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Oogenesis is the process of forming the female gamete, i.e., the ovum or egg. In *Caenorhabditis elegans*, gametes derive from a tissue called the germ line, which is specified early in embryonic development. Two major events occur during oogenesis: the oocyte precursor germ cell undergoes meiotic division and it accumulates substantial cytoplasm. In meiosis, two sequential rounds of cell division produce a haploid egg, with only one copy of each chromosome, from the diploid oocyte precursor cell. Simultaneously, a large volume of cytoplasm is accumulated; it contains yolk and numerous other components that are essential for early embryonic development. Meiotic progression seems to be an integral part of oogenesis, since a number of proteins are required meiotic progression and for the development of functional oocytes. For example, GLD-1, an RNA-binding protein, is required for maintenance of oocyte precursors in pachytene stage (see below); in its absence, female germ cells will enter meiosis and progress to pachytene stage, but then exit meiosis and return to mitotic proliferation. In contrast, male germ cells do not require GLD-1 for meiosis and gametogenesis.

The *C. elegans* gonad is a U-shaped tube and has a distal-to-proximal polarity with respect to germline development. Germ cells at the distal end of the tube are proliferative (mitotic) and germ cells located more proximally are meiotic; sperm and mature oocytes are present at the proximal end. Certain somatic gonad cells, the distal tip cells, maintain a mitotic germ cell population in the distal gonad by signaling the germ line to proliferate. Most of the *C. elegans* germ line is technically a syncytium with nuclei arranged toward the outside and a common cytoplasmic core that is critical for oogenesis. However, each nucleus is associated with local cytoplasm and partially enclosed by a plasma membrane; therefore, for ease of description, it is often referred to as a germ 'cell.' The *C. elegans* hermaphrodite produces sperm during mid-late larval development and abruptly begins to produce oocytes at approximately the time of the larval-to-adult molt; oogenesis continues throughout adulthood. Conse-

quently, the hermaphrodite germ line is considered to be male during larval development and become female just prior to the adult molt through the regulation of a set of sex determination genes. Oocyte precursors located just proximal to the distal proliferative region enter meiosis and proceed fairly rapidly through early meiotic stages (leptotene and zygotene stages of prophase I of meiosis). They progress very slowly through pachytene stage of prophase I during which time oocyte cytoplasmic contents are synthesized. By synthesizing components of the oocyte cytoplasm, the oocyte precursor cells also act as support cells; they are analogous to germline 'nurse' cells found in some other animal species.

The late-stage *C. elegans* oocyte has a cytoplasmic volume far larger than the average cell in the body. It contains materials essential for embryonic development in general and early embryogenesis in particular, including factors that facilitate metabolism and the rapid DNA replication and cell cleavages characteristic of early development. It also includes specialized proteins and messenger RNAs required for setting up the embryonic body plan and distinguishing the fate of various early embryonic cells. Evidence suggests that many of these components are synthesized by pachytene germ cells and are moved into the common cytoplasmic core, which is eventually included in the growing oocytes. In contrast, yolk proteins are synthesized in the intestine (see below).

Most developing oocytes located at and proximal to the bend in the gonad exit pachytene stage and proceed further through meiosis to diakinesis stage of prophase I. They also begin to change morphologically, becoming progressively larger and eventually taking on the block-like morphology of mature oocytes. Most of this growth occurs while cells are in diakinesis. Other oocyte precursors at the bend do not develop further, but instead undergo programmed cell death, perhaps to provide room for the remaining oocytes to grow. In the loop region and proximal gonad, cells of the somatic gonad, the 'sheath' cells, form an epithelium that encloses the germ line and regulates oogenesis in at least two ways. First, together with cells in distal spermatheca, the sperm storage vesicle, sheath cells appear to signal meiotic progression beyond pachytene stage. Signaling may be accomplished via gap junctions that are observed between sheath cells and maturing oocytes. Progression past the pachytene stage also depends on MAPK signaling in the germ line, which is perhaps triggered by the proximal sheath cell/distal spermathecal signal. Second, the proximal sheath cells act as an oviduct. Contractions of the sheath cell epithelium, together with dilation of the spermatheca, allow oocytes to be ovulated and subsequently fertilized. Evidence

suggests that the oocyte may actively regulate ovulation by modulating sheath cell contractions and by signaling spermathecal dilation. Sheath cells may also play a role in yolk uptake. Yolk proteins are synthesized in the intestine and transported to the proximal gonad as yolk particles. They are taken up by oocytes in the proximal gonad through specialized pores in the sheath cells.

As the proximal-most oocyte completes differentiation, it pinches off from the syncytium and is ovulated into the spermatheca where it is fertilized. At ovulation, the oocyte is triggered to complete meiosis by interaction with sperm cells. In the absence of sperm cells (e.g., in an old hermaphrodite that is purged of sperm), oocytes do not progress beyond diakinesis. As the oocyte fuses with a sperm cell, it resumes meiotic progression and undergoes the two rounds of meiotic cell division. To preserve the large egg volume, these divisions are extremely asymmetric: the first division (MI) produces a large diploid oocyte and a tiny diploid polar body; the second division (MII) produces a large haploid oocyte and a tiny haploid polar body. The haploid oocyte and sperm nuclei (technically called pronuclei) can now fuse, allowing fertilization to be completed. A protective eggshell is subsequently deposited on the egg.

Systematic screens for oogenesis-defective mutants have not been carried out in *C. elegans*, but oogenesis is clearly a complex process that depends on a wide variety of gene products. Mutations in *gld-1* and components of the MAPK signaling pathway disrupt meiotic progression. Mutations in many genes will decrease the rate of ovulation, thereby disrupting

the normal process of oocyte maturation. Numerous other gene products have been identified that are important for production of functional oocytes, yet do not seem to regulate meiotic progression. These genes have oogenesis-defective (Oog) mutant phenotypes. In general, their primary function during germline development is not clear, but mutants produce small oocytes incapable of supporting embryonic development.

Further Reading

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See also: 0492, 0494, 0563, 0797, 0807