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Non-reciprocal intragenic mitotic recombination in *Drosophila melanogaster*

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SUMMARY

X-ray-induced mitotic recombination within the lozenge locus of *Drosophila melanogaster* was found to be non-reciprocal. Recombination was detected by the presence of faceted spots in a smooth (lozenge) eye. Markers were present so that if recombination were reciprocal, equal numbers of vermilion and apricot-vermilion-coloured faceted spots would be formed. Of 19 faceted spots found among more than 60000 eyes examined, 10 were vermilion, 7 variegated (some vermilion and some apricot-vermilion-coloured facets), and 2 probably variegated. None was uniformly apricot-vermilion in colour. Four mechanisms for the formation of faceted spots are discussed: double reciprocal recombination, misrepair or gene conversion before chromatid replication, misrepair or gene conversion after chromatid replication, and misrepair or gene conversion followed by chromosome loss. The evidence most strongly supports the hypothesis that all faceted spots were formed by either misrepair following X-irradiation or gene conversion and were originally vermilion in colour. Subsequent chromosome loss from these vermilion cells led to the production of variegated spots. Variegated spots were generally smaller than those uniformly vermilion in colour, indicating that chromosome loss may occur with greater frequency in older irradiated larvae.

1. INTRODUCTION

Reciprocal intergenic mitotic recombination was first found in *D. melanogaster* in 1936 (Stern, 1936). More recently, mitotic recombination has been reported within the white locus of the same organism (Stern, 1969). However, in the latter study it was not possible to determine whether the intragenic recombination was reciprocal or non-reciprocal. The present experiments were undertaken to determine (1) whether intragenic recombination occurs within the lozenge locus (*lz*; I:27·7) of *D. melanogaster*, and (2) whether such recombination is reciprocal or non-reciprocal.

Lozenge is a recessive X-linked gene. Flies hemi- or homozygous for *lozenge* have facetless eyes. Only females were scored in these experiments. Each fly had two non-complementing alleles of *lozenge* in the trans position

$$\left(\frac{+ \quad lz^{y4}}{lz^{36} \quad +}\right).$$

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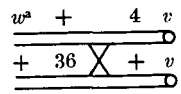
The eyes of such flies are facetless. Somatic recombination between the lozenge sites leads to a wild-type (faceted) spot in a largely facetless eye. As Table 1 indicates, reciprocal somatic recombination events would lead to equal numbers of vermilion and apricot-vermilion faceted spots. However, no uniformly apricot-vermilion spots were found, suggesting that recombination within the lozenge locus is non-reciprocal. Non-faceted spots, whether formed by recombination within or outside the lozenge locus were not analysed.

Table 1. *Phenotypes of facets* (lz+) *produced by reciprocal recombination between* 4 *and* 36



Genotypes produced		Phenotypes of facets
(1, 4)	$\frac{w^a \; + \; 4 \; v}{+ \; 36 \; + \; v}$	Facets absent
(2, 3)	$\frac{+ \; 36 \; 4 \; v}{w^a \; + \; + \; v}$	Vermilion
(1, 3)	$\frac{w^a \; + \; 4 \; v}{w^a \; + \; + \; v}$	Apricot-vermilion
(2, 4)	$\frac{+ \; 36 \; 4 \; v}{+ \; 36 \; + \; v}$	Facets absent

2. MATERIALS AND METHODS

The recessive *lozenge* (*lz*; I: 27·7) mutants used in these experiments were obtained from Dr M. M. Green, University of California, Davis. Mutant sites of these alleles are located at opposite ends of the locus with lz^{y4} more proximal than lz^{36} (Green & Green, 1956). Hereafter, the lozenge alleles will be referred to as *4* and *36*, respectively. Eyes of flies hemi- or homozygous for *4* have occasional rounded bumps on the eye surface, but normal facets are absent; flies hemi- or homozygous for *36* have smooth, facetless eyes (Clayton, 1954).

In addition to *lozenge* at 27·7 units, flies in these experiments were heterozygous for apricot and homozygous for vermilion:

$$\frac{w^a \; + \; 4 \; v}{+ \; 36 \; + \; v}$$

(w^a: apricot at 1·5; *v*: vermilion at 33·0). Such flies have facetless eyes with occasional bumps. Eye colour is light mottled orange with a darker orange rim. Markers in these experiments were chosen to ensure visibility of even a few facets on the orange lozenge background. The alleles *4* and *36* produce 16% and 0% respectively of the red pigment found in wild-type eyes (Green, 1948). The combination of *vermilion* and *lozenge* further reduces eye pigment and ensures visibility

of facets (Lindsley & Grell, 1967). *Apricot* was used as a marker because the combination of *vermilion* and *apricot* produces a light pinkish yellow colour distinct from both the background orange and the vermilion colour of the other expected recombinant type (see Table 1).

Eggs were deposited from 12 to 24 h. Larvae between 19·5 and 60 h old were irradiated in standard Drosophila media. An Andrex 150 kV, 5 MA industrial X-ray unit with 1·5 mm aluminum inherent filtration was used to administer 1002–1292 R over 10–17 min. Following eclosion, flies were aged at least 2 days before scoring, since the amount of red pigment increases until the fifth day (Ephrussi & Herold, 1944).

A zoom dissecting microscope producing a total magnification of from 60× to 120× was used. Both eyes of live or recently killed flies were examined. (The colour of facets cannot be determined well after flies are placed in 100% alcohol.) Eyes were illuminated by direct reflected light. The presence of occasional bumps on the eye surface made the lower limit of detection two facets.

To obtain photographs with the scanning electron microscope, flies were anesthetized, then attached to a copper mount using silver paint as a conducting adhesive. The scanning electron microscope (a modified Japan Electron Optics Laboratory Model JSM-1) was operated at 25 kV with a specimen current of 2×10^{-11} A. The specimen-beam angle (viewing aspect) was 45°. Type 42 Polaroid roll film was used in all photographs.

3. RESULTS

In scoring the eyes of 30704 phenotypically lozenge females

$$\left(\frac{w^a \quad + \quad 4 \quad v}{+ \quad 36 \quad + \quad v}\right),$$

19 faceted (lz^+) spots were found. Of these 19 spots, 10 were vermilion in colour and 7 were variegated. Variegated spots contained some vermilion facets and some apricot-vermilion facets. The two remaining faceted spots were probably variegated, but an exact notation of their phenotype was not made before the flies died.

The presence of faceted spots in facetless eyes indicates that recombination did occur within the lozenge locus. However, equal numbers of vermilion and apricot-vermilion spots were not obtained. In fact, no faceted spots were uniformly apricot-vermilion in colour. Instead, apricot-vermilion facets were always found in variegated spots, which also contained vermilion-coloured facets.

A description of the faceted spots is given in Table 2. Spots are listed in order of size, but numbered in order of discovery. As Table 2 indicates, the larger and intermediate-sized spots are all vermilion in colour. Of the small spots (less than 20 facets) only one is uniformly vermilion in colour. Variegated spots were not only smaller than most vermilion spots, but also (with one exception) were found only in the groups irradiated at a later larval age (35–60 h). Vermilion spots, on

the other hand, were larger and usually found in the groups irradiated at an earlier age (19·5–47·5 h). Although the times of irradiation overlap, the sizes of the two types of spot (with one exception) do not. It is therefore likely that vermilion spots were formed in larvae irradiated at younger ages, while the variegated spots, being smaller, were formed in larvae irradiated at older ages.

Table 2. *Size and phenotype of faceted* (lz$^+$) *spots found in* w^a 4 v/+ 36 v *flies irradiated as larvae*

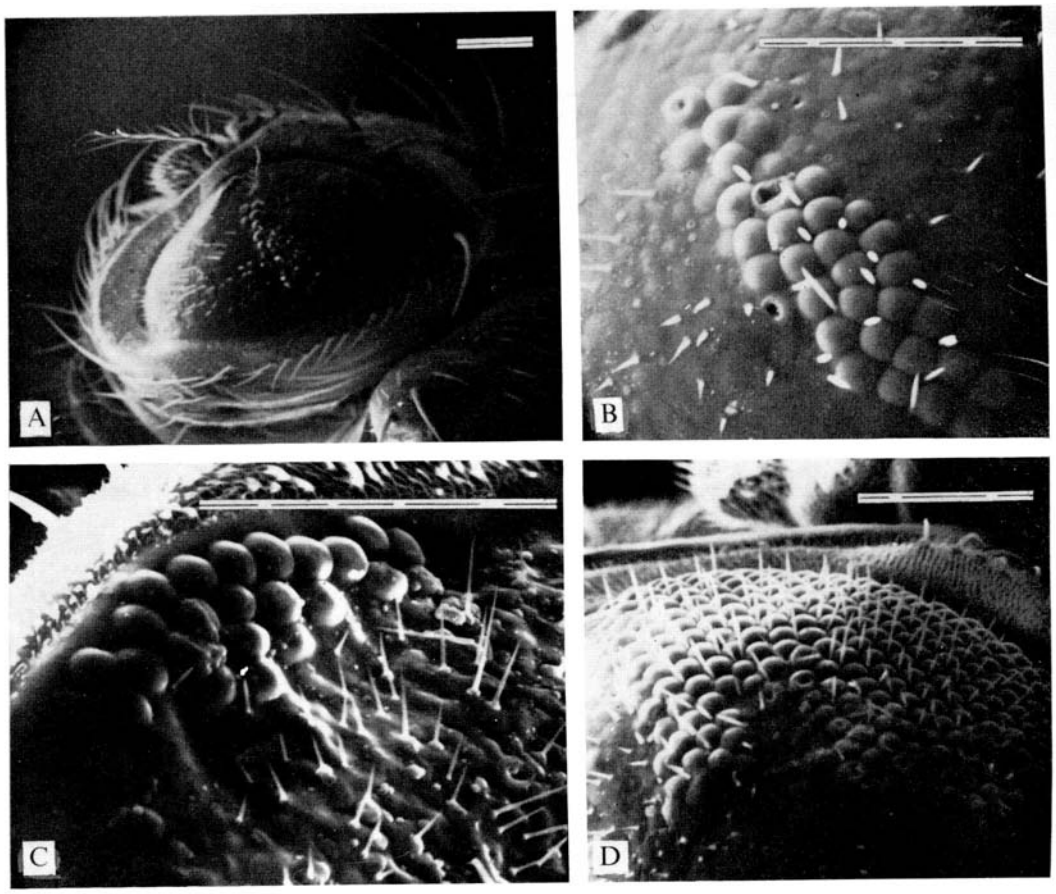
Spot no.*	No. of facets	Phenotype	Larval age at time of irradiation (h)	
3	*c.* 250	Vermilion	Early	(19·5–43·5)
15	*c.* 100	Vermilion	Late	(36–60)
9	*c.* 85	Vermilion	Late	(35–59)
6	*c.* 75	Vermilion	Early	(24–47·5)
4	*c.* 65	Vermilion	Early	(24–47·5)
8	38	Vermilion	Late	(35–58)
1	*c.* 30	Vermilion	Early	(19·5–43·5)
7	*c.* 25	Vermilion	Early	(24–48)
2	24	Vermilion	Early	(20–44)
13	18	Variegated	Early	(25–47)
16	18	Variegated	Late	(36–60)
11	17	Variegated?	Late	(35–59)
18	16	Variegated	Late	(36–60)
10	15	Variegated	Late	(35–59)
17	12	Variegated	Late	(36–60)
5	*c.* 10	Vermilion	Early	(24–47·5)
14	6	Variegated	Late	(36–59)
12	6	Variegated?	Late	(35–59)
19	6	Variegated	Late	(36–60)

* Spots are numbered in order of discovery.

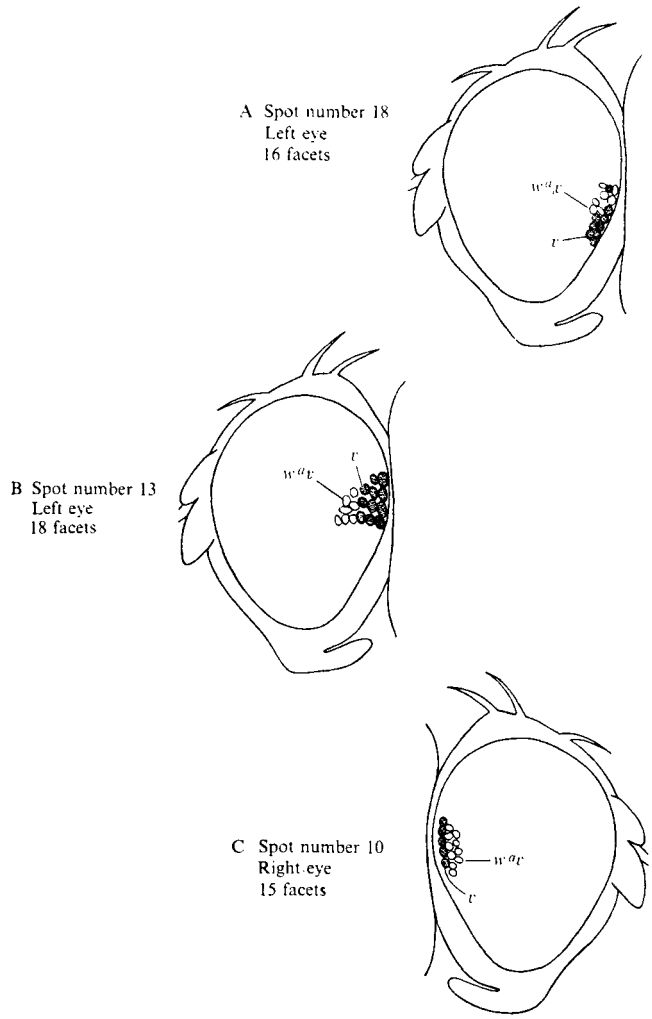
In three of the variegated spots, several rows of facets were one colour and the remaining rows the other colour. In four other variegated spots, the differently coloured facets were not as strictly segregated, giving the spot a mottled look. The distributions of facet colours for three variegated spots are illustrated in Text-fig. 1.

What is the evidence that vermilion and variegated facet phenotypes accurately reflect the *v* and *w^{a}v* genotypes? Since *lozenge* also influences colour, diffusion of pigment from unfaceted to faceted cells (or vice versa) might cause genotypically *vermilion* or *apricot-vermilion* spots to appear variegated. However, demonstration of the autonomy of *lz* and *lz$^+$* would provide evidence against diffusion of pigment between cells. In females containing one ring *X* chromosome and one normal *X* chromosome marked with *lozenge-spectacled* (*lz^s*; yellow brown in colour, no facets), the ring *X* chromosome was frequently lost during development, resulting in the formation of eyes containing a small area of *lz^s* in a largely *lz$^+$* eye. The reverse was also found, indicating that both *lz* and *lz$^+$* act autonomously.

With the exception of one variegated spot, faceted spots were at or near the



Scanning electron photographs showing faceted spots rising from a lozenge background. (A) An entire eye, showing facets in the centre (× 100). (B) An enlargement of A (× 300). (C) Facets near the eye edge showing absence of setae between facets (× 460). (D) Faceted spot with setae between facets (× 230).



Text-fig. 1. Sketches of three faceted (lz^+) spots showing the relative positions of vermilion- and apricot-vermilion-coloured facets.

eye edge. Plate 1 illustrates faceted spots rising from the lozenge (facetless) background, as seen with the scanning electron microscope. There is a clear demarcation between the faceted area and the background. Holes in three facets in Plate 1B (an enlargement of Plate 1A) are artifacts caused by the scanning electron microscope. Note that in Plate 1C, where facets are at the eye edge, no setae are present between facets. In a scanning electron microscope study, Hartman & Hayes (1971) found that setae are absent or scarce near the edge of wild-type eyes. Note that facets in Plates 1B and 1C are not all hexagonal in shape, as one would expect in wild-type flies. Also, they are not tightly packed as in Plate 1D (a larger spot) and wild-type flies. The regular shape of tightly packed facets is probably due at least in part to the pressure of facets on each other. Spots con-

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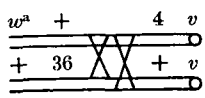
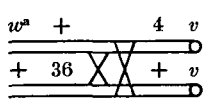
taining relatively few facets would have less pressure on each facet, with a resulting irregular shape.

4. DISCUSSION

Of the 19 faceted spots observed, none was uniformly apricot-vermilion, although reciprocal mitotic recombination within the lozenge locus would result in an equal number of apricot-vermilion and vermilion-coloured faceted spots (Table 1). The lack of uniformly apricot-vermilion spots indicates that some process other than reciprocal mitotic recombination is responsible for the formation of the faceted spots found in these experiments. Four alternative mechanisms for the formation of faceted spots are suggested.

Table 3. *Phenotypes of facets produced by double reciprocal recombination within the lozenge locus*

Strands involved in crossover*	Genotypes produced		Phenotypes of facets
1, 4 and 1, 3†	(1, 4)	$\frac{+\ 36\ 4\ v}{+\ 36\ +\ v}$	Facets absent
	(2, 3)	$\frac{w^a\ +\ 4\ v}{w^a\ +\ +\ v}$	Apricot-vermilion
	(1, 3)	$\frac{+\ 36\ 4\ v}{w^a\ +\ +\ v}$	Vermilion
	(2, 4)	$\frac{w^a\ +\ 4\ v}{+\ 36\ +\ v}$	Facets absent
1, 4 and 2, 3‡	(1, 4)	$\frac{+\ 36\ 4\ v}{w^a\ +\ +\ v}$	Vermilion
	(2, 3)	$\frac{+\ 36\ 4\ v}{w^a\ +\ +\ v}$	Vermilion
	(1, 3)	$\frac{+\ 36\ 4\ v}{w^a\ +\ +\ v}$	Vermilion
	(2, 4)	$\frac{+\ 36\ 4\ v}{w^a\ +\ +\ v}$	Vermilion

* Reverse order of same strands results in same phenotypes.

† The same phenotypes are obtained when the crossover strands are 2, 3 and 2, 4; 1, 4 and 2, 4; or 1, 3 and 2, 3.

‡ The same phenotypes are obtained when the crossover strands are 1, 3 and 2, 4.

(i) *Double reciprocal recombination*

Tables 3 and 4 illustrate the phenotypes expected if double reciprocal recombination occurs either entirely within the lozenge locus or within the lozenge locus and between *36* and w^a. Each of these models leads to uniformly vermilion or uniformly apricot-vermilion-faceted spots. The presence of variegated spots and absence of uniformly apricot-vermilion spots in the experiments reported here indicates that double reciprocal recombination cannot explain the results obtained.

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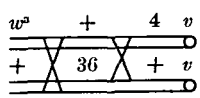
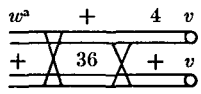
Table 4. *Phenotypes of facets produced by double reciprocal recombination both within the lozenge locus and between* w^a *and the centromere**

Strands involved in crossover†	Genotypes produced		Phenotypes of facets
1, 4 and 1, 3‡ 	(1, 4)	$\frac{+\ 36\ 4\ v}{w^a\ 36\ +\ v}$	Facets absent
	(2, 3)	$\frac{w^a\ +\ 4\ v}{+\ +\ +\ v}$	Vermilion
	(1, 3)	$\frac{+\ 36\ 4\ v}{+\ +\ +\ v}$	Vermilion
	(2, 4)	$\frac{w^a\ +\ 4\ v}{w^a\ 36\ +\ v}$	Facets absent
1, 4 and 2, 4§ 	(1, 4)	$\frac{+\ +\ 4\ v}{w^a\ +\ +\ v}$	Vermilion
	(2, 3)	$\frac{w^a\ 36\ 4\ v}{+\ 36\ +\ v}$	Facets absent
	(1, 3)	$\frac{+\ +\ 4\ v}{+\ 36\ +\ v}$	Facets absent
	(2, 4)	$\frac{w^a\ 36\ 4\ v}{w^a\ +\ +\ v}$	Apricot-vermilion

* The same phenotypes are obtained if crossing over is between *v* and 4 or between 36 and w^a.

† Reverse order of same strands results in same phenotypes.

‡ The same phenotypes are obtained when the crossover strands are 2, 3 and 2, 4; 1, 4 and 2, 3; or 1, 3 and 2, 4.

§ The same phenotypes are obtained when the crossover strands are 1, 3 and 2, 3.

(ii) *Misrepair following X-irradiation or gene conversion before chromatid replication*

Both mammalian cells and bacteria are able to repair DNA damaged by X-irradiation (see Painter, 1971). In *D. melanogaster*, Valencia & Plaut (1969) found evidence of repair replication in salivary-gland chromosomes following X-irradiation. It therefore seems likely that repair mechanisms also exist in *D. melanogaster*. In the present experiments, if mistakes or misrepair occasionally occur so that either *4* or *36* is repaired as +, a faceted spot will be formed. Gene conversion of *4* or *36* to + can also result in faceted spots. To date, mitotic conversion, or the recovery of non-reciprocal recombinant products, has been found in yeast and fungi (see Fogel & Mortimer, 1971). Non-reciprocal products of *meiosis* have been reported in three *D. melanogaster* loci: garnet (Chovnick, 1961; Hexter, 1963, 1964), maroon-like (Finnerty, Duck & Chovnick, 1970) and rosy (Chovnick *et al.* 1970; Ballantyne & Chovnick, 1971).

As shown in Table 5, faceted spots resulting from misrepair or gene conversion before chromatid replication are either entirely vermilion or entirely apricot-vermilion. The colour of the spot depends on the manner in which the chromosomes

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Table 5. *Phenotypes of facets produced by misrepair following X-irradiation or gene conversion before chromatid replication*

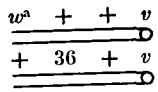
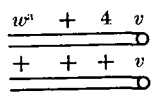
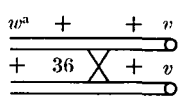
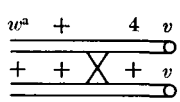
Events	Genotypes produced		Phenotypes of facets
I. No recombination after chromatid replication			
A. *4* changed to +	(1, 4)	$\frac{w^a \; + \; + \; v}{+ \; 36 \; + \; v}$	Vermilion
	(2, 3)	$\frac{w^a \; + \; + \; v}{+ \; 36 \; + \; v}$	Vermilion
	(1, 3)	$\frac{w^a \; + \; + \; v}{+ \; 36 \; + \; v}$	Vermilion
	(2, 4)	$\frac{w^a \; + \; + \; v}{+ \; 36 \; + \; v}$	Vermilion
B. *36* changed to +	(1, 4)	$\frac{w^a \; + \; 4 \; v}{+ \; + \; + \; v}$	Vermilion
	(2, 3)	$\frac{w^a \; + \; 4 \; v}{+ \; + \; + \; v}$	Vermilion
	(1, 3)	$\frac{w^a \; + \; 4 \; v}{+ \; + \; + \; v}$	Vermilion
	(2, 4)	$\frac{w^a \; + \; 4 \; v}{+ \; + \; + \; v}$	Vermilion
II. Recombination within the lozenge locus after chromatid replication			
A. *4* changed to +	(1, 4)	$\frac{w^a \; + \; + \; v}{+ \; 36 \; + \; v}$	Vermilion
	(2, 3)	$\frac{+ \; 36 \; + \; v}{w^a \; + \; + \; v}$	Vermilion
	(1, 3)	$\frac{w^a \; + \; + \; v}{w^a \; + \; + \; v}$	Apricot-vermilion
	(2, 4)	$\frac{+ \; 36 \; + \; v}{+ \; 36 \; + \; v}$	Facets absent
B. *36* changed to +	(1, 4)	$\frac{w^a \; + \; 4 \; v}{+ \; + \; + \; v}$	Vermilion
	(2, 3)	$\frac{+ \; + \; 4 \; v}{w^a \; + \; + \; v}$	Vermilion
	(1, 3)	$\frac{w^a \; + \; 4 \; v}{w^a \; + \; + \; v}$	Apricot-vermilion
	(2, 4)	$\frac{+ \; + \; 4 \; v}{+ \; + \; + \; v}$	Vermilion

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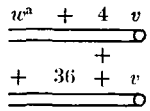
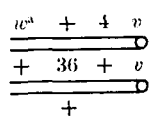
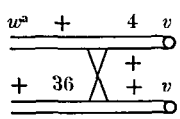
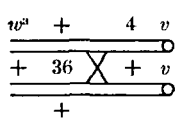
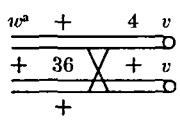
Table 6. *Phenotypes of facets produced by misrepair following X-irradiation or gen conversion after chromatid replication*

Events	Genotypes produced		Phenotypes of facets
I. No recombination after chromatid replication			
A. *4* converted to +	(1, 4)	$\frac{w^a \; + \; 4 \; v}{+ \; 36 \; + \; v}$	Facets absent
	(2, 3)	$\frac{w^a \; + \; + \; v}{+ \; 36 \; + \; v}$	Vermilion
	(1, 3)	$\frac{w^a \; + \; 4 \; v}{+ \; 36 \; + \; v}$	Facets absent
	(2, 4)	$\frac{w^a \; + \; + \; v}{+ \; 36 \; + \; v}$	Vermilion
B. *36* converted to +	(1, 4)	$\frac{w^a \; + \; 4 \; v}{+ \; + \; + \; v}$	Vermilion
	(2, 3)	$\frac{w^a \; + \; 4 \; v}{+ \; 36 \; + \; v}$	Facets absent
	(1, 3)	$\frac{w^a \; + \; 4 \; v}{+ \; 36 \; + \; v}$	Facets absent
	(2, 4)	$\frac{w^a \; + \; 4 \; v}{+ \; + \; + \; v}$	Vermilion
II. Recombination after chromatid replication			
A. *4* converted to +	(1, 4)	$\frac{w^a \; + \; 4 \; v}{+ \; 36 \; + \; v}$	Facets absent
	(2, 3)	$\frac{+ \; 36 \; + \; v}{w^a \; + \; + \; v}$	Vermilion
	(1, 3)	$\frac{w^a \; + \; 4 \; v}{w^a \; + \; + \; v}$	Apricot-vermilion
	(2, 4)	$\frac{+ \; 36 \; + \; v}{+ \; 36 \; + \; v}$	Facets absent
B. *36* converted to +	(1, 4)	$\frac{w^a \; + \; 4 \; v}{+ \; + \; + \; v}$	Vermilion
(1) Recombination between strands 2 and 3	(2, 3)	$\frac{+ \; 36 \; 4 \; v}{w^a \; + \; + \; v}$	Vermilion
	(1, 3)	$\frac{w^a \; + \; 4 \; v}{w^a \; + \; + \; v}$	Apricot-vermilion
	(2, 4)	$\frac{+ \; 36 \; 4 \; v}{+ \; + \; + \; v}$	Vermilion
(2) Recombination between strands 2 and 4	(1, 4)	$\frac{w^a \; + \; 4 \; v}{w^a \; + \; + \; v}$	Apricot-vermilion
	(2, 3)	$\frac{+ \; + \; 4 \; v}{+ \; 36 \; + \; v}$	Facets absent
	(1, 3)	$\frac{w^a \; + \; 4 \; v}{+ \; 36 \; + \; v}$	Facets absent
	(2, 4)	$\frac{+ \; + \; 4 \; v}{w^a \; + \; + \; v}$	Vermilion

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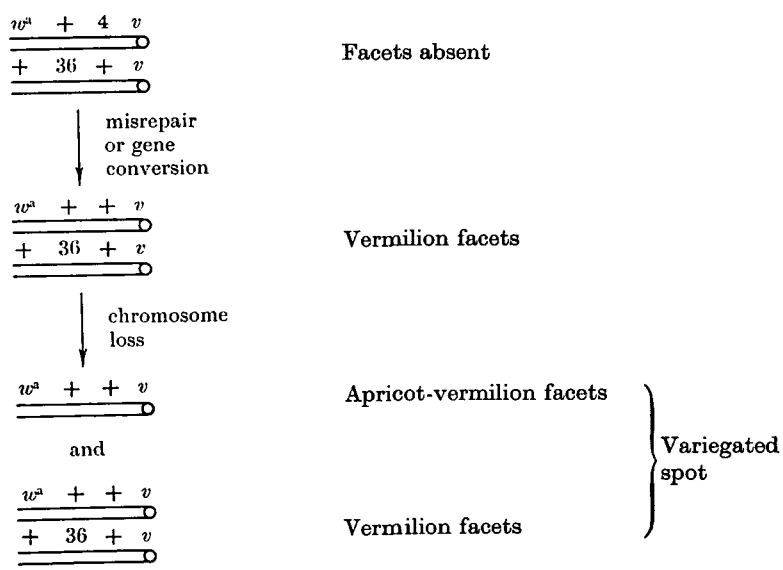
segregate during mitosis. That is, in part IIA of Table 5, one expects *either* an apricot-vermilion *or* a vermilion spot, but not both. Only in one segregation type in part IIB of Table 5 does one expect both vermilion and apricot-vermilion facets from the same mitotic division. If the two phenotypically different products of part IIB remain together during development, a variegated spot, consisting of both vermilion and apricot-vermilion facets, might be seen. However, if variegated spots were formed in this manner, one wonders why other similar events (e.g. Table 5, part IIA) which lead to entirely apricot-vermilion spots do not occur.

(iii) *Misrepair following X-irradiation or gene conversion after chromatid replication*

Faceted spots are expected in the present experiments if misrepair or gene conversion of either *4* or *36* to + occurs after chromatid replication (Table 6). As with gene conversion before chromatid replication, these spots are expected to be either uniformly vermilion or uniformly apricot-vermilion, except for one instance (Table 6, part IIB). In both Tables 5 and 6 it can be seen that vermilion and apricot-vermilion products are expected from a single mitotic event only when: (1) recombination occurs in addition to misrepair or conversion *and* (2) the misrepaired or converted strand is not involved in the recombination process. If variegated spots are produced by misrepair or conversion of this sort, one wonders (as in the previous model) why no entirely apricot-vermilion spots have been found.

Table 7. *Formation of variegated spots by misrepair or gene conversion, followed by chromosome loss*



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(iv) *Misrepair or gene conversion followed by chromosome loss*

Variegated spots were generally found in larvae irradiated at later ages, while vermilion spots were found in larvae irradiated earlier. This suggests a fourth mechanism for faceted spot formation. Tables 5 and 6 show that more entirely vermilion than entirely apricot-vermilion spots are expected during misrepair and conversional processes. It is therefore possible that all spots were originally vermilion, formed by misrepair or conversion, probably without recombination. In larvae irradiated at a later age, chromosome loss may occur more frequently than in larvae irradiated earlier. Some such chromosome losses will lead to apricot-vermilion cells (Table 7). These apricot-vermilion cells would be closely associated with vermilion cells, due to their common origin. Together, vermilion and apricot-vermilion cells would produce variegated spots. Apricot-vermilion cells would be monosomic for the *X*-chromosome. Since whole flies are known to be viable if monosomic for the *X*-chromosome, monosomic apricot-vermilion cells are also expected to be viable.

Of the four models presented – double reciprocal recombination, misrepair or gene conversion before chromatid replication, misrepair or gene conversion following chromatid replication, and misrepair or gene conversion followed by chromosome loss – the last most satisfactorily accounts for: (1) the presence of variegated and vermilion faceted spots in approximately equal numbers, (2) the absence of uniformly apricot-vermilion spots, (3) the correlation between larval age at the time of irradiation and size and colour of faceted spots.

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