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Evolution of maternal control of axial patterning in insects

Jeremy A Lynch

Positional and cell fate cues provided maternally to eggs are important factors in the development of many animals. The insects are a model clade where maternal establishment of embryonic axes is widespread and has been a topic of intense classical and molecular embryological analysis. Recently, significant progress has been made in revealing the molecular basis of some classical embryological experiments. In addition, observations of novel forms of maternal positional cues have been made. Finally, it has become increasingly clear that no maternal source of positional information acts alone without input and feedback from zygotic target genes to ensure precise and repeatable pattern formation in the early embryo. These advances will be discussed in the context of historical experiments, our current understanding of how positional cues can be generated, stored, and transmitted in insect ovaries and eggs, and how the nature of the cues can change in evolution.

Address

University of Illinois at Chicago, Chicago, IL, USA

Corresponding author: Lynch, Jeremy A (jlynch42@uic.edu)

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Unique features of insect ovaries

Insect ovaries have an anterior–posterior (AP) polarity that typically follows that of the female. Typically, a germline stem-cell resides at the anterior end (Figure 1a). When this stem cell divides to produce a gametic progenitor (Figure 1b), the latter moves posteriorly and begins differentiation. Repetition of this process leads to the production of a string of differentiating germ cells of increasing age from anterior to posterior. Thus, each developing oocyte is flanked by a younger oocyte progenitor at its anterior, and an older one to its posterior (Figure 1c,d). If this asymmetric information could be transmitted and stored, it would be a potent source of positional cues. That such transmission occurs was clear

well before the molecular era, as it was observed that the anterior–posterior polarity of insect eggs almost always is tightly correlated to the AP polarity of the ovariole [1,2].

Another intrinsic property of the insect oocyte is the asymmetric movement of the germinal vesicle (oocyte nucleus) from a symmetric position in the central column of cytoplasm (Figure 1d) to a highly asymmetric location at the plasma membrane (Figure 1e). This movement is necessary to prepare the oocyte nucleus for the resumption and completion of meiosis when the egg is laid and activated [3]. The importance of this movement was also strongly implied by early investigators, where it was observed that position of the oocyte nucleus very often marks the dorsal pole of the egg and embryo [4,5].

Crucially, there is a strong interaction between germline cells and somatic cells in the insect ovary. A single layer of somatic cells surrounds a single germline cell (Figure 1c–e), or a clone of sister germline cells, forming the functional unit of the insect ovary, the egg chamber. The somatic cells surrounding the germline cells are called follicle cells, and these cells can receive, store, and transmit positional information through communication among themselves and with the germ cells [2]. Since the follicle cells secrete the eggshell, information can be stored in structure of the eggshell layers, or in the fluid that separates the egg from the innermost eggshell layer. Thus, information can be passed to the developing embryos (Figure 1f), even after follicle cells are gone.

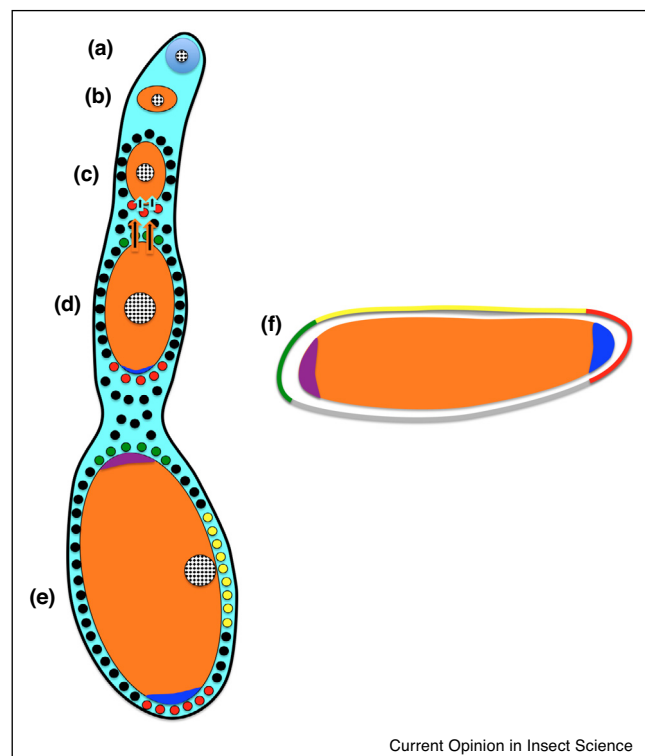
Finally, communication among the germline and somatic cells can lead to the polarization of the oocyte itself, allowing for the differential localization of macromolecules at different poles of the egg (Figure 1d,e), which are also maintained in the embryo (Figure 1f).

Maternal patterning information in *Drosophila melanogaster*

The molecular basis of maternal positional information has been intensively studied in insects, primarily in *D. melanogaster*. A relay system involving Jak/STAT and Notch signaling operates in the ovary to position the oocyte correctly within the egg chamber, and pass positional information from the older egg chambers to the newly specified oocyte [6]. This relay system leads to the establishment of AP polarity within the oocyte, and the proper localization of mRNA for the anterior determinant *bicoid* and posterior/germ cell determinant *oskar* at their respective poles. Localized *bcd* mRNA gives rise to a

2 Development and regulation

Figure 1



Generation and storage positional information in the insect ovary. Ovariole highly schematic to represent common features of all types of oogenesis. **(a)** Anteriorly localized germline stem cell. **(b)** Differentiating oocyte. **(c)** Oocyte surrounded by follicle cell layer (solid black circles). Blue arrows indicate oocyte receiving signals from specialized follicle cells (solid red circles), leading to polarization of the embryo. In this case, it is a hypothetical situation, drawn from knowledge gained from *D. melanogaster*. **(d)** Maturing egg chamber with polarized oocyte (indicated by posteriorly localized blue), sending signals (orange arrows) to anterior follicle cells (green), which in turn signal to the next younger oocyte to induce polarity (again a hypothetical mechanism). **(e)** Late stage egg chamber. The oocyte nucleus (black and white checkered circle) has migrated to the cortex, where it induces signaling to and differentiation of, the overlying follicle cells (yellow circles). **(f)** Schematic representation of a typical insect embryo, with regions of potential eggshell modification and embryonic RNA localization marked with colors corresponding to their origin the ovary (c-f).

87 gradient of protein that acts as a morphogen to establish
88 cell fates in the anterior half of the embryo. Oskar protein
89 is crucial for assembling the germplasm (which specifies
90 the primordial germ cells) and stabilizing *nanos* mRNA.
91 Posterior Nanos protein plays a permissive role in pre-
92 venting the early translation of maternal *hunchback* (*hb*)
93 mRNA [7].

94 The molecular basis of maternal establishment DV polar-
95 ity is also well described in *D. melanogaster*. mRNA for the
96 EGF ligand *gurken* (*grk*) is localized around the oocyte
97 nucleus which becomes localized at an asymmetric loca-
98 tion at the anterior. Grk protein is secreted and activates

99 EGF receptor expressed in the follicle cells. This leads to
100 a ventrally localized modification of the eggshell. This
101 information stored in the eggshell is then transmitted
102 back to the embryo through localized processing of the
103 Toll ligand Spatzle to the ventral half of the egg. Again,
104 this leads to a graded source of patterning information,
105 this time in the form of nuclear uptake of the Toll target
106 transcription factor Dorsal. The Dorsal gradient also
107 regulates its targets in a concentration dependent fashion,
108 and has been described as a morphogen [8].

Maternal contribution to AP patterning in other insects

Establishing oocyte polarity

109 Whether the developmental and molecular bases of
110 inducing AP polarity in the oocyte are conserved outside
111 of *D. melanogaster* is an interesting topic, especially in light
112 of the variability in the structure of ovaries across insects.
113 *D. melanogaster* has polytrophic meroistic ovaries, which
114 means that the oocyte is one of a clone of sister germline
115 cells. The other germline cells become 'nurse cells' which
116 are specialized to produce macromolecules provided to
117 the oocyte. These germ cells are surrounded as a unit by
118 follicle cells to form egg chambers. Many insects have
119 telotrophic meroistic ovaries, where a common pool of
120 nurse cells located toward the anterior end of the ovary
121 feed oocytes that become encapsulated by follicle cells as
122 they mature and move posteriorly. Finally, panoistic
123 ovaries lack nurse cells, and each oocyte is encapsulated
124 singly by follicle cells [2,8].

125 Since the polarization of the *D. melanogaster* oocyte occurs
126 in the context of the selection and migration of the oocyte
127 in the context of the selection and migration of the oocyte
128 in the context of its sister cells in the specialized poly-
129 trophic ovaries of the fly [6], it might stand to reason that
130 the *D. melanogaster* system may not be broadly conserved,
131 especially in systems with different ovary types. Indeed,
132 it appears that JAK/STAT signaling does not have a role
133 in establishing AP polarity of the oocyte in the telotrophic
134 ovaries of the beetle *Tribolium castaneum*, despite a par-
135 tially conserved role in specifying the stalk cells that
136 separate egg chambers from each other [9]. On the other
137 hand, Notch signaling between the germline and soma
138 appears to have a conserved role in establishing AP
139 polarity with in the *T. castaneum* oocyte [10]. Examination
140 of Notch signaling in the cockroach *Blattella germanica*
141 indicates that signaling between germline and soma is
142 conserved, but any effect on oocyte polarity is yet to be
143 shown [11].

Diverse roles of localized mRNAs

144 Although *bcd* is the absolutely crucial anterior determi-
145 nant in *D. melanogaster* and its relatives in the Brachycera,
146 it has long been known that this molecule is a novelty
147 within this group, and that other molecules must be used
148 in other species [12,13]. A wide variety of such anterior
149 determinants have been found, and evidence indicates
150
151

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