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Lethal effect of attached-*X* deletion in *Drosophila melanogaster*

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1. INTRODUCTION

A portion of the heterochromatin near the centromere is lost when two *X* chromosomes join as in an attached-*X* stock of *Drosophila melanogaster*. This loss is normally covered or compensated for by an homologous region in the heterochromatic *Y* chromosome. An interesting phenomenon has been uncovered, however, in crosses involving echinus deltex males and attached-*X* females. The only offspring of such a cross, ignoring the small number of crossover products for the present, are echinus deltex males. No attached-*X* females survive. The echinus deltex stock *Y* chromosome has accordingly been shown to possess a deletion which, when homozygous with the deletion believed to occur in attached-*X* stocks, is lethal.

2. STOCKS

The following stocks were used in the course of this investigation. For detailed description of mutants, see Lindsley & Grell (1967). Attached-*X* stocks: (1) *y w f.* = /Y, $X^{c2}yf$; (2) *y f*: = /Y, *y w m f*; (3) *y w f.* = /sc^8 Y, y^+/ Bascy; (4) *y f*: = /Y, *y cv m f car*; (5) B^SY^SX. (FR-1, $3a^R$), B^SY^S *y cv v f.*/$Y^{L'C}$ & *y v f.* = ; other stocks: (6) *ec dx*; (7) In (1) K2, $y\,cv\,f^5$; (8) $y\,w^a$ *spl rb*; (9) $Y^SX.Y^L$ ($F2\text{-}1^L$, $u\text{-}8d^R$), $Y^S\,y\,w^a$ *cv v f.*Y^L; (10) Y^S/g^2 B.Y^L & *y f*: = (dp^{olv}) (Stern).

Attached-*X*, or compound (1), stocks 1 and 3 are reversed metacentrics, in which the two *X* chromosomes are attached proximally to the same centromere. Stock 2 is a compound (1) double *X*, or a reversed acrocentric, in which the proximal end of one *X* chromosome is attached to the distal end of the other.

All parents were premated for one day in vials, then transferred to half-pint bottles containing an agar–cornmeal medium (Demerec & Kaufmann, 1964). Parents were left in the bottles for 3 days, transferred to a second bottle for 3 days, then discarded. Counts of the offspring were made for up to 7 days to allow slowly developing attached-*X* females to eclose, if present.

3. RESULTS

Attached-X crosses involving ec dx *males*. Four different crosses were made between attached-*X* females and *ec dx* males. The F_1 in each case was predominantly, if not wholly, male (Table 1). The females which did occur were wild type for the markers in the cross, and usually possessed notched wings and abnormally segmented abdomens. The occurrence of these fertile females can be explained as the result of the breakdown of the attached-*X* system by crossing over between the homologous heterochromatic regions of the *X* and short arm of the *Y* chromosomes. The separated *X*'s would then possess a short arm and a long arm of the *Y*, respectively. When either was later paired with an *ec dx* chromosome, the resulting phenotype would be that of a wild-type female.

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The abnormal appearance of the wings and abdomen was possibly due to the abnormal heterochromatic constitution. The occasional *y w f* male in crosses with *y w f* attached-*X* females was, similarly, a result of the combination of the cross-over *X* and the *ec dx* parent male *Y* chromosome. The high number of breakdown products was not expected, however. They are believed to have been caused by the use of parent attached-*X* females that were in the process of breaking down as a stock. The breakdown products will be investigated further.

Table 1. *Attached-*X *females* × ec dx *males*

Attached-*X* stock*	Females (wild-type)†	Males (*ec dx*)‡
1	42	280
—	4	83
—	0	75
2	0	32
3	9	86
4	1	47

* See list of stocks. † Wings often notched, see text.
‡ Plus rarely occurring *y* males (breakdown products).

Table 2. *Backcross results*

Attached-*X* stock	Females (matroclinous)	Males (*ec dx*)
1	138	179
2	293	224
3	144	208

Reciprocal crosses made between males from attached-*X* stocks and *ec dx* females resulted in the normal 1:1 sex ratio.

Back-crosses were made to show whether the *ec dx Y* were definitely responsible for the death of the females. Male offspring were collected from crosses between attached-*X* females and *ec dx* males. All such F_1 males possessed the *Y* chromosome originally carried by the attached-*X* females. When these males were mated to attached-*X* females, offspring were recovered in the normal 1:1 sex ratio (Table 2). Thus, the attached-*X* stock *Y* chromosome introduced through *ec dx* males allowed the flies to survive, whereas the presence of the *ec dx* stock *Y* chromosome was lethal.

Introduction of ec dx Y *through different genotypic backgrounds.* The *ec dx Y* chromosome was introduced into attached-*X* crosses in two different genotypic backgrounds to investigate the possibility that the *ec dx* autosomes affected the deletion lethality. This was accomplished by mating In (1) K2, *y cv* f^5 (and in a parallel test, *y* w^a *spl rb*) females to *ec dx* males, selecting F_1 males with their mother's *X* and their father's '*ec dx*' *Y* chromosome, and mating them to attached-*X* females. The results (Table 3) were reminiscent of the original crosses and support the idea that the *ec dx Y* chromosome, rather than the autosomes, was responsible for the loss of the attached-*X* females.

Localization to Y^S-. The deletion was localized to the short arm of the *Y* chromosome by crossing stock 3 attached-*X* females to B^SY^S *y cv v f*/$Y^{L'C}$ males (stock number 5). The F_1 included ten *y f B*/+ females with notched wings, 89 B^S+^{v} *cv v f* males, and 1 *y cv f* male. The absence of attached-*X* females indicates that the deletion was not covered by the long arm of the Y ($Y^{L'C}$). The required region must then be on the short arm of the Y.

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Supporting evidence was obtained by crossing stock 2 attached-X females with stock 10 free-Y^S males. The F_1 females of such a cross have the attached-X from the mother and the short arm of the Y chromosome from the father. The males have the paternal X and Y chromosome from the mother. Counts of F_1 offspring produced an approximate 1:1 sex ratio, with 86 females and 67 males. Thus, the deletion was covered by the Y^S fragment.

When stock three attached-X females were mated with stock nine males (males without a free Y chromosome), the following were recovered: 2 *y w*^{a} *f* females (breakdown products), and 83 + ^{v} *w*^{a} *cv v f* males. The attached-X chromosome was not recovered when present without a compensating Y chromosome.

No cytological evidence is available to indicate the nature or extent of the deletion.

Table 3. *Introduction of* ec dx Y *through different genotypic backgrounds*

Stock	Females	Males
7	0	73
8	0	156

SUMMARY

Attached-X stocks appear to be deficient in a small region, probably heterochromatic, which is normally covered by an homologous region on the short arm of the Y chromosome. There is an homologous deficiency in the *ec dx* stock Y chromosome. When this Y^S deficiency occurs in crosses involving attached-X stocks, the matroclinous females are not recovered.

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