisms of major evolutionary change, including the supposition of unfortunately named "hopeful monsters" (Goldschmidt, 1940), percolated through the literature but were largely dismissed by the Synthesis. Decades later, Davidson and others proposed that regulation of gene expression was a principal mechanism of developmental evolution (Britten and Davidson, 1969). The theoretical importance of gene regulatory control was augmented by the discovery of extensively conserved developmental "toolkit" genes, such as the *Hox* genes in diverse animals (McGinnis et al., 1984). Together, these ideas issued a major challenge to both evolutionary and developmental biologists studying a wide variety of organisms: if disparate species share such similar genes that control key developmental processes, how do gene regulatory networks shape an organism and generate species diversity?

We started graduate school at a time when the zebrafish was considered an "emerging model system", and there was some trepidation at the time in the greater field of developmental genetics. What could one learn from the zebrafish that couldn't be studied in a mouse? Would findings in the zebrafish be fish-specific and therefore "uninteresting"? Over the past two decades, we witnessed a rapid emergence of molecular studies of evolution and development and a remarkable expansion of the number of study species. In retrospect, the focus on model systems in developmental genetics was essential to pioneer powerful experimental approaches that ultimately benefit studies of evolutionary diversity. Complex molecular methods once limited functional experiments such as gene targeting to this small number of model species. More recently, the explosion of new genome editing technologies has begun to allow specific engineering – deletion, insertion, or replacement – in the genomes of a multitude of species (Gaj et al., 2013). In parallel, technical advances driven by sequencing the genomes of human and model species have dramatically driven down costs and improved ease of assembly and annotation. As a result, there are currently over 3,000 sequenced eukaryotic genomes with an anticipated acceleration as more species are added to cover phylogenetic diversity and to address problems of economic and health importance (diArk, http://www.diark.org/diark). Hence, we have now entered an exciting period in evolutionary and developmental genetics. Instead of relying exclusively on a small group of traditional model organisms, we can now select appropriate animal models to understand specific traits and processes based upon their biology rather than historical precedence.

These opportunities raise a set of big picture "existential" questions for the field of evo devo. Within the broader field of evolutionary biology, can we relate principles of population genetics and selection to the molecular regulation of development? How does phenotypic variation in a population offset developmental canalization to provide the material for natural selection? Can we define a set of developmental "rules" for evolution on par with the statistical and theoretical framework of the Modern Synthesis,

Article is online at: http://onlinelibrary.wiley.com/doi/10.1002/dvdy.24346/abstract

or does evolution of development follow myriad and unpredictable paths? What can we learn by synthesizing studies from a broad phylogenetic sample rather than further subdividing species by phenomenology?

These are big questions that will likely require bold approaches and many years of dedicated research efforts. Given the historical focus of developmental genetics on a small number of species, the first steps require understanding genetic and developmental variation at both the macro (between species) and microevolutionary (among populations) levels throughout the tree of life. Both levels of analysis have their strengths: comparisons among species can help us understand key developmental events that drove major evolutionary transformations, while studies of diversity within and among conspecific populations can identify causal genotypes underlying phenotypic variation. These may appear to be individual case studies for some time, but a survey of mechanisms across the phylogeny of life will be essential to identify the broader rules, if any, that govern the evolution of organismal diversity.

In this context, the special issue of *Developmental Dynamics: Evolution and Morphological Diversity* comes at an exciting time as we seek to establish a collective identity for our field and define our objectives. We have assembled a body of literature that includes research articles, reviews, and topical critical commentaries. Together, these papers provide an illuminating perspective on a rapidly growing field that spans taxa, experimental approaches, and evolutionary scales.

One of the more "mature" evo devo study organisms is the cavefish, *Astyanax mexicanus*, which serves as a model for the evolution of morphologies and behaviors common to diverse cave-adapted taxa. Gross and colleagues review the origins and evolution of the field of cavefish biology starting with the earliest discovery of cave populations and continuing through the characterization and genetic analysis of derived phenotypes (Gross et al., 2015). They end with a forward-looking perspective on the potential to leverage this historically important organism using modern approaches in functional genomics, opportunities that were not possible until recently and for which the cavefish is especially well-positioned.

Other areas of evo devo are at earlier stages of study where valuable contributions focus on a deep and quantitative analysis of phenotypes over developmental and evolutionary time. The Arctic charr, for example, exhibits intraspecific diversity in morphology of the cranial bones. A thorough understanding of the extent and developmental timing of morphological divergence will ultimately provide an opportunity to connect genotype and phenotype within variable populations (Kapralova et al., 2015). Smith and colleagues apply a broadly similar approach to quantify the developmental timing of morphological divergence at the macroevolutionary level among avian species. The authors find that closely related birds, chick and quail, are quantitatively more similar than the divergent face of the developing duck (Smith et al., 2015). Each of these stories will no doubt inspire further analyses of the mechanisms that generate this phenotypic diversity.

Several articles in this special issue take a multi-organismal approach to understand evolutionary transformations of body plan evolution. Diogo and Ziermann provide a consolidated review of the literature with detailed anatomical and temporal (in evolution and in ontogeny) analyses of cranial musculature in basal chordates, and highlight implications for the origin of vertebrate head muscles (Diogo and Ziermann, 2015). This is accompanied by a review focusing within diverse vertebrate taxa on the anatomy and homologies of the early axon scaffold that sets the stage to understand mechanisms underlying the elaboration of neuronal pattern in vertebrate evolution (Ware et al., 2015). The topic of neuronal elaboration in vertebrates is further bolstered by an investigation of *neurogenin* expression in lamprey; the subfunctionalization of paralogues to encompass nearly all of the conserved neurogenic domains runs deep in the vertebrate lineage (Lara-Ramírez et al., 2015).

Stepping backward in ontogeny, two papers focus on aspects of the earliest stages of gastrulation in distantly related clades. Fish and amphibians gastrulate via the blastopore, while amniotes such as birds and mammals ingress cells of the mesoderm and endoderm via the primitive streak. Stower and colleagues investigated the veiled chameleon, *Chamaeleo calyptratus*, as a candidate transitional state and identified a hybrid bimodal mechanism of gastrulation that occurs by spatially distinct blastopore-like involution together with streak-like ingression (Stower et al., 2015). Working more basally in the metazoan phylogeny, Perry and coauthors address the developmental lineage and gene network homologies of two bipotential progenitors of mesoderm in spiralians, the endomesoderm (thought to be homologous to mesoderm in bilateria) and a uniquely spiralian ectomesoderm (Perry et al., 2015). They find extensively shared gene regulatory networks between these distinct origins of mesoderm suggesting co-option or derivation from a common progenitor.

Each of these approaches leverage phylogenetic relationships to identify key taxa for comparative analyses to understand evolutionary transitions from basal to derived states. Organ and colleagues make a strong case in their critical commentary that modern statistical phylogenetic approaches, paired with a growing collection of fossilized embryos of extinct taxa, provide new opportunities to strengthen and test hypotheses in evo devo (Organ et al., 2015). Newly developed statistical methods enable identification of rates of evolutionary change (early burst, punctuated, gradual) and test models of correlated evolution, convergence, and constraint. Morphometry, gene expression patterns, cell/tissue lineage, and sequence information together with character states preserved in fossilized specimens provide the data on which to build and test these models.

We have so far focused on what evo devo stands to add to the field of evolution and vice versa, but there is an equivalent interconnection between evo devo and developmental biology. Classic developmental genetics has established the foundation for investigations of the molecular mechanisms of developmental evolution. Pairing model species with non-traditional species is a powerful approach to gain insight into fundamental mechanisms of development and diversification. For example, *Drosophila melanogaster* has long been a workhorse model in developmental genetics, and essential conserved mechanisms of patterning and morphogenesis have been identified via the well-studied wing. These critical studies of *D. melanogaster* now provide a foundation to explore the mechanisms of wing size and shape variation in other *Drosophila* species (Matamoro-Vidal et al., 2015). Other research, primarily in *D. melanogaster*, promises to shed light on the mysterious mechanisms of phenotypic plasticity in traits that vary in response to environmental conditions, including the weaponry of horned beetles and caste traits in social insects. The critical commentary by Gotoh and colleagues connects local tissue signaling pathways to the endocrine system and proposes a promising mechanism by which specific structures may be more

sensitive to nutrient availability than the body as a whole (Gotoh et al., 2015).

Among the vertebrates, the zebrafish serves as a close comparative model to the Mexican cavefish. In *Astyanax mexicanus*, the morphologies of eye orbital bones in cave morphs share some similarities and minor differences with mutant zebrafish and both zebrafish and surface *Astyanax* with lenses removed (Dufton and Franz-Odendaal, 2015). Future studies will likely focus on the mechanisms of developmental constraint and flexibility in shaping the orbital bones.

Experiments in the chick and mouse identified a signaling center in the forebrain that promotes outgrowth of the facial primordia. By building on their phylogenetic morphometry (Smith et al., 2015) and extending the observations in these two model systems, Hu and colleagues demonstrate correlated differences in facial shape and *shh* expression domains in a variety of avian species (Hu et al., 2015). Interspecific transplantation experiments suggest that signals from the forebrain shape the face in these divergent species, thereby providing a role for tissue interactions in shaping morphology.

Plant genetics provides an excellent opportunity to model and experimentally test the relationship between genotype and phenotype (Rodríguez-Mega et al., 2015). As with each of the model/non-model species pairs highlighted above, studies of flower development in *Arabidopsis thaliana* can be leveraged to understand morphological diversity across lineages of plants, including floral morphology of the gingers, Zingiberales. To this end, Rocha de Almieda and colleagues provide an ultrastructural analysis of petal and petal-like structures together with an investigation of expression of genes thought to control flower evolution (Rocha de Almeida et al., 2015). Their findings suggest floral evolution may be more complex than previously modeled and will undoubtedly lead to a deeper exploration of putative mechanisms.

The overarching goal of evolutionary developmental biology is to take all of these contributions, and many more, to a deep genetic understanding of the relationship between genotype and phenotype and the types of developmental changes that diversify life. We are well on this path to incorporate developmental biology into a new "postmodern" evolutionary synthesis, as evidenced by this selection of papers representing the current state of the field, and we look forward to its continued evolution.

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