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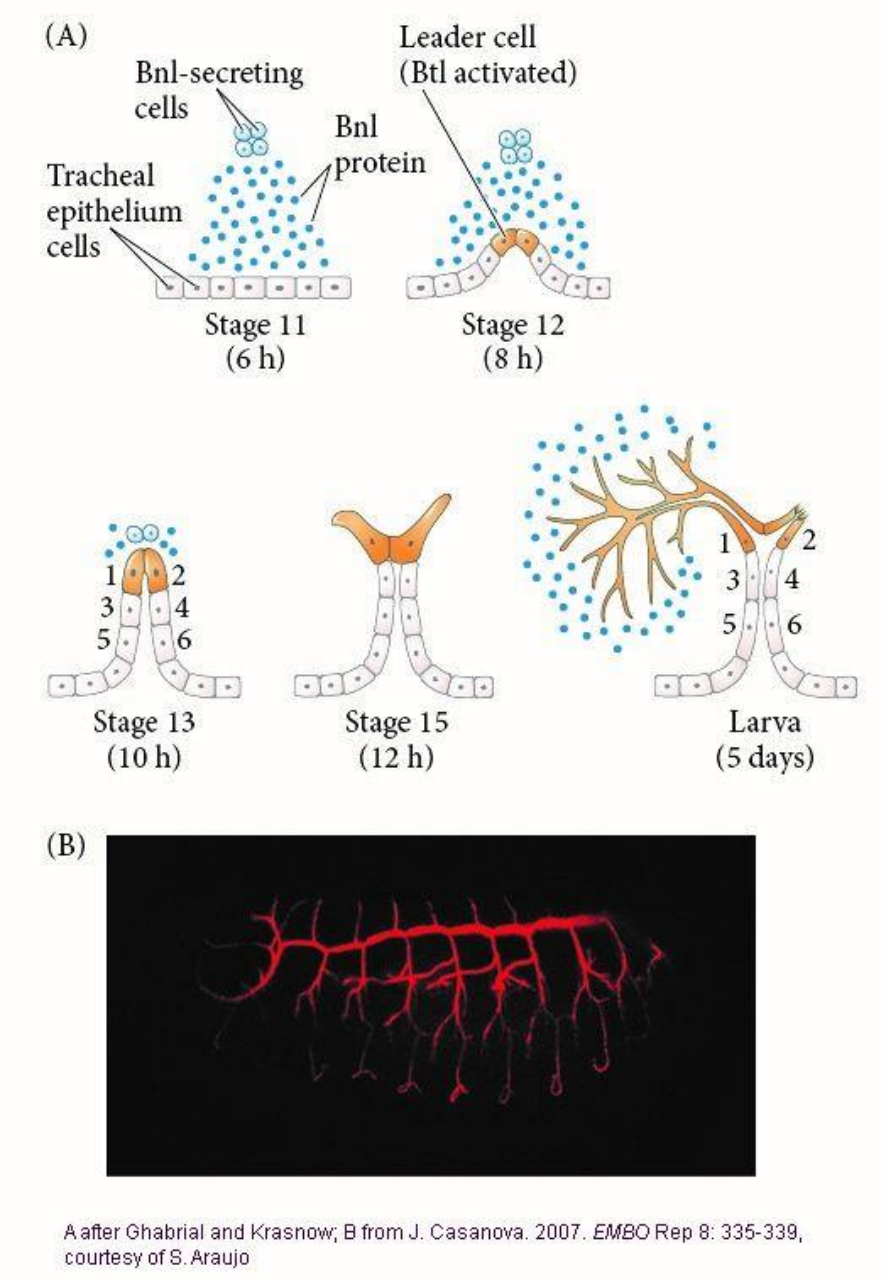
The Insect Trachea: Combining Inductive Signals with Cadherin Regulation

Earlier in this chapter we talked about the shared role of cadherins and actinomyosin cortical contraction in mediating cell-to-cell adhesions involved in tissue morphogenesis. Instructions from outside the cell can influence cell shape change through modulation of the cadherin-actinomyosin mechanism. For instance, the tracheal (respiratory) system in *Drosophila* embryos develops from epithelial sacs. The approximately 80 cells in each of these sacs become reorganized into primary, secondary, and tertiary branches without any cell division or cell death (Ghabrial and Krasnow 2006). This reorganization is initiated when nearby cells secrete a protein called Branchless, which acts as a chemoattractant (usually a diffusible molecule that attracts a cell to migrate along an increasing concentration gradient toward the source secreting the factor).[i] Branchless binds to a receptor on the cell membranes of the epithelial cells. The cells receiving the most Branchless protein lead the rest, whereas the followers (connected to one another by cadherins) receive a signal from the leading cells to form the tracheal tube (Figure 1). It is the lead cell that will change its shape (by rearranging its actin-myosin cytoskeleton via a Rho GTPase-mediated process) to migrate and form the secondary branches. During this migration, cadherin proteins are regulated such that the epithelial cells can migrate over one another to form a tube while keeping their integrity as an epithelium (Cela and Llimagas 2006).



A after Ghabrial and Krasnow; B from J. Casanova. 2007. *EMBO* Rep 8: 335-339, courtesy of S. Araujo

Figure 1 Tracheal development in *Drosophila.* (A) Diagram of dorsal tracheal branch budding from tracheal epithelium. Nearby cells secrete Branchless protein (Bnl; blue dots), which activates Breathless protein (Btl) on tracheal cells. The activated Btl induces migration of the leader cells and tube formation; the dorsal branch cells are numbered 1 through 6. Branchless also induces unicellular secondary branches (stage 15). (B) Larval *Drosophila* tracheal system visualized with a fluorescent red antibody. Note the intercalated branching pattern. (A after Ghabrial and Krasnow 2006; B from Casanova 2007.)

Another external force is also at work, however. The dorsalmost secondary branches of the sacs move along a groove that forms between the developing muscles. These tertiary cell migrations cause the trachea to become segmented around the musculature (Franch-Marro and Casanova 2000). In this way, the respiratory tubes are placed close to the larval musculature.

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[i]There are also *chemorepulsive* factors that send the migrating cells in an opposite direction. Generally speaking, chemotactic factors—soluble factors that cause cells to move in a particular direction—are assumed to be chemoattractive unless otherwise described.