

## Probing Cell-Type Specific Gene Expression in the Ovarian Cells of *Drosophila* by P-Element Mediated Enhancer Detection

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**P-element mediated enhancer detector lines (EDLs) were screened for reporter gene (*lacZ*) expression in the ovary of *Drosophila melanogaster*. Cell-type specific *lacZ* expression can be grouped into three parts such as in the germline, soma, and both. *LacZ* expression in germline cells was divided into 2 types; expression in nurse cells or in both of the nurse cells and oocyte. In the stage-9 to stage-10 follicles, *lacZ* expression was observed either in the whole follicle cells around oocyte or in the subpopulation of follicle cells in egg chamber. *LacZ* expression in the subset of follicle cells are showed in the centripetal follicle cells or the columnar follicle cells except centripetal follicle cells. Several lines showed anterior to posterior gradient pattern of *lacZ* expression in the follicle cells. Interestingly there were 3 lines in which *lacZ* was expressed in the polar cells and/or the border cells of egg chamber. These *lacZ* expression patterns in the different ovarian cells of independent EDLs reflect the cell type-specific expression of maternal genes near the P-element insertion, and might provide a basis for cloning of genes involved in oogenesis of *Drosophila*.**

**KEY WORDS: P-Element, Oogenesis, *Drosophila***

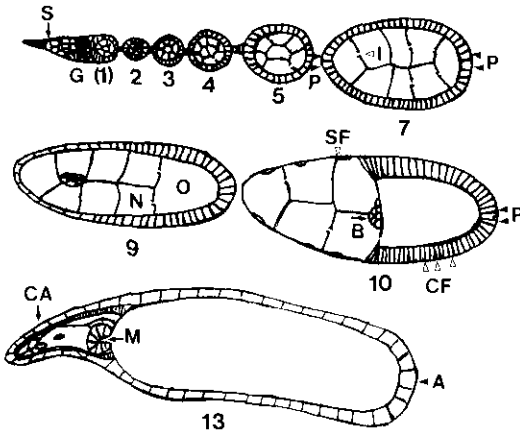
Two basic cell types can be distinguished during the oogenesis in *Drosophila*: the germline, consisting of fifteen nurse cells and an oocyte, as well as surrounding these, the somatically derived follicle cells. Germline and follicle cells interact during oogenesis for normal egg production (Schüpbach, 1987; Parks and Spradling, 1987). The function of the nurse cells is to produce maternal transcripts and proteins required for normal embryonic development. Early in oogenesis, the follicular epithelial cells divide as the follicle enlarges, but they eventually cease division and become polyploid (Mahowald *et al.*, 1979). Before the secretion of the vitelline

membrane around the developing oocyte, there is a general migration of follicle cells to produce a dense columnar epithelium over the oocyte itself and a thin squamous epithelium over the nurse cells (King and Vanoucek, 1960). Also during this time, a group of 6-10 follicle cells (the 'border' cells) leaves from the anterior end of the epithelium and migrates between the nurse cells, to the anterior pole of oocyte. Later, these border cells make the micropylar apparatus at the anterior end of the egg (Zarani and Margaritis, 1985). Finally, the follicle and nurse cells degenerate, leaving the mature egg (Fig. 1).

Temporally and spatially regulated gene expression is an important feature of development of an organism. Different transcriptional activity in

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**Fig. 1.** Diagram of the oogenesis in *Drosophila melanogaster*. Numbers below the egg chambers indicate stage of oogenesis. S, stem cell; G, germarium; N, nurse cell; O, oocyte; M, micropyle; A, aeropyle; CA, chorionic appendage; SF, squamous follicle cell; CF, columnar follicle cell; B, border cell; P, polar cell; I, intercellular bridge (adopted from King, 1970).

the specific sets of cells of same lineage is important for differentiation of these cells. Highly organized structure of the *Drosophila* ovary makes it an ideal system for studying mechanism of differential gene expression. Many maternal genes have been tested for somatic- or germline-dependent functions, using pole cell (Wieschaus *et al.*, 1978), or ovary (Clancey and Beadle, 1937) transplantation experiments or mitotic recombination (Wieschaus *et al.*, 1981; Perrimon and Gans, 1983). For the genes required for uniquely during oogenesis, both germline- (Wieschaus *et al.*, 1978; Schüpbach and Wieschaus, 1986b) and soma- (Perrimon and Gans, 1983; Schüpbach, 1987) dependent gene activities have been reported.

A P-element mediated enhancer detector method described by O'Kane and Gehring (1987) is widely used to monitor the gene expression in certain tissue. Briefly, position- and temporal-specific regulatory elements can be revealed, by inserting a ubiquitously acting promoter linked to the structural gene for  $\beta$ -galactosidase at random into the genome.  $\beta$ -galactosidase enzyme can then be monitored in the individual lines obtained, and X-Gal staining pattern reflects regulatory elements

in the different cell types (Wilson *et al.*, 1989). The P-element mediated enhancer detector system can be effectively used for the study of transcriptional activity among the specific set of cells during development. On the other hand, change in the genomic structure caused by P-element insertion provides an information about the regulatory elements which positively or negatively regulate transcription of nearby genes (Logan and Wensink, 1990; Jin and Petri, 1993).

In an effort to clone the genes involved in oogenesis of fruit flies, we made ovarian enhancer-detector lines (EDLs) using the germline transformation (Rubin and Spradling, 1982) of P [IArB] (Bellen *et al.*, 1989). Here we report cell type specific expression of *lacZ* in the independent EDLs which reflect transcriptional activities of genes during the oogenesis in *Drosophila melanogaster*.

## Materials and Methods

### Flies

Flies were reared in uncrowded half-pint glass bottles on standard medium (cornmeal, sugar, agar and yeast) containing propionic acid as mold inhibitor and maintained 70-80% humidity at  $24 \pm 1^\circ\text{C}$  under a photoperiodic regime (12L:12D).

### Establishment of enhancer detector lines

P [IArB] (Bellen *et al.*, 1989) was used as an enhancer detector (Fig. 2). Flies carrying the enhancer detector P [IArB] on a CyO second chromosome were mated to flies carrying the transposase source P [ry<sup>+</sup> $\Delta$ 2-3]. Progenies were screened by eye color. Male flies having wild type eye and normal wing (jump start male) were selected and each was crossed with cantonized ry<sup>506-iso</sup> females. *LacZ* expression in the ovary was examined and positive (enhancer detector) lines were maintained.

### X-gal staining

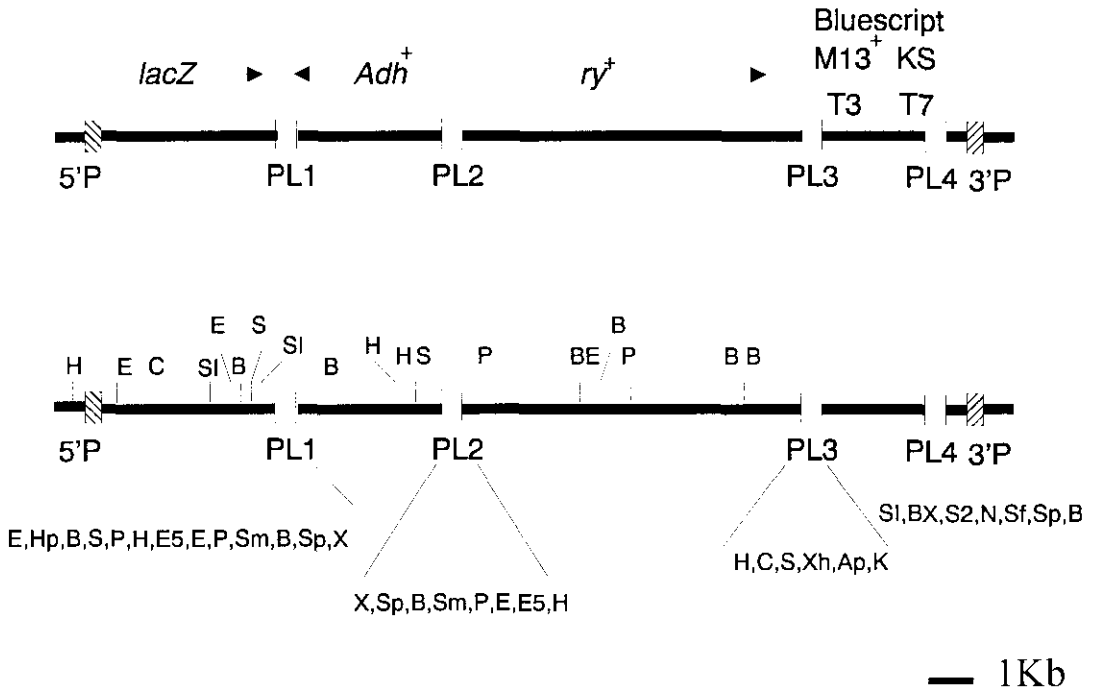
Flies were collected at varying time after eclosion and washed in Ringer's solution (Tris buffer, pH 7.1, 0.1% Triton X-100). Ovaries were dissected in Ringer's solution under the

stereomicroscope. The dissected ovaries were fixed for 5 min in fixation solution (1% formalide in Ringer's solution) and washed for 5-10 min with Ringer's solution. X-gal stock sol (8% in DMSO) was added to preincubated X-gal staining buffer (50 mM sodium phosphate, monobasic, 50 mM sodium phosphate, dibasic, 150 mM NaCl, 1 mM MgCl<sub>2</sub>, 9.3 mM K<sub>4</sub>[Fe(CN)<sub>6</sub>], 9.3 mM K<sub>3</sub>[Fe(CN)<sub>6</sub>], 0.3% Triton X-100) to be final 0.2% and incubated for 5 min at 37°C. This mixture was spinned down and yellow supernatant was applied

to ovaries and covered with parafilm. Ovaries were incubated in X-gal staining solution for overnight at 37°C. After staining, ovaries were mounted on slide with PBS/glycerol (1:1) mixture and observed under stereomicroscope.

**Results**

Unique temporal and spatial patterns of *lacZ* expression in different cells of egg chambers were



**Fig. 2.** Map of P[ArB]. Originally described by Bellen *et al.* (1989). Restriction sites on the polylinker 3 are not present on the 3' of P-element. *Ap*, *Apal*; *B*, *BamHI*; *BX*, *BstXI*; *C*, *Clal*; *E*, *EcoRI*; *E5*, *EcoRV*; *H*, *HindIII*; *Hp*, *HpaI*; *K*, *KpnI*; *N*, *NotI*; *P*, *PstI*; *S*, *Sall*; *S1*, *SacI*; *S2*, *SacII*; *Sf*, *SfiI*; *Sm*, *SmaI*; *Sp*, *SpeI*; *Xh*, *XhoI*.

**Table 1.** General distribution of staining patterns in ovarian cell of independent EDLs

Types of cells	Total (%)	Remarks
Germline cells	31 (16.1)	
nurse cell only	7 (3.6)	
Follicle cells	38 (19.7)	
polar cells and/or border cells	3 (1.6)	EDL149, insertion on X chromosome
posterior follicle cells	1 (0.5)	EDL108
Germline cells and follicle cells	28 (14.5)	
No staining in the ovarian cells	96 (47.7)	
Total	193 (100.0)	



**Fig. 3.** Transposants expressing *lacZ* in germlines and soma of egg chambers. (A) EDL41. Staining was observed in nucleus of the nurse cells (asterisk) and the oocyte (filled arrowhead) of stage-10 follicles. Open arrowhead indicates the early stage of follicles. (B) EDL681. Positive staining in the oocyte nucleus (filled arrowhead) and nurse cell nucleus (white arrowhead) in nearly all stages of oogenesis. Some follicle cells around oocyte were also stained (open arrowhead). Nurse cells of the early stage of egg chamber showed faint signal (arrow). (C) EDL462. Both of the nurse cells and oocyte nucleus (filled arrowhead) in all stages of follicles, and follicle cells around the egg chamber were stained (open arrowhead). (D) EDL153. Positive staining in germarium (filled arrowhead) and nurse cells of late stage-10 follicles (asterisk). (E) EDL29. Germarium (arrow), nurse cells of stage-5 to -10 follicles (white arrowhead), and oocyte nucleus of stage-10 to -11 egg chambers (filled arrowhead) were stained. *LacZ* expression ceased in stage-11 egg chamber onward (asterisk). (F) EDL71. Staining occurred in nurse cell (white arrowhead) and follicle cells of lateral side of stage-10 egg chamber (filled arrowhead). Centripetal follicle cells were free from staining (open arrowhead). (G) EDL56. Staining occurred in germarium (arrow) and nurse cells of all stage of oogenesis (white arrowhead). At stage-10 follicles, follicle cells around oocyte were exclusively stained (open arrowhead). Filled arrowheads indicate border cells. (H) EDL679. Staining pattern was similar to (G) but follicle cells around the mature oocyte of stage-11 follicle (white arrowhead) were also stained. (I) EDL82. Staining was observed in nurse cells (asterisk) and centripetal follicle cells near the nurse cell-oocyte border (filled arrowhead) of stage-10 egg chamber. Chorionic appendages were stained in egg chamber of stage-11 onward (open arrowhead).



**Fig. 4.** Transposants expressing *lacZ* in the follicle cells. (A) EDL454. Follicle cells of early stage of egg chamber were intensively stained (filled arrowheads). Staining occurred in the follicle cells around oocyte at stage-10 follicles (open arrowheads). Follicle cells at the posterior end (white arrowheads) of egg chamber and chorionic appendages (arrow) were stained in stage-13 egg chambers. (B) EDL636. Follicle cells around oocyte at stage-10 follicle were intensively stained (white arrowhead). At later stage, staining occurred in chorion (filled arrowhead). Arrowhead indicates dechorionated egg free from staining. (C) EDL13. Follicle cells near the nurse cell-oocyte border (filled arrowheads) were stained. Open arrowheads indicate follicle cells around the nurse cells. (D) EDL678. Columnar follicle cells around lateral side of oocyte (white arrowheads) but not the centripetal follicle cells (open arrowheads) were exclusively stained. (E) EDL142. Staining pattern is similar to (D), but the follicle cells at anterior part of egg chamber were more intensively stained (filled arrowheads). At stage-12 follicles, staining occurred at chorionic appendages (open arrowhead). (F) EDL55. Follicle cells around oocyte of stage-10 egg chamber were exclusively stained (filled arrowheads). Oocyte-nurse cell border showed weak staining (open arrowhead). (G) EDL674. All kinds of follicle cells including border cells (open arrowhead), polar cell (filled arrowhead) and squamous follicle cells (white arrowheads) were stained. (H) EDL694. Staining occurred in the follicle cells of all stage of oogenesis. At later stage, Note staining in the chorion with stripe (filled arrowheads) and chorionic appendages (open arrowhead). (I) EDL149. Border cells (filled arrowheads) and posterior polar cells of stage-10 egg chamber were stained (open arrowheads). Inset, early stage follicle showing staining of polar cells at both pole of egg chamber (arrows). Open arrowhead denotes the posterior polar cells. (J) EDL108. Staining exclusively occurred in the posterior follicle cells including polar cells (filled arrowheads) of stage-9 follicle (asterisk) onward. Staining intensities of stage-11 to -12 egg chambers were decreased (open arrowheads).

examined. A total of 193 lines were screened and the results were summarized in Table 1.  $\beta$ -galactosidase expression was detected in the ovary of 97 (52.3%) EDLs. Cell type specific *lacZ* expressions were grouped into the germline expression (Fig. 3 A, D, and E), somatic follicle cells expression (Fig. 4 A - J), or the both (Fig. 3 B, C, F, G, H, and I).

The *lacZ* expression in germ line cells of ovary was observed in 31 lines. In these lines, cell-type specific expression pattern was further divided into 2 types: nurse cell expression (Fig. 3 D, F, H, and I) and both of the nurse cells and the oocyte expression (Fig. 3 A, B, C, E, and G). The majority of nurse cell-EDLs showed maximum *lacZ* expression at stage-10 and thereafter ceased reported gene expression (Fig. 3 C, E, H, and I). There were two types of *lacZ* expression in nurse cells EDLs; expression exclusively in the stage-10 egg chamber (Fig. 3 A and I) or from stage-2 to 10 (Fig. 3 B, C, D, E, F, G, and H).

Insertions which expressed  $\beta$ -galactosidase limited to the follicle cells occurred in 38 lines. Some of these lines showed *lacZ* expression in the subset of follicle cells of stage-10 egg chambers: staining in the centripetal follicle cells (Fig. 4 A, B, C, and E) or all columnar follicle cells except centripetal follicle cells (Fig. 4 D and F). *LacZ* expression in the follicle cells were characterized by existence of anterior to posterior gradient in follicle cells (Fig. 4 E). Interestingly there were 3 lines in which *lacZ* was expressed in the polar cells and/or the border cells (Figs. 3 G, and 4 G and I). In one line, both of the polar cells and border cells were exclusively stained (Fig. 4 I). One line showed *lacZ* expression in the posterior follicle cells of an egg chamber (Fig. 4 J). Many of the follicle cell-EDLs showed *lacZ* expression with stripe on the chorionogenic cells of late stage of egg chamber (Fig. 4 B and H).

## Discussion

Many germline-EDLs were isolated through screening, and most of these showed *lacZ* expression in both of the nurse cells and oocyte in the egg chamber. Although we could not isolate

oocyte-only-EDL, it could be obtained by increasing the number of screening. In the majority of nurse cell-EDLs, *lacZ* expressions were burst at stage-8 and reached to maximum at stage-10 egg chamber (Fig. 3 C, E, H, and I). It coincides with the period of rapid growing of germline cells. Cytoplasmic transport from nurse cells to oocyte leading to increase in oocyte volume proceed during the stage-2 to 12 of oogenesis. And during the stage-10B, terminal injection of nurse cells cytoplasm to oocyte rapidly occurs (for review, Mahajan-Miklos and Cooley, 1994). Therefore *lacZ* expressions in each nurse cells-EDLs reflect active transcription of genes encoding the maternal factors accumulated during the growth of oocyte or the machineries required for cytoplasm transport.

In many follicle cells-EDLs showing the *lacZ* expression in the stage-10 egg chamber, chorionic components were stained in more later staged egg chamber (Figs. 4 B and H). Message sequences unique to the follicle cells include those coding for proteins of vitelline membrane (Burke *et al.*, 1987) and chorion (Parks and Spradling, 1987). Chorion gene clusters encoding protein components of chorion exist in both X and third chromosome (Spradling *et al.*, 1980). Interestingly there was an EDL in which *lacZ* expression was exclusively occurred in the polar cells of both ends of egg chamber of stage-2 to -8. In this line, migrating border cells of stage-8 to stage-10 follicles were also labeled (Fig. 4 I). The function of the polar cells has been proposed to be involved in the control of the polarity of developing egg chamber (Brower *et al.*, 1981). The potential for gene activity in either one or both poles of the embryo was suggested by the existence of certain germline-dependent mutations. These affect the development and differentiation of anterior, posterior, or both poles of the embryo (Schüpbach and Wieschaus, 1986a; Frohnhöfer and Nüsselein-Volhard, 1986), or the oocyte and the embryo (Frey and Gutzeit, 1986). Gene which controls the *torso-like* activity is expressed in the somatic follicle cells located at the poles of the oocyte (Stevens *et al.*, 1990). *Sibo* (slow border cell migration) encoding the protein homologue to the CCAAT/enhancer-binding protein (C/EBP) family

of transcription factors, is the gene firstly identified to be expressed in border cells during oogenesis of *Drosophila* (Montell *et al.*, 1992) and control the differentiation of follicle cells (Montell, 1994). Border cells was known to make the micropylar apparatus at the anterior end of the egg (Zarani and Margaritis, 1985). But even in mutant carrying the the severe alleles of *slbo*, neither malformed micropyle nor the absence of this extra embryonic structure was reported. P-element insertion site of border cell-EDL (EDL149) revealed by genetic crosses was on the X chromosome (data not shown). Hence EDL149 did not showed abnormality in micropyle and whether the gene trapped in EDL149 encodes the extracellular component of egg chamber is unknown, we supposed that the gene involved in the maintenance of identity of polar cell-originated follicle cells must be trapped in this line. Now we are undergoing cloning of the gene near the P-element insertion in EDL149.

*LacZ* expression pattern in the subset of follicle cells is of interest. *LacZ* expression with spreading or gradient pattern in the subset of cells of same lineage is often observed in both germline (Fig. 3 A - H) and soma (Fig. 4 A - J) in independent ovary-EDLs. Especially expression of *lacZ* in columnar follicle cells with anterior to posterior gradient (Fig. 4 E) suggested that genes with different transcriptional activities in the same lineage of follicle cells be trapped in these EDLs. These genes might be under control of polarity within the egg chamber which is possibly controlled by transcription factors derived from the nurse cells or the oocyte. Several maternal transcripts or translational products was reported to be actively engaged in the construction of polarity within the egg chamber and control the down stream events during embryonic development (Stevens *et al.*, 1990). Change of cell shape and functional differentiation of germline cells or somatic follicle cells steadily proceeded throughout the oogenesis, and it requires precisely regulated switching of transcription of gene(s) needed. Therefore gradient expressions of *lacZ* in the cells of the same lineage reflects that transcriptional activities may be differentially regulated among the these cells of

same lineage.

So far, several ovarian enhancer elements such as *oe1* of yolk protein gene (Logan and Wensink, 1990), developmental control element 2 (DCE2) (Jin and Petri, 1993), and transcriptional control element of the *hsp26* (Frank *et al.*, 1992) were reported to be responsible for cell type specific gene expression in *Drosophila* ovary. DCE2 was revealed to govern the expression of the vitelline gene in the follicle cells, and change in repressor element result in *lacZ* expression in the border cells ectopically (Jin and Petri, 1993). Therefore the possibility that *lacZ* expression in the specific set of ovarian cells is actually caused by change in the control elements by P-element insertion could not be ruled out.

Insertions that gave *lacZ* expression in the ovarian cells occurred with relatively high frequencies. Therefore before cloning the gene of interesting expression pattern, the phenotype associated caused by P-element insertion should be confirmed. Plasmid having the genomic insert could be rescued by using the cloning vector within *P[ArB]*. Genomic structure and regulatory element near the P-element insertion in the independent EDLs of interest would provide valuable information about the genes expressed during the oogenesis in *Drosophila*.

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## References

- Bellen, H.B., C.J. O'Kane, C. Wilson, U. Grossniklaus, R.K. Pearson, and W.J. Gehring, 1989. P-element-mediated enhancer detection: a versatile method to study development in *Drosophila*. *Genes & Dev.* **3**: 1288-1300.
- Brower, D.L., R.J. Smith, and M. Wilcox, 1981. Differentiation within the gonads of *Drosophila*

- revealed by immunofluorescence. *J. Embryol. Exp. Morphol.* **63**: 233-242.
- Burke, T., G.L. Waring, E. Popodi, and P. Minoo, 1987. Characterisation and sequence of follicle cell genes selectively expressed during vitelline membrane formation in *Drosophila*. *Dev. Biol.* **124**: 441-450.
- Clancey, C.W. and G.W. Beadle, 1937. Ovary transplants in *Drosophila melanogaster*. *Biol. Bull. (Woods Hole)* **72**: 47-56.
- Frank, L.H., H.-K. Cheung, and R.S. Cohen, 1992. Identification and characterization of *Drosophila* female germ line transcriptional control element. *Development* **114**: 481-491.
- Frey, A. and H. Gutzzeit, 1986. Follicle cells and germ line cells both affect polarity in dicephalic chimeric follicles of *Drosophila*. *Wilhelm Roux's Arch. Dev. Biol.* **195**: 527-537.
- Frohnhofer, H.G. and C. Nüsslein-Volhard, 1986. Organization of anterior pattern in the *Drosophila* embryo by the maternal gene bicoid. *Nature* **324**: 120-125.
- Jin, J. and W.H. Petri, 1993. Developmental control elements in the promoter of a *Drosophila* vitelline membrane gene. *Dev. Biol.* **156**: 557-565.
- King, R.C., 1970. *Ovarian Development in Drosophila melanogaster*, Academic Press, New York.
- King, R.C. and K.G. Vanoucek, 1960. Oogenesis in adult *Drosophila melanogaster*. X. Studies on the behavior of the follicle cells. *Growth* **25**: 333-338.
- Logan, S.K. and P.C. Wensink, 1990. Ovarian follicle cell enhancers from the *Drosophila* yolk protein genes: Different segments of one enhancer have different cell-type specificities that interact to give normal expression. *Genes & Dev.* **4**: 613-623.
- Mahajan-Miklos, S. and L. Cooley, 1994. Intercellular cytoplasm transport during *Drosophila* oogenesis. *Dev. Biol.* **165**: 336-351.
- Mahowald, A.P., J.H. Caulton, M.K. Edward, and A.D. Floyd, 1979. Loss of centrioles and poly-ploidization in follicle cells of *Drosophila melanogaster*. *Exp. Cell Res.* **118**: 404-410.
- Montell, D.J., 1994. Moving right along: regulation of cell migration during *Drosophila* development. *Trends Genet.* **10**: 59-62.
- Montell, D.J., P. Rorth, and A.C. Spradling, 1992. *Slow border cells*, a locus required for a developmentally regulated cell migration during oogenesis, encodes *Drosophila C/EBP*. *Cell* **71**: 51-62.
- O'Kane, C. and W.J. Gehring, 1987. Detection in situ of genomic regulatory elements in *Drosophila*. *Proc. Natl. Acad. Sci. USA* **84**: 9123-9127.
- Parks, S. and A.C. Spradling, 1987. Spatially regulated expression of chorion genes during *Drosophila* oogenesis. *Genes & Dev.* **1**: 497-509.
- Perrimon, N. and M. Gans, 1983. Clonal analysis of the tissue specificity of recessive female sterile mutations of *Drosophila melanogaster* using a dominant female sterile mutation *Fs(1)K1237*. *Dev. Biol.* **100**: 365-373.
- Rubin, G.M. and A.C. Spradling, 1982. Genetic transformation of *Drosophila* with transposable element vectors. *Science* **218**: 348-353.
- Schüpbach, T., 1987. Germline and soma cooperate during oogenesis to establish the dorsoventral pattern of the eggshell and embryo in *Drosophila melanogaster*. *Cell* **49**: 699-707.
- Schüpbach, T. and E. Wieschaus, 1986a. Maternal effect mutation altering the anterior-posterior pattern of the *Drosophila* embryo. *Wilhelm Roux's Arch. Dev. Biol.* **195**: 302-317.
- Schüpbach, T. and E. Wieschaus, 1986b. Germline autonomy of maternal-effect mutations altering the body pattern of *Drosophila*. *Dev. Biol.* **113**: 443-448.
- Spradling, A.C., M.E. Digan, A.P. Mahowald, M. Scott, and E.A. Craig, 1980. Two clusters of genes for major chorion proteins of *Drosophila melanogaster*. *Cell* **19**: 905-914.
- Stevens, L.M., H.G. Frohnhofer, M. Klingler, and C. Nüsslein-Volhard, 1990. Localized requirement for torso-like expression in follicle cells for development of terminal anlagen of the *Drosophila* embryo. *Nature* **346**: 660-663.
- Wieschaus, E., C. Audit, and M. Masson, 1981. A clonal analysis of the roles of somatic cells and germ line during oogenesis in *Drosophila*. *Dev. Biol.* **88**: 92-103.
- Wieschaus, E., J.L. Marsh, and W.L. Gehring, 1978. *Fs(1)K10*, a germline-dependent female sterile mutation causing abnormal chorion morphology in *Drosophila melanogaster*. *Wilhelm Roux's Arch. Dev. Biol.* **184**: 75-82.
- Wilson, C., R.K. Pearson, H.J. Bellen, C.J. O'Kane, U. Grossniklaus, and W.J. Gehring, 1989. P-element-mediated enhancer detection: an efficient method for isolating and characterizing developmentally regulated genes in *Drosophila*. *Genes & Dev.* **3**: 1301-1313.
- Zarani, F.E. and L.H. Margaritis, 1985. The eggshell of *Drosophila melanogaster*. V. Structure and morphogenesis of the micropylar apparatus. *Can. J. Zool.* **64**: 2509-2519.

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P-요소를 이용한 노랑초파리 난소에서의 세포특이적 유전자발현의 검출  
 계명찬 · 조경상 · 김경진 · 이정주<sup>1</sup>(서울대학교 분자생물학과 및 세포분화연구센터,  
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P-element의 germ line transformation을 이용하여 초파리 난소에서의 세포특이적 유전자발현 양상을 조사하였다. 표지유전자인 *lacZ*의 발현양상은 생식세포, 체세포, 두 종류의 세포에서 모두 발현되는 경우로 대별되며, 생식세포에서 *lacZ*의 발현은 조세포 또는 조세포와 난자에서 동시에 발현되는 경우로 구분되었다. 난자주변 난포세포에서의 *lacZ* 발현은 난자형성 9-10기 난포의 경우 모든 세포에서 균일하게 발현되거나 일부 세포에서만 발현되는 양상으로 구분되었다. 일부의 난포세포에서 발현되는 경우 난자와 조세포 경계의 난포세포에서 발현되는 경우, 이들을 제외한 난포세포에서 발현되는 경우로 구분되었다. 난자주위의 난포세포에서 난자의 전후축을 따른 구배현상도 관찰되었다. 극세포 또는 경계세포에서 발현되는 3개의 독립라인을 분리하였다. 독립된 EDI의 난소에서 나타난 *lacZ*의 발현양상은 초파리 난자형성에 관여하는 유전자의 시간과 공간적인 발현을 반영하며 이들 유전자 분리의 기초를 제공할 것으로 사료된다.