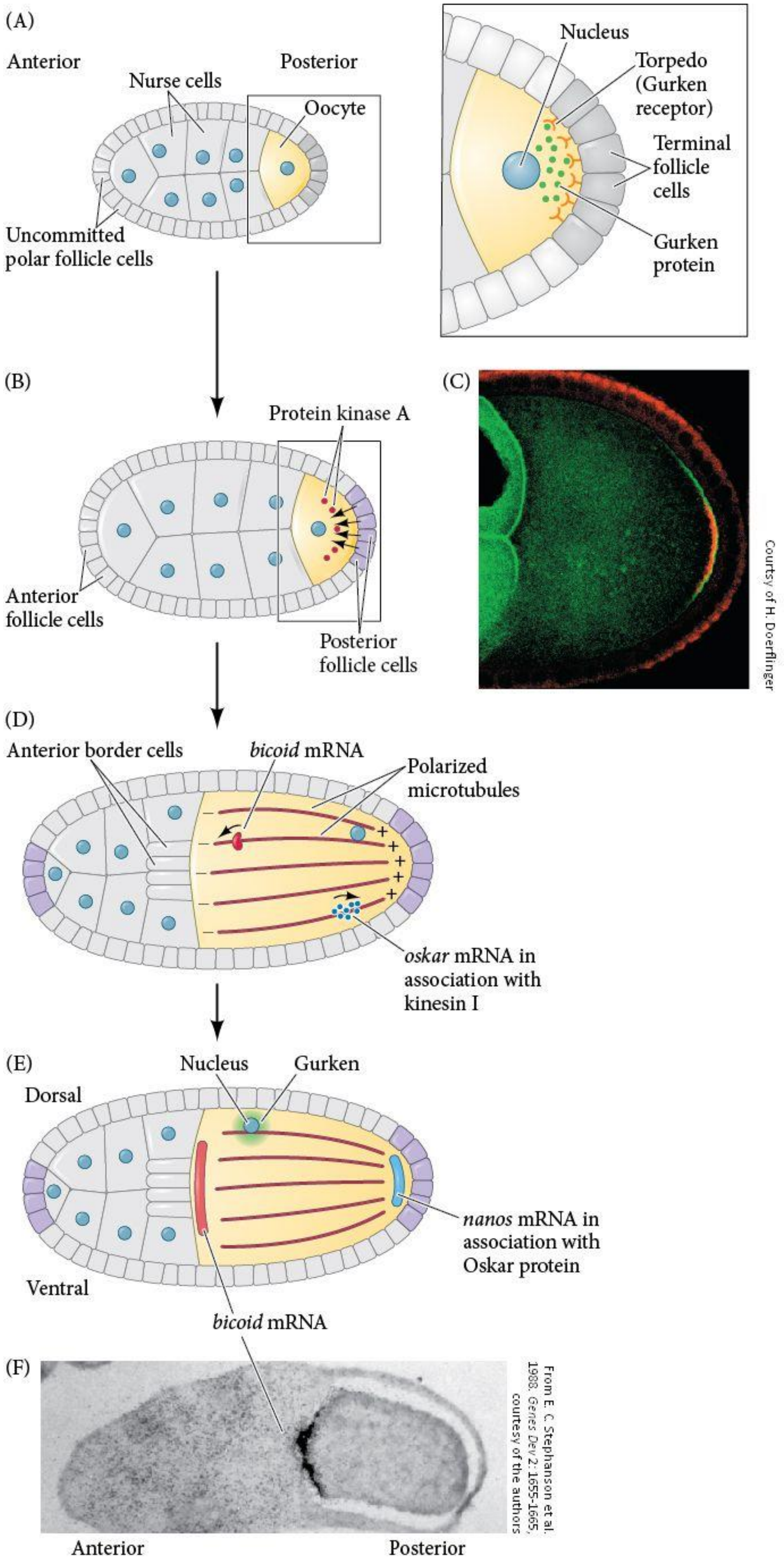
<Further Development 10_03>

Anterior-Posterior Polarity in the Oocyte

The anterior-posterior polarity of the embryo is established while the oocyte is still in the egg chamber, and it involves interactions between the developing egg cell and the follicular cells that enclose it. The follicular epithelium surrounding the developing oocyte is initially uniform with respect to cell fate, but this uniformity is broken by two signals organized by the oocyte nucleus. Interestingly, both of these signals involve the same gene, *gurken*. The *gurken* message appears to be synthesized in the nurse cells, but it is transported into the oocyte. Here it becomes localized between the oocyte nucleus and the cell membrane, and it is translated into Gurken protein (Cáceres and Nilson 2005). At this time the oocyte nucleus is very near what will become the posterior tip of the egg chamber, and the Gurken signal is received by the follicle cells at that position through a receptor protein encoded by the *torpedo* gene[i] (Figure 1A). This signal results in the "posteriorization" of these follicle cells (Figure 1B). The posterior follicle cells send a signal back into the oocyte. This signaling activates a lipid kinase that recruits the Par-1 protein to the posterior edge of the oocyte cytoplasm (Figure 1A; Doerflinger et al. 2006; Gervais et al. 2008). Par-1 protein organizes microtubules specifically with their minus (cap) and plus (growing) ends at the anterior and posterior ends of the oocyte, respectively (Gonzalez-Reyes et al. 1995; Roth et al. 1995; Januschke et al. 2006).

The orientation of the microtubules is critical, because different microtubule motor proteins will transport their mRNA or protein cargoes in different directions. The motor protein kinesin, for instance, is an ATPase that will use the energy of ATP to transport material to the plus end of the microtubule. Dynein, however, is a "minus-directed" motor protein that transports its cargo in the opposite direction. One of the messages transported by kinesin along the microtubules to the posterior end of the oocyte is *oskar* mRNA (Zimyanin et al. 2008). The *oskar* mRNA is not able to be translated until it reaches the posterior cortex, at which time it generates the Oskar protein. Oskar recruits more Par-1 protein, thereby stabilizing the microtubule orientation and allowing more material to be recruited to the posterior pole of the oocyte (Doerflinger et al. 2006; Zimyanin et al. 2007). The posterior pole will thereby have its own distinctive cytoplasm, called pole plasm, which contains the determinants for producing the abdomen and the germ cells.

This cytoskeletal rearrangement in the oocyte is accompanied by an increase in oocyte volume, owing to transfer of cytoplasmic components from the nurse cells. These components include maternal messages such as the *bicoid* and *nanos* mRNAs. These mRNAs are carried by motor proteins along the microtubules to the anterior and posterior ends of the oocyte, respectively (Figure 1D-F). The protein products encoded by *bicoid* and *nanos* are critical for establishing the anterior-posterior polarity of the embryo.



Courtsy of H. Doerflinger

From E. C. Stephanson et al. 1988. *Genes Dev* 2: 1655–1665, courtesy of the authors

Figure 1 The anterior-posterior axis is specified during oogenesis. (A) The oocyte moves into the posterior region of the egg chamber, while nurse cells fill the anterior portion. The oocyte nucleus moves toward the terminal follicle cells and synthesizes Gurken protein (green). The terminal follicle cells express Torpedo, the receptor for Gurken. (B) When Gurken binds to Torpedo, the terminal follicle cells differentiate into posterior follicle cells and synthesize a molecule that activates protein kinase A in the egg. Protein kinase A orients the microtubules such that the growing (plus) ends are at the posterior (depicted in panel D). (C) Par-1 protein (green) localizes to the cortical cytoplasm of nurse cells and to the posterior pole of the oocyte. (The Staufen protein marking the posterior pole is labeled red; the red and green signals combine to fluoresce yellow.) (D) *bicoid* mRNA binds to dynein, a “minus-directed” motor protein associated with the non-growing end of microtubules; dynein moves the *bicoid* mRNA to the anterior end of the egg. *oskar* mRNA becomes complexed to kinesin I, a “plus-directed” motor protein that moves it toward the growing end of the microtubules at the posterior region, where Oskar protein can bind *nanos* mRNA. (E) The nucleus (with its associated Gurken protein) migrates along the microtubules to the dorsal anterior region of the oocyte and induces the adjacent follicle cells to become the dorsal follicle cells. (F) Photomicrograph of *bicoid* mRNA (stained black) passing from the nurse cells and localizing to the anterior end of the oocyte during oogenesis.

Literature Cited

Cáceres, L., L. A. Nilson. 2005. Production of gurken in the nurse cells is sufficient for axis determination in the *Drosophila* oocyte. *Development* 132(10):2345-53.
PubMed Link

Doerflinger, H., R. Benton, I. L. Torres, M. F. Zwart and D. St. Johnston. 2006.*Drosophila* anterior-posterior polarity requires actin-dependent PAR-1 recruitment to the oocyte posterior. *Curr. Biol.* 16(11): 1090–1095.
PubMed Link

Gervais, L., S. Claret, J. Januschke, S. Roth, and A. Guichet. 2008. PIP5K-dependent production of PIP2 sustains microtubule organization to establish polarized transport in the *Drosophila* oocyte. *Development* 135: 3829–3838.
PubMed Link

Gonzalez-Reyes, A., H. Elliott and D. St. Johnson. 1995. Polarization of both major body axes in *Drosophila* by gurken-torpedo signalling. *Nature* 375: 654–658.
PubMed Link

Januschke, J., L. Gervais, L. Gillet, G. Keryer, M. Bornens and A. Guichet. 2006. The centrosome nucleus complex and microtubule organization in the *Drosophila* oocyte. *Development* 133: 129–139.
PubMed Link

Roth, S., F. S. Neuman-Silberberg, G. Barcelo and T. Schüpbach. 1995.*cornichon* and the EGF receptor signaling process are necessary for both anterior-posterior and dorsal-ventral pattern formation in *Drosophila*. *Cell* 81: 967–978.
PubMed Link

Stephanson, E. C., Y.-C. Chao and J. D. Frackenthal. 1988. Molecular analysis of the swallow gene of *Drosophila melanogaster*. *Genes Dev.* 2: 1655–1665.
PubMed Link

Zimyanin, V., N. Lowe, D. St. Johnston. 2007. An oskar-dependent positive feedback loop maintains the polarity of the *Drosophila* oocyte. *Curr Biol* 17(4):353-9.
PubMed Link

Zimyanin, V. L., K. Belaya, J. Pecreaux, M. J. Gilchrist, A. Clark, I. Davis and D. St. Johnston. 2008. In vivo imaging of *oskar* mRNA transport reveals the mechanism of posterior localization. *Cell* 134(5): 843–853.
PubMed Link

---

[i] Gurken protein is a member of the EGF (*e*pidermal *g*rowth *f*actor) family, and `torpedo` encodes a homologue of the vertebrate EGF receptor (Price et al. 1989; Neuman-Silberberg and Schüpbach 1993).