Evolutionary biology

The ancestry of segmentation

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Until recently, most evolutionary biologists would have agreed that the segments of an arthropod, such as an insect, and of the backbone of a vertebrate were independent ('convergent') solutions to a functional need for building bilaterally symmetrical body plans using modular units. The work reported by Linda Holland and colleagues in the May issue of *Development*¹ is bound to change that view.

Holland and colleagues find that a homologue of the *engrailed* gene is expressed in the posterior half of each of the first eight segments (somites) of amphioxus (Fig. 1). In *Drosophila*, the *engrailed* gene encodes a DNA-binding protein that specifies the posterior compartment of each segment. Amphioxus has a notochord but not vertebrae, and is very useful in evolutionary studies because it appears to have retained many of the characteristics of the archetypal chordate ancestor that gave rise to the vertebrates². The fact that *engrailed* is expressed in both *Drosophila* and chordate metameres¹ tells us that segmentation was present in the common ancestor from which the insect and chordate lineages diverged 500 million years ago,

Figure 1 Expression of *engrailed* mRNA in the posterior portion of each of the five somites that have been formed in a 12-hour amphioxus embryo. The sixth stripe is in the somite that is about to be formed in the posterior (to the right). (Photo courtesy of Linda Holland, from ref. 1.)

the Urbilateria (Ur, primaeval; Bilateria, bilateral animal)³. The report on amphioxus *engrailed* follows soon after the discovery of *her1*, a homologue of the hairy DNA-binding protein that is expressed in every other forming somite in the zebrafish⁴. In *Drosophila*, *hairy* is a 'pair-rule' gene required for the formation of alternating segments. The pair-rule expression of *her1* in zebrafish led Kimmel to propose that Urbilateria was segmented⁵.

The Nobel prize-winning screen for *Drosophila* embryonic lethal mutations⁶ provided researchers with many pair-rule and segment-polarity genes, but their homo-

logues were not implicated in the formation of vertebrate somites. In fact, many homologues of *Drosophila* segment-polarity genes (such as *engrailed*, *wingless*, *armadillo*, *hedgehog* and *patched*) have been found to have other functions in vertebrates, such as the formation of the midbrain–hindbrain border and dorsoventral patterning of the neural tube. The new work¹ will undoubtedly stimulate a second, hard look for expression of these homologues in forming somites in regions such as the tailbud of the vertebrate embryo.

In zebrafish, chick and mouse, *engrailed* homologues are expressed in subsets of cells in the somites^{7,8}, but only after somites have been formed. This is different from amphioxus *engrailed* or zebrafish *her1*, which form bands of expression before morphological signs of segmentation are detectable^{1,4}. There are three *engrailed* genes in zebrafish and only one in amphioxus^{1,7}. Although one could argue that an as yet undiscovered *engrailed* homologue might explain the failure to detect early expression, it is more likely that the differences from amphioxus are due to the mode of somite formation. Amphioxus has 50 or more somites but the *engrailed* bands are observed only in the first eight, which are formed by a primitive mechanism by which epithelial outpockets are pinched off the primitive gut ('enterocoely'), whereas more posterior somites are formed from mesenchymal cell blocks which are then subdivided into seg-

Evolving protostomes and deuterostomes

Zoologists classify bilateral animals that possess a coelomic cavity into two fundamental groups: the protostomes – such as arthropods, annelids and molluscs; and the deuterostomes – such as echinoderms and chordates (chordates include ascidians, amphioxus and vertebrates). In protostomes, the mouth is formed at or close to the initial site (proto, first; stomo, mouth) of the blastopore, the site at which the endomesoderm, shown here in mauve, involutes into the interior of the embryo. In many protostomes the anus is formed at the blastopore as well. In deuterostomes, the mouth is formed secondarily (deutero, second) by a perforation of the ectoderm, and the anus is formed at or close to the site of the original blastopore. In addition, most protostomes have a ventral nerve cord which is traversed by the mouth and connects to a supraesophageal ganglion (brain) in the anterior. In most deuterostomes the central nervous system (CNS, in red) is dorsal and is not traversed by the gut. There are other differences, but these suffice for the present discussion.

Developmental studies suggest that protostomes and deuterostomes had a

common ancestor that was complex and segmented, raising the question of how such different body plans evolved. We of course do not know how the adult Urbilateria looked; it could have had either an open gut/blastopore (not shown) or it could have resembled an adult protostome or deuterostome (bottom diagrams). However, by modifying the blastopore during gastrulation it is possible to envisage how the transition could have happened, provided one assumes that the CNS is formed near the blastopore⁹.

As shown in the figure, in protostomes such as annelids the slit-

like ventral blastopore gives rise to the mouth and anus by closing along its central portion. The fusion of the lateral blastopore lips results in the dorsoventral inversion of the CNS, generating posteriorly a nerve cord ventral to the gut, and anteriorly a supraesophageal ganglion (bottom left). In deuterostomes the anterior part of the blastopore, corresponding to the mouth, does not form at all and endomesodermal involution takes place from the posterior, eventually leading to formation of the anus. The CNS is induced in nearby ectoderm by proteins secreted by the invaginating endomesoderm, and by the end of gastrulation the deuterostome mouth is perforated secondarily, with the gut and CNS remaining in different sides of the animal throughout their length. The deuterostome depicted here is a frog tadpole, which if inverted would adopt its normal dorsoventral position. Thus, although the Urbilateria ancestor was complex in its adult form (presumably having segments, heart, eyes and appendages), the potential to give rise to widely divergent body plans resided in its mechanisms of embryonic development. **E.M.DeR.**