

Meeting report
Spiralians in the limelight
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A report on the meeting 'Developmental Basis of Evolutionary Change', University of Chicago, USA, 16-18 October 2003.

The meeting, organized by R. Adam Franssen and Rebecca M. Shearman, two research students at the University of Chicago, brought together nearly 200 participants to discuss recent trends in evolution and development ('evo-devo'). This report focuses on two of the themes covered: the relationship between gene regulation and species divergence (interconnecting the fields of ecology, development and evolution), and spiralian evolution and development. Linda Holland (Scripps Institution of Oceanography, University of California, San Diego, USA) summarized the first theme by concluding that "the distance between micro- and macro-evolution is shrinking, in conjunction with genomics, and this meeting has done an excellent job in bringing these sides together." As to the second theme, the Spiralia - organisms such as molluscs and annelids, which have a spiral pattern of cleavage of the early embryo - are the core group of the Lophotrochozoa, representing a major evolutionary branch of higher animals that is under-represented in research so far. The meeting made clear that this gap needs to be filled to obtain a more complete and reliable picture of animal evolution and development.

Ecology, development and evolution

One cannot understand large transitions in evolution without understanding the small ones. Thus, the rapprochement between micro- and macro-evolutionary fields is obvious and manifold, and various examples of this were presented at the meeting. Scott Gilbert (Swarthmore College, Swarthmore, USA) referred to recent broadening of the fields of development and evolution into new side-disciplines, and focused on one of these: the field of 'eco-devo,' which integrates ecology, development and evolution. On one hand, this field explores the environmental, and thus

epigenetic, control of development. On the other, it explores how ecology determines the course of molecular evolution, population genetics being one facet of this. The environmental regulation of developmental gene expression can occur in a variety of ways, such as through differential DNA methylation (as in *viable-agouti* mice) or through chemical induction (for example, the stimulation of intestinal angiogenesis by gut microbes). Environmental regulation is most obvious in the action of the neuroendocrine system, which is capable of translating environmental sensory input into highly specific control of gene expression in the developing body, by the release of metabolites and neuropeptides that act selectively and at a distance. One example of this is the case of the tropical butterfly *Bicyclus*, where the release of ecdysone from the brain controls a temperature-mediated polyphenism (that is, the occurrence of several phenotypes in a population that are not due to different genotypes). Gilbert summarized eco-devo as "a major processing center to integrate the cellular and molecular levels of biology with the organismal and population areas of the biological sciences."

Michael Lynch (Indiana University, Bloomington, USA) and Allan Force (Virginia Mason Research Center, Seattle, USA) discussed their work on exploring the interrelation between genome evolution and population genetics using mathematical modeling. One starting point is the basal rate of gene duplication common to eukaryotic genomes. A frequent fate of the duplicated genes is subfunctionalization, meaning that different subfunctions of the initial gene are kept in distinct duplicates, in a complementary manner. Because subfunctionalized duplicated genes should each be less pleiotropic (that is, act at fewer different sites in the organism) than the parental gene, in the end subfunctionalization facilitates adaptive evolution. Lynch and Force calculated the survival rates of subfunctionalized alleles as a function of mutation rate and population size, and concluded that survival rates are highest in small populations that allow for genetic drift. This prompted Lynch to state that "genome complexity arises as a pathological response to small population size and degenerative mutations." At first, the increasing genome

complexity is near-neutral with respect to phenotypic selection, and would only later open up novel pathways to morphological evolution. This model has interesting implications. First, it makes adaptive evolution a secondary consequence of genome complexity, and not the other way round, and second, it implies that large and fast evolutionary transitions are more likely to occur in small populations.

Eric Haag (University of Maryland, College Park, USA) reported another case of molecular microevolution interwoven with population genetics. Comparing sex-determination mechanisms in three *Caenorhabditis* nematode species, Haag focused on the proteins FEM-3 and TRA-2. These specifically interact with each other within the two species, but each protein from one species will not interact with the other from the other species, indicating compensatory coevolution. When Haag compared the protein-interaction domains of both FEM-3 and TRA-2 to other regions of the proteins, however, he found them specifically non-conserved, representing a striking case of hypervariability. What is the driving force for these changes and the mechanism underlying them? To gain further insight into the quantity and types of changes that occur in wild populations, Haag presented a collection of FEM-3 variants from *Caenorhabditis remanei*. From these, and from computer simulations done in collaboration with Michael Molla (University of Wisconsin, Madison, USA), Haag suggested a model in which selection episodically drives adaptive compensatory changes to fixation. These fixation events would, however, alternate with longer periods of more neutral change. Haag's group is also working to establish *Caenorhabditis briggsae* as a *bona fide* system for forward and reverse genetics, for the purpose of comparing its sex-determination mechanisms with those of *C. elegans*. One striking difference that has already emerged is that the *fem* genes, which are essential for hermaphroditism in *C. elegans*, are dispensable for this in *C. briggsae*.

Lophotrochozoan development and evolution

The Spiralia are a large group of marine invertebrates that represent the main body of the Lophotrochozoa - one of the three branches of the Bilateria, alongside the Deuterostomia, which includes the vertebrates, and the Ecdysozoa, which includes insects and nematodes. The meeting assembled the growing community of researchers on the molecular genetics and development of spiralian. Several talks featured the polychaete annelid *Platynereis dumerilii*, a new spiralian model organism for which molecular resources are being generated on a large scale. *Platynereis* has been selected because it shows prototypical spiralian development and anatomy and exhibits many features considered ancestral in the Bilateria.

Gastrulation is one example of a process in which polychaete development follows ancestral paths. During polychaete gastrulation, the blastopore forms a slit and gives rise to both

mouth and anus. This pattern is called amphistomy, and it is the likely evolutionary precursor of protostomy and deuterostomy (where the blastopore gives rise exclusively to the mouth or anus, respectively). I reported our group's study of *Platynereis* amphistomous gastrulation movements using *in vivo* time-lapse recordings on whole-mount preparations. We have traced at cellular resolution the morphogenetic transformation of the spirally cleaved embryo, with approximate radial symmetry, into the bilateral body of the mature larva, and this enables us to compare polychaete and vertebrate gastrulation movements. We have also started molecular analysis of the mechanisms driving these gastrulation movements. Genes specifically active in the vertebrate Spemann organizer (which releases signals to organize the early embryo), such as *dickkopf* or *noggin*, have been found in lophotrochozoan expressed sequence tag (EST) collections, including our own for *Platynereis*, but apparently do not exist in *C. elegans* or *Drosophila*.

In *Platynereis* most of the segments are morphologically similar (homonomous). This is different not only from many other segmented animals, such as insects, most crustaceans and vertebrates, but also from other polychaetes; in all these animals the fate of distinct groups of segments is more diverse (heteronomous). Nevertheless, homonomy is considered the ancestral state of segmentation in all segmented animal groups. What, then, are the roles in *Platynereis* development of genes orthologous to *Drosophila* genes that control segmentation? The *Drosophila* segment-polarity genes *engrailed* and *wingless* are expressed in transverse stripes in each segment early in development; Guillaume Balavoine (Centre de Génétique Moléculaire CNRS, Gif-sur-Yvette, France) reported that the *Platynereis* orthologs were also expressed in transverse stripes in each of the nascent segments, a pattern compatible with a role in segmentation. When he compared the segmental pattern of *engrailed* and *wingless* stripes in *Platynereis* with that in *Drosophila*, however, he noted that the patterns were out of register: instead, one segment in *Platynereis* corresponded to one parasegment in the *Drosophila* embryo (parasegments are transitory metamer units that form ahead of the later segments and are out of phase with them by half a segment). Balavoine proposed that in a remote insect ancestor some kind of 'resegmentation' - a phase shift of segmental units - might have occurred, possibly driven by the evolution of the jointed appendages such as legs and antenna (*Platynereis* has unjointed parapodial appendages).

In a complementary approach involving similar genes but different polychaete species, Elaine Seaver (Kewalo Marine Laboratory, University of Hawaii, USA) presented expression data on segmentation genes for *Capitella*, *Chaetopterus* and *Hydroides*. These species differ in their life cycle and in the way segments develop, and they show segmental heteronomy to distinct degrees. Each of these species has a distinct body plan and/or life cycle, and all differ in segment formation and

segment diversification. Although segmental expression of *engrailed* orthologs is also observed in these species, the onset of *engrailed* expression was reported only after the segments had initially formed. These findings seem to preclude an ancestral role of *engrailed* in the segmentation machinery proper but would support an ancestral role in specifying cell types in a given segment, such as certain types of neurons or chaetoblasts, the cells that produce the chaetae (the stiff bristles sitting on the parapodial appendages).

Contradicting the beliefs of generations of spiralian embryologists, evidence is accumulating that the determinate and highly conserved pattern of spiral cleavage does not involve invariant blastomere fates. Instead, the same fate can be produced by dissimilar blastomeres in two species, or within one species after experimental manipulation. Adriaan Dorresteyn and co-workers (University of Giessen, Germany) have treated consecutive cleavage stages of *Platynereis* embryos with agents inhibiting the progression of cytokinesis. Dorresteyn reported that using the *twist* gene as a mesodermal marker, they found that the mesodermal fate of the blastomere called the 4d cell - which is normally to make mesoderm - is not fully determined, but instead depends on further cell division taking place. If cell division is inhibited, *twist* is not expressed and the mesoderm derived from this cell is never generated. This finding corroborates previous reports of considerable temporal and spatial plasticity in spiralian mesoderm formation.

Mark Martindale (Kewalo Marine Laboratory, University of Hawaii, USA) came to similar conclusions on the basis of a survey of mesoderm formation in various spiralian groups. Comparing the blastomeres that produce the second type of spiralian mesoderm, the so-called ectomesenchyme, Martindale and co-workers observed a great deal of plasticity. By extending the mesodermal cell-lineage studies to the phoronids - a phylum that form an outgroup to the spiralian within the Lophotrochozoa - Martindale has found that the lophotrochozoan mesoderm always arises at the interface between ectoderm and endoderm but that the contributions of individual blastomeres can vary. Interestingly, the same plasticity also holds true for the eye-forming blastomeres, as evidenced by the non-canonical origin of the eye behind the prototroph, an equatorial ciliated band, in the trochophore larva of chitons (a type of mollusc).

Finally, Svetlana Maslakova (George Washington University, Washington DC, USA) presented a pioneering study on the fascinating development of the nemerteans or ribbon worms, another group of mostly marine, spiralian worms, recognized by the presence of an eversible proboscis. The nemertean pilidium larva is unique among lophotrochozoans in that the adult body develops from imaginal discs and 'hatches' via a drastic metamorphosis. So far, the evolutionary origin of this larva has been enigmatic. By studying the larva of a basal nemertean species, *Carinoma tremaphoros*,

Maslakova has now revealed clear affinities to the prototype spiralian trochophore larva. She proposed that development with a modified trochophore is ancestral for nemerteans and that development with drastic metamorphosis is derived. This study impressively illustrated the richness and surprises that the study of spiralian evolution and development has in store.

This meeting on the developmental basis of evolutionary change, a continuation of the 1999 and 2001 conferences of the same name, was again a clear success in assembling a good part of the world's community of evolutionary developmental biologists. The program is available at the conference website [<http://evodevo.bsd.uchicago.edu/index.html>]