Review of the Fifth UK Evolutionary Developmental Biology Meeting

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The Fifth one-day Evolutionary Developmental Biology Meeting was recently held in Oxford (September 13, 2004) and attracted a considerable crowd of researchers in the field from the UK and from overseas. The talks represented a variety of different approaches and perspectives in evolutionary developmental biology: from the mechanisms that produce developmental variation within populations to the patterns and processes of evolution across phyla and even the animal kingdom as a whole. Many of the speakers used some combination of mechanistic and comparative approaches, and the integration of these methods will surely produce further progress in the field.

The program started with a talk by Tim Littlewood (Natural History Museum, London) on the evolution of life cycles in flatworms. Littlewood used a phylogenetic approach to track the history of the evolution of parasitic life styles. He demonstrated that drastic changes of life cycles and modes of transfer between hosts have occurred multiple times, and switches even between higher taxa of hosts have repeatedly occurred. As a result, the phylogenetic "ages" of the parasite and their host taxa do not coincide, contrary to a widespread view. Parasitism is an intriguing opportunity for studying the evolution of development, because the development of the parasite is intimately tied to that of its hosts throughout the life cycle.

Peter Holland (University of Oxford) discussed the origin of multicellular animals. He first briefly discussed whether the origin of multicellularity might have coincided with a wholesale genome duplication. Comparisons between metazoan and yeast genomes do not support this hypothesis, but indicate that metazoans possess many families of genes that are not found in yeast or other eucaryotes. The problem with this comparison is that yeast is too distantly related to the metazoans to be fully informative. This gives a new urgency to the long-standing problem regarding the uncertainty about the sister-group of metazoans. Holland's lab has conducted phylogenetic analyses that clearly point to choanoflagellates, a heterogenous group with mainly single-celled and a few colonial species, as the sister-group of the metazoans. First results from genome studies in the choanoflagellate *Monosiga ovata* are most promising. Holland presented the example of the *Hoglet* gene of *M. ovata* and its similarity to the *hedgehog* gene family of the metazoans. *Hoglet* and the *hedgehog* genes share an autocatalytic domain with similar characteristics. Hoglet is a protein that undergoes autocatalytic cleavage just as *hedgehog* genes do, but it differs from them because it is not a signaling molecule. Its function is unclear—it contains a CBD-II (cellulose-binding domain) not found in metazoans, as well as a very long threonine repeat. *Hoglet* and the *hedgehogs* provide a fascinating opportunity for studying the evolution of signaling, one of the central features of multicellularity. Further studies of the genomes of choanoflagellates and the basal metazoans (sponges, Placozoa, etc.) are likely to shed more light on this question in the near future.

Claudio Alonso (University of Cambridge) and Adam Wilkins (*BioEssays*) presented a shared talk in which they challenged the view that enhancer elements are the only, or the predominant, sites for genetic control of gene regulation, and therefore are the primary target for the evolution of developmental processes. In the first section of the talk, Alonso showed some quotes from prominent evo-devo researchers stating forcefully that *cis*-regulatory control is all evolution is about, and that indeed there is a sort of "enhancer cult." He then went on to point out how many different players are involved in the regulation of gene expression, both at the transcriptional and posttranscriptional levels: the whole transcriptional machinery and the basal promoter to which it binds, translational regulation, and alternative splicing. All these components, or alternative regulatory points (ARPs), might well contribute to variation that is relevant for the evolution of gene expression. But do they? A short survey of some examples illustrated that mutations of ARPs have been described often, and that a large proportion of mutations may affect ARPs. Around 10–15% of known human disease mutations are at splice sites, and it is likely that splicing is also affected by additional mutations that are not located directly at these sites. Moreover, about 75% of human genes undergo alternative splicing, providing scope for considerable variation in expression. And splicing is just one example of an ARP. Wilkins outlined that ARPs have many of the features, like flexibility and modularity, which have made enhancers attractive as a mechanism for explaining standing genetic

variation in populations. Moreover, they may evolve in concert with enhancers, so that it may be difficult to tease apart their relative roles. The conclusion is not that it is one or the other, but that ARPs as well as the enhancers contribute to the developmental genetic variation in natural populations, which is the raw material for phenotypic evolution.

Claude Desplan (New York University) gave an overview of primary axis formation in insects, showing that the *Drosophila*-centered view of most developmental biology texts is only a part of the picture. The interaction of maternal Bicoid and Nanos with the gap gene *hunchback* is critical for anterior–posterior patterning in *Drosophila*, but appears to be a special case limited to "higher" flies—*bicoid* seems to be exclusive to this group. In other insects, *hunchback* is regulated in a different manner, and it is not always a "gap gene" in other species, because it has different mutant effects. Mutants of *hunchback* in the parasitic wasp *Nasonia*, a long-germ-band insect like *Drosophila*, have effects that resemble *bicoid* mutants of *Drosophila*. Also, zygotic genes are "in charge" earlier in *Nasonia* than in *Drosophila* development, where maternally provided RNA plays a greater role. Overall, it becomes apparent that there are a multitude of ways to set up the embryonic axes in insects, and exploring them in a comparative framework is promising many new discoveries.

In the otherwise animal-dominated program, Jane Langdale (University of Oxford) represented the Plant Kingdom, providing an overview of the evolution and development of leaves. Plant development is driven by meristems, localized growth zones consisting of undifferentiated cells that proliferate indeterminately and give rise to the different plant organs. In contrast, growth in a leaf is determinate, so cells need to switch from an indeterminate to a determinate mode of proliferation. The indeterminate type of meristematic proliferation is maintained by *knox* genes. Therefore, repression of *knox* in leaf primordia is required, and overexpression of *knox* genes in leaf tissue can produce indeterminate growth. The repression of *knox* genes in leaves is achieved by *ARP* genes (*ARP* stands for the *as1*, *rs2*, and *phan* genes, and has no relation to the ARPs of Alonso and Wilkins). Studies in the lycophyte *Selaginella* indicate that this mechanism has been conserved through much of land plant evolution, and Langdale presented a hypothesis of how changes in *knox* and *ARP* gene expression could lead to the evolution of complex leaf structure. Langdale also reviewed work on mechanisms by which plants control the development of chloroplasts, and also found functional conservation, as transgenes from mosses can rescue mutants in *Arabidopsis*.

Methodology for comparative studies of gene function is making fast progress. Michalis Averof (Institute of Marine Biology and Biotechnology, Iraklio, Greece) reported on RNAi experiments in the branchiopod crustacean *Artemia* and the beetle *Tribolium*, as well as on transgenesis in *Tribolium* and the amphipod crustacean *Parhyale*. Clearly, these organisms are becoming new study systems providing valuable new information in addition to the classical models like *Drosophila*.

The final talk, by Detlev Arendt (European Molecular Biology Laboratory, Heidelberg, Germany), presented new ideas and results on studying the evolution of cell types in the nervous systems across the Bilateria. Arendt suggested that the detailed analysis of cell types can resolve problems in the large-scale phylogenetic comparisons. A cell type is characterized by the deployment of similar combinations of orthologous transcription factors and it can be traced to a cell type in the last common ancestor. In contrast, sister cell types evolve by duplication of cell types in an evolutionary lineage and tend to use paralogous effector genes. Arendt illustrated these ideas with a comparison of brains and photoreceptors between the annelid *Platynereis* and vertebrates (i.e., a protostome–deuterostome comparison). He found common patterns of gene expression in many sensory and neurosecretory cell types.

About a decade after evo-devo became a fashionable subject, the discipline is clearly thriving. The talks at the Oxford meeting illustrated some trends that promise many new insights in the years to come. There is a closer link to neighboring fields, both traditional and new, such as phylogenetics and genomics, which provide the tools that can be combined to address a broad range of questions in new and powerful ways. Moreover, an increasing number of species is being converted to model systems that are amenable to detailed genetic and developmental study in the laboratory, providing a denser phylogenetic coverage and therefore a higher resolution for reconstructing the evolution of development.

The UK evo-devo meetings are an annual opportunity to take stock of these trends, and they have become a tradition that seems to be well established now. The next meeting of the series will be in Manchester in September 2005. But having become a tradition does not keep the meetings from growing and evolving. Alessandro Minelli announced that he will organize a meeting in the spring of 2006 in Venice, providing increased opportunities for communication among evo-devo researchers at the European level.