

The Terminal Gene Group

In addition to the anterior and posterior morphogens, there is a third set of maternal genes whose proteins generate the unsegmented extremities of the anterior-posterior axis: the acron (the terminal portion of the head that includes the brain) and the telson (tail). Mutations in these terminal genes result in the loss of the acron and the most anterior head segments as well as the telson and the most posterior abdominal segments (Degelmann et al. 1986; Klingler et al. 1988).

A critical gene here appears to be *torso*, a gene encoding a receptor tyrosine kinase (RTK; see Chapter 3). The embryos of mothers with mutations of *torso* have neither acron nor telson, suggesting that the two termini of the embryo are formed through the same pathway. The *torso* mRNA is synthesized by the ovarian cells, deposited in the oocyte, and translated after fertilization. The transmembrane Torso protein is not spatially restricted to the ends of the egg but is evenly distributed throughout the cell membrane (Casanova and Struhl 1989). Indeed, a gain-of-function mutation of *torso*, which imparts constitutive activity to the receptor, converts the entire anterior half of the embryo into an acron and the entire posterior half into a telson. Thus, Torso must normally be activated only at the ends of the egg.

Stevens and her colleagues (1990) have shown that this is the case. Torso protein is activated by the follicle cells only at the two poles of the oocyte. Two pieces of evidence suggest that the activator of Torso is probably the Torsolike protein: first, loss-of-function mutations in the *torsolike* gene create a phenotype almost identical to that produced by *torso* mutants; and second, ectopic expression of Torsolike protein activates Torso in the new location.

The *torsolike* gene is usually expressed only in the anterior and posterior follicle cells, and secreted Torsolike protein can cross the perivitelline space to activate Torso in the egg membrane (Martin et al. 1994; Furriols et al. 1998). In this manner, Torsolike activates Torso in the anterior and posterior regions of the oocyte membrane.

The end products of the RTK cascade activated by Torso diffuse into the cytoplasm at both ends of the embryo. These kinases are thought to inactivate the Capicua protein, a transcriptional repressor of the *tailless* and *huckebein* gap genes (Ajuria et al. 2011); it is these two gap genes that specify the termini of the embryo. The distinction between the anterior and posterior termini depends on the presence of Bicoid. If *tailless* and *huckebein* act alone, the terminal region differentiates into a telson. However, if Bicoid is also present (at the anterior end), the terminal region forms an acron (Pignoni et al. 1992).

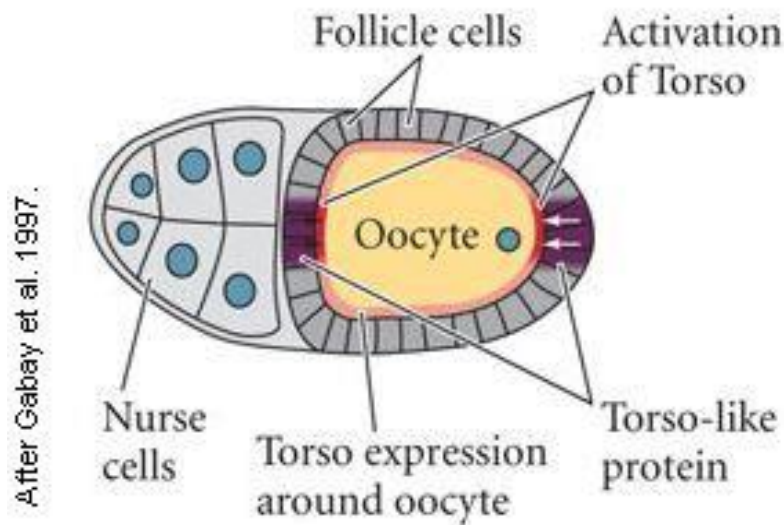


Figure 1 Formation of the unsegmented extremities by Torso signaling. Torsolike protein is expressed by the follicle cells at the poles of the oocyte. Torso protein is uniformly distributed throughout the cell membrane of the oocyte. Torsolike activates Torso at the poles (see Casanova et al. 1995).

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