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Meeting Review: the Microevolution of Development

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What can the study of variation within populations bring to the macroevolutionary transitions that have generally been the province of evolutionary developmental biology? This past September 6–8, a diverse group of biologists gathered in Bloomington, Indiana to address just this question. The occasion was a mini-symposium organized by students affiliated with the National Science Foundation-funded Integrative Graduate Education and Research Training (IGERT) program in Development, Evolution, and Genomics at the University of Oregon and Indiana University, Bloomington. The meeting's stated goal, expressed by IGERT co-PI Michael Lynch, was to emphasize studies of populations or very closely related species, as opposed to "macro" studies comparing distantly related species. The promise of such studies is that the tracks left by the evolutionary process on developmental systems might still be visible.

The meeting was started, somewhat paradoxically, by Thom Kaufman, a noted "macro" researcher who deftly catalogued the types of seemingly abrupt shifts in arthropod segmental arrangements and the Hox patterns that specify them. However, rather than being largely ignored as the meeting turned to its stated emphasis, his talk served as a recurring foil for the following talks, a challenge to those assembled to remember that at the end of the day (or the era), big changes do happen and need to be explained. An oft-debated point of friction between neo-Darwinians and many evolutionary developmentalists is whether the evolution of truly novel features require especially rare and/or large quanta of variation or whether the more subtle sort constantly around us is sufficient. Two speakers showed that we may actually live to see some progress made on this front.

The first was William Jeffery (University of Maryland, College Park), who discussed his laboratory's detailed characterization of the development and evolution of blindness in the Mexican cave fish, *Astyanax.* Jeffery showed that blindness is accompanied by, and dependent on, the expansion of *sonic hedgehog* expression in the embryonic brain midline. With this expansion, eye reduction and feeding apparatus enlargement occur in a coordinated syndrome that could be easily envisioned as a gradual process driven by selection for enhanced feeding in a new environment and the tolerance of eye loss in the dark. Thus, though a key mechanism in the evolution of cave fish involves a favorite gene of developmental biologists, one need not invoke saltations to explain how it can guide adaptation. More directly hitting the theme, Antonia Monteiro (SUNY Buffalo) addressed how standing variation in the butterfly wing eyespot is revealed through laboratory selection experiments. Selection for divergent color schemes produced marked differences over only nine generations, for example, making a half black, half gold spot almost entirely one color or the other. She plans to test whether these rapid shifts in phenotype are tied to parallel shifts in the expression of genes thought to pattern the spots, *engrailed* and *spalt*, and whether selection acts on the genes themselves or on their upstream regulators. These two talks together emphasized just how quickly highly conserved developmental regulators can be put to work in the factory of variation.

The quantitative trait loci (QTL) method of associating genomic regions with variable phenotypes is arguably the most prominent population-based approach currently being applied to development and its evolution. Representing this growing area were Cynthia Weinig (University of Minnesota) and Andrew Doust (University of Missouri, St. Louis), who performed genome-wide scans for QTL that affect different aspects of plant variation. Weinig reported results of an enormous collaborative study of *Arabidopsis* by researchers at North Carolina State University and Brown University, in which a highly replicated set of recombinant inbred lines were planted both in North Carolina and Rhode Island in two different seasons. One result of special interest pertained to bolting time. In each condition significant QTL were discovered, but they showed little or no overlap between treatment groups, indicating that different environments can coax different components of a single genotype to serve similar ends. Doust has studied the domestication of foxtail millet, *Setaria italica*, from its wild ancestor, *S. viridis.* This study serves as an interesting parallel to that of John

Doebley and his colleagues on the domestication of another grass, *Zea mays.* Indeed, in at least a few cases Doust's QTL seems to match ones in the other system. But numerous unique QTL exist in millet as well, indicating that domestication of grasses is flexible.

Both Weinig and Doust noted the challenges of trying to go from QTL to actual genes of known sequence and function and were counting on well-mapped candidate genes to shorten the process. Greg Gibson (North Carolina State University) noted that in his system, the *Drosophila* wing and its shape, most of the genome still falls in the "statistical shadow" of one or more QTL in a whole-genome scan. Cutting straight to candidate genes, he described work attempting to link single nucleotide polymorphisms in key wing patterning genes to phenotypic variation. Although some significant relationships were found, Gibson noted that single nucleotide polymorphisms in a second "control" gene thought to have nothing to do with wing shape also gave statistically significant associations. He cautioned participants that the kind of resolution needed to get truly gene-level QTL required dense markers and numerous repetitions, a sobering thought for the biologist on a budget.

David Parichy (University of Texas, Austin) and Scott Baird (Wright State University) both made ample use of interspecies hybrids to study variation among sister taxa. Parichy is interested in the mechanisms that distinguish the different pigmentation patterns of the zebrafish, *Danio rerio*, from those of other *Danio* species. The genus abounds with modifications of the ancestral striping pattern retained by *D. rerio*, and in hybrids the ancestral pattern is largely dominant. But in a clever next step, Parichy's group then tested various pigmentation-disrupting *D. rerio* mutants in the same hybrids. Although *leopard*, which is spotted, was complemented by hybridization with the normally stripeless *D. albolineatus*, hybrids using the *panther* mutant remained stripeless. Thus *panther*, encoding a receptor tyrosine kinase, is neatly implicated as an especially important candidate gene, and *leopard* is excluded.

Baird has recently discovered that the genetically male hybrids produced by crossing the nematodes *Caenorhabditis briggsae* and *C. remanei* are feminized. This unusual mechanism for implementation of Haldane's Rule is even more unusual because the feminization can be suppressed by using different strains of either species. This implies that hidden variation in sex determination genes exists in populations and is only uncovered by putting them in a novel context, a result seen previously in flour beetle hybrids by Michael Wade and his coworkers. Eric Haag (University of Maryland, College Park) also described work on the evolution of nematode sex determination. He detailed the rapid concerted evolution of two *Caenorhabditis* proteins that physically interact as part of the cascade of repressive interactions that specifies sex. One of these, FEM-3, is so different in sister species that it can barely be recognized, yet its interaction with TRA-2 is maintained (but species-specific) in the three species studied. This suggests that a potential mechanism for Baird's result may be a failure of heterologous sex determination proteins to interact normally.

Holding down the theoretical fort, Allan Force presented his work on gene duplications and their fate. After summarizing his influential model for the subfunctionalization of genes, he explained how population size is predicted to greatly influence the path that gene duplicates take to become fixed. More speculatively, Force proposed that the resolution of gene duplications could have the general effect of promoting the duplication of spatial modules (such as arthropod segments). Though this may be hard to imagine, we currently have few alternatives by which to envision how the gain or loss of segmented parts occurs.

How successful the meeting was should be judged more by how far we have come rather than how far we still have to go. True, the old matter of whether development is "creative" or "merely limiting" still came up, but considerable common ground has been landfilled in recently. First, both fervent Fisherians and enthusiast evo-devoists can be heard talking about the importance of identifying the specific genes controlling variation. Second, there is growing acceptance of, and interest among, developmental biologists in epistasis and dominance (i.e., functional context dependence) and their effect on developmental genes. Third, there is a common appreciation that hidden variation is rife at all levels of comparison, with the implication that much of the evolution of development is not adaptive in any obvious way. Finally, we now know that genes capable of producing massive shifts in morphology in the laboratory are also capable of producing smaller ones in natural populations. If the question was once "does development evolve via the genes studied by developmental biologists, or by countless small changes all over the genome?" then the answer may very well be "yes."