S6

Directed dilation

Hydrostatic pressure can provide the force for morphogenesis in various situations. We have already seen how an increase in hydrostatic pressure inside the mammalian blastocyst causes an increase in volume and maintains the blastocyst in a roughly spherical shape (see Section 7.8). Here, we consider examples of **directed dilation**, where an increase in internal hydrostatic pressure causes a distinct asymmetric change in shape as a result of the particular properties of the structure. For example, if the circumferential resistance of a stretchable tube to internal pressure is much greater than the resistance lengthways, then an increase in the internal pressure will cause an increase in length (Fig. S6.1).

S6.1 Later extension and stiffening of the notochord occurs by directed dilation

After the *Xenopus* notochord has formed, its volume increases threefold, and there is considerable further lengthening as it straightens and becomes stiffer. At this stage, the notochord has become surrounded by a sheath of extracellular material, which because of its molecular structure restricts circumferential expansion but does allow expansion in the antero-posterior direction. The flat cells within the notochord develop fluid-filled vacuoles and the rod of cells expands in volume in an antero-posterior direction. Cells are initially flat and are restricted in the direction in which they swell by junctional connections, with the result that cell expansion is exerting force lengthways along the notochord. The sheath contains helically wound collagen fibrils, which make it resistant to outward expansion but make it elastic as well, and so it can lengthen. The hydrostatic pressure exerted by the cells, combined with the composition of the sheath enables the notochord to undergo directed dilation. Circumferential expansion of the notochord is prevented by the resistance of the sheath, and this ensures that the increase in volume (dilation) is directed along the notochord's long axis, enabling the notochord to lengthen, straighten and stiffen without buckling.

The vacuoles in the notochord cells are filled with glycosaminoglycans which, because of their high carbohydrate content, tend to attract water into the vacuoles by osmosis. This produces the hydrostatic pressure that causes the increase in cell volume, and the consequent stiffening and straightening of the notochord. Changes in the structure of the sheath during the period of notochord elongation fit well with the proposed hydrostatic mechanism. The sheath contains both glycosaminoglycans, which have little tensile strength, and the fibrous protein collagen, which has a high tensile strength; during notochord dilation the number of collagen fibers increases, providing resistance to circumferential expansion. The crucial role of the sheath in dilation and elongation is shown by the fact that if it is digested away, the notochord buckles and folds and the notochord cells, instead of being flat, become rounded.

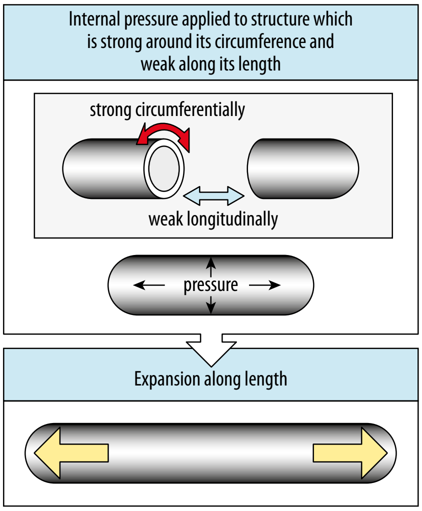

Fig. S6.1 Directed dilation. Hydrostatic pressure inside a constraining sheath or membrane can lead to elongation of the structure. If the circumferential resistance is much greater than the longitudinal resistance, as it is in the notochord sheath, the rod of cells inside the sheath lengthens.

S6.2 Circumferential contraction of hypodermal cells elongates the nematode embryo

During the early development of the nematode there is little change in body shape from the ovoid form of the fertilized egg, even during gastrulation. After gastrulation, about 5 hours after fertilization, the embryo begins to elongate rapidly along its antero-posterior axis. Elongation takes about 2 hours, during which time the embryo decreases in circumference about threefold and undergoes a fourfold increase in length.

This elongation is brought about by a change in shape of the hypodermal (epidermal) cells that make up the outermost layer of the embryo; their destruction by laser ablation prevents elongation. During embryo elongation, these cells change shape so that, instead of being elongated in the circumferential direction, they become elongated along the antero-posterior axis (Fig. S6.2). Throughout this elongation the hypodermal cells remain attached to each other by cell junctions. The junctions are also linked within the cells by actin-containing fibers that run circumferentially, and these fibers appear to shorten as the cells elongate. The disruption of actin filaments and inhibition of actin polymerization by cytochalasin D treatment blocks elongation, and so it is very likely that the contraction of the actin-containing fibers brings about the change in cell shape. Circumferential contraction of the hypodermal cells causes an increase in hydrostatic pressure within the embryo, forcing an extension in an antero-posterior direction. Circumferentially oriented microtubules may also have a mechanical role in constraining the expansion, in the same way as the sheath of the *Xenopus* notochord described earlier. Increase in nematode body length is thus another example of directed dilation.

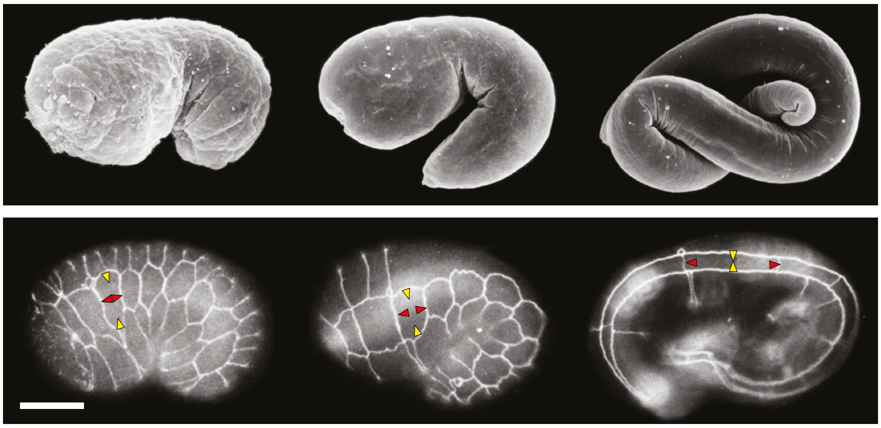

Fig. S6.2 Increase in nematode body length by directed dilation. The change in body shape over 2 hours is illustrated in the top panel. The increase in length is due to circumferential contraction of the hypodermal cells, as shown in the bottom panel. The change in shape of a single cell can be seen in the cell marked with arrows. Scale bar = 10 μm. Photographs reproduced with permission from *Priess, J.R., Hirsh, D.I.:* Caenorhabditis elegans **morphogenesis: the role of the cytoskeleton in elongation of the embryo**. Dev. Biol. *1986,* **117***: 156–173. © 1986 Academic Press.*

SUMMARY

Directed dilation results from an increase in hydrostatic pressure inside a structure, and unequal peripheral resistance to this pressure. Extension of the notochord is brought about by directed dilation. The notochord interior increases in volume while its circumferential expansion is constrained by the notochord sheath, forcing it to elongate. Similarly, the nematode embryo elongates after gastrulation as a result of a circumferential contraction of the outer hypodermal cells that generates pressure on the internal cells, forcing the embryo to extend in an antero-posterior direction.

S6.1 Later extension and stiffening of the notochord occurs by directed dilation

Adams, D.S., Keller, R., Koehl, M.A.: **The mechanics of notochord elongation, straightening and stiffening in the embryo of *Xenopus laevis***. *Development* 1990, **110**: 115–130.

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