

Drosophila Oogenesis: An Elegant Model System in Cell and Developmental Biology

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Editorial

Oogenesis in Drosophila was initially studied as a model system to investigate the patterning of embryonic axis, however, it has since become a powerful model system for investigating various aspects of cellular, molecular and developmental biology. Oogenesis in Drosophila melanogaster is a complex developmental process which involves extensive cellular remodeling and communication [1-3]. The entire process of oogenesis occurs within Drosophila ovary which harbors 16 to 20 long tube-like structures known as ovarioles. These ovarioles are held together by an enveloping peritoneal sheath consists of a network of muscle fibers. Each ovariole represents an individual linear array of egg assembly, with younger egg chambers near the anterior and a series of progressively older egg chambers towards posterior end. Egg chamber, the functional unit of oogenesis is produced in the germarium which localizes at the anterior-most region of the ovariole. The development of the egg chamber in each ovariole has been subdivided into a series of 14 consecutive stages and the approximate age of an egg chamber can be determined by morphological features [1].

At the beginning of oogenesis, a stem cell residing at the tip of the germarium divides to produce two unequal daughters. One daughter cell remains a stem cell while the other daughter cell (cystoblast) undergoes four rounds of divisions with incomplete cytokinesis to generate a cyst of 16 interconnected cells. One of the 16 germline cells in a cyst differentiates into the oocyte while the other 15 become nurse cells [1]. The connective bridges of these germ cells are referred as ring canals. Ring canals exhibit stereotyped arrangement which connects the nurse cells with each other and with the growing oocyte. As the germline cyst moves through the germarium, it becomes enclosed by a layer of somatically derived follicle cells [1]. Subsequently, oocyte becomes positioned at the posterior of the germline cyst by a process mediated by several signaling events along with DE-cadherine and βcatenin dependent adhesion between oocyte and follicle cells [4,5]. Once differentiated, the developing oocyte nucleus becomes transcriptionally inactive, and therefore, most of the maternal products required for oocyte maturation and early embryogenesis are synthesized in the nurse cells and subsequently transported to the oocyte through the network of ring canals [6].

The follicular epithelium is a key player that participates in establishing both the anterior-posterior and dorsal-ventral egg axes [4]. The patterning of the follicular epithelium and polarization of the oocyte axis by differential localization of maternal mRNAs are achieved during oogenesis. Determination of oocyte involves multiple reciprocal communication events between the germline and somatic components of the egg chamber [7,8]. The oocyte polarity is defined by two signaling events, both of which are induced by the epidermal

growth factor receptor (Egfr) ligand, Gurken (Grk), associated with the oocyte nucleus [7,8]. Therefore, formation of proper dorsal ventral axis requires the controlled export of gurken mRNA from the nurse cells to oocyte, and thereafter, regulated distribution of the gurken RNA and protein at the antero-dorsal corner of the oocyte, ensuring precisely localized signaling [8]. The first Grk signal induces the follicle cells overlying the oocyte to take on posterior fate. The posterior follicle cells respond by sending an unidentified signal back to the oocyte. In response to this signal, the Microtubule Organizing Centre (MTOC) at the posterior of the oocyte disassembles and microtubules (MTs) nucleate from the anterior and lateral cortices of the oocyte [9,10]. This reorganization of the MT network is necessary for migration of the oocyte nucleus and associated Gurken to an antero-lateral position [11,12]. Thereafter, a second Gurken signal at stage 9 induces adjacent follicle cells to adopt dorsal fate. After determination of D/V axis, size of the oocyte rapidly increases. During advance stages (stage 10B onwards) of egg chamber development, the polyploid nurse cells contract and rapidly transfer the residual of their cytoplasmic contents to the oocyte. This process is referred to as "cytoplasmic dumping" [1,13].

During egg chamber development and axes determination, a dynamic cytoskeleton is critical for generating epithelial polarity, intercellular transport, stable intercellular bridges, cell migrations, cell shape changes, nurse cell contraction and specific subcellular localization of many oocyte-patterning determinants [13,14]. Mutations, which interfere with cytoskeletal integrity and arrangement of follicle cells, exhibit abnormalities in various aspects of oogenesis. Several genes such as armadillo, DE-cadherine, egghead, a- spectrin, merlin etc. are known to be required for maintenance of epithelial integrity during progression of oogenesis [15-18]. Mutations in junction-associated membrane proteins like Disk-large and Scribble also disrupt follicle cell proliferation and polarity [19,20]. In addition, several genes involved in actin biogenesis are also critically important for egg chamber development [13,21]. Taken together, Drosophila oogenesis has provided important insight of cellular functioning and development in the past and expected to continue to do so in the future.

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