

Gastrulation in Tunicates

Tunicates, like sea urchins and vertebrates, follow the deuterostome pattern of gastrulation in which the blastopore becomes the anus. Tunicate gastrulation is characterized by the invagination of the endoderm, the involution of the mesoderm, and the epiboly of the ectoderm. About 4–5 hours after fertilization, the vegetal (endoderm) cells assume a wedge shape, expanding their apical margins and contracting near their vegetal margins. The A8.1 and B8.1 blastomere pairs appear to lead this invagination into the center of the embryo. The invagination forms a blastopore whose lips will become the mesodermal cells. The presumptive notochord cells are now on the anterior portion of the blastopore lip, while the presumptive tail muscle cells (from the yellow crescent) are on the posterior lip. The lateral lips comprise those cells that will become mesenchyme.

The second step of gastrulation involves the involution of the mesoderm. The presumptive mesoderm cells involute over the lips of the blastopore and, by migrating over the basal surfaces of the ectodermal cells, move inside the embryo. The ectodermal cells flatten and epiboly over the mesoderm and endoderm, eventually covering the embryo. After gastrulation is complete, the embryo elongates along its anterior-posterior axis. The dorsal ectodermal cells that are the precursors of the neural tube invaginate into the embryo and are enclosed by neural folds. This process forms the neural tube, which will form a brain anteriorly and a spinal chord posteriorly. Meanwhile, the presumptive notochord cells on the right and left sides of the embryo migrate to the midline and interdigitate to form the notochord. The 40 cells of the notochord rearrange themselves from a 4 × 10 sheet of cells into a single row of 40 cells, extending the body axis along the anterior-posterior dimension (Figure 1; Jiang et al. 2005). This intercalation and migration of notochord cells is another example of convergent extension, a phenomenon seen throughout development. Indeed, the convergent extension of notochordal precursor cells is characteristic of all chordates.

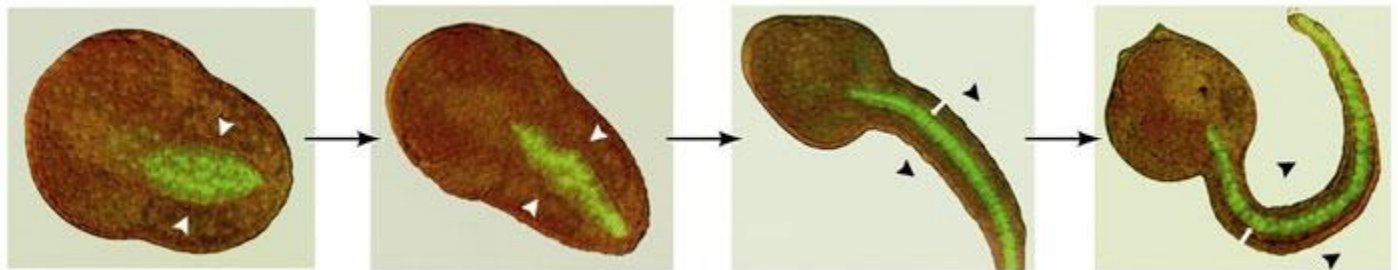


Figure 1 Convergent extension of the tunicate notochord. The notochord is visualized by a green fluorescent protein (GFP) probe fused to a promoter of the *Brachyury* gene, which is usually expressed in the notochord. The notochordal precursor cells converge and extend the notochord down the length of the animal's tail. (From Deschet et al. 2003, courtesy of the authors.)

The muscle cells of the tunicate tail differentiate on either side of the neural tube and notochord (Jeffery and Swalla 1997). This forms the tadpole-like body of the larva (see the final panel of Figure 2). At the 110-cell stage, the B7.5 blastomere pairs express the conserved heart transcription factor *Mesp*. The anterior daughters of these B7.5 blastomeres respond to FGF signals to activate the cytoskeletal genes responsible for migration as well as the genes responsible for heart differentiation. These two cells migrate to form two regions of cardiac mesoderm on the left and right ventral sides of the tadpole, just anterior to the tail. Like the heart precursor cells of vertebrate embryos, these two cell clusters migrate to meet at the ventral midline of the larva (Davidson and

Levine 2003; Satou et al. 2004; Christiaen et al. 2008). After metamorphosis, they will form the functional heart of the adult. During this metamorphosis, the tail and brain degenerate and the tunicate no longer moves.ⁱ

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ⁱ Such a process, according to neurobiologist Rudolfo Llinás (1987) is “paralleled by some human academics obtaining university tenure.”