

Table 1. Frequencies of yellow, Minute and dumpy mutations observed after irradiation of immature oocytes with 3000 rad of  $\gamma$ -rays at 3000 rad/min and at 30 rad/min.

Dose rate (rad/min)	Mutation frequency (%)		
	yellow	Minute	dumpy
Control	0.0000 (0/13587)	0.0442 (6/13587)	0.0000 (0/24113)
3000	0.2254 (15/6654)	0.7364 (49/6654)	0.1023 (12/11733)
30	0.0781 (9/11529)	0.2342 (27/11529)	0.0894 (18/20141)

mutations are considerably lower after irradiation at 30 rad/min than after irradiation at 3000 rad/min. Statistical tests by the use of Kastenbaum and Bowman's tables (1970) showed that such differences were highly significant, but the difference observed for dumpy mutations was far from significant. The simplest, although not only, interpretation for the relative lack of dose-rate effect on dumpy mutations may be ascribed to the fact that these mutations originate from point mutational events as well as from breakage events (Carlson and Southin 1962; Fujikawa and Inagaki 1979), while the majority of the yellow mutations induced in scute<sup>8</sup> chromosome (the one used) and Minute mutations are known to

involve minute deficiencies (see Frye 1961, and Lindsley and Grell 1968). An association of yellow mutations with minute deletions was confirmed in the present study. Almost all of the yellow mutants recovered after irradiation either at 3000 rad/min or at 30 rad/min were male lethals in the progeny test. On the other hand, it was found that 9 out of 18 dumpy mutants isolated in the low dose-rate series and 5 out of 12 in the high dose-rate series were the (ol, lv, o, v) types, a class of dumpy mutations which are usually free from aberration phenomena (Carlson and Southin 1962; Fujikawa and Inagaki 1979). The remainder were the olv types, which often originate from deficiencies or rearrangements. However, no Minute bristles were observed in the olv mutants, although a locus whose deficiency results in a Minute phenotype lies close to the dumpy locus (see Carlson and Southin 1962).

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References: Carlson, E.A. and I.I. Oster 1962, Genetics 47:561-576; Carlson, E.A. and J.L. Southin 1962, Genetics 47:321-336; Frye, S.H. 1961, Genetics 46:865-866; Fujikawa, K. and E. Inagaki 1969, Mutation Res. 63:139-146; Kastenbaum, M.A. and K.O. Bowman 1970, Mutation Res. 9:527-549; Lindsley, D.L. and E.H. Grell 1968, Genetic Variation of *D. melanogaster*.

Futch, D.G. San Diego State University, San Diego, California. Crossing over in a hybrid *D. ananassae*-*D. pallidosa* X-chromosome.

In the course of my studies on the comparative genetics of the two interfertile sibling species, *D. ananassae* and *D. pallidosa*, I have found a certain synthesized X-chromosome to be very useful, especially as a marker chromosome in the analysis of parthenogenic strains of the two

species. The chromosome is marked with the three mutations yellow, forked, and white and has been integrated by repeated (13 generations) backcrossing into otherwise normal strains of *ananassae* and *pallidosa*.

This particular chromosome was obtained from F<sub>1</sub> interspecific hybrid females heterozygous for an *ananassae* X-chromosome marked with yellow and a *pallidosa* X-chromosome marked with forked and white and resulted from a single crossover between y and f. Several genetic maps have been constructed for the *ananassae* X-chromosome with these three mutations arranged in the sequence y f w (see Moriwaki and Tobar 1975). The three alleles in this hybrid chromosome, y<sup>d</sup> (*ananassae*) and f and w (*pallidosa*), were reported by me in DIS 50 (1973). The forked mutant which has a very strong bristle effect was mistakenly identified as a singed mutant in that report because of its phenotypic resemblance to singed and because it seemed to complement another allele of forked (probably f<sub>49</sub>) carried in one of my *ananassae* stocks. However, mapping results have subsequently placed this mutant at the forked locus and closer inspection of hybrid females heterozygous for the two alleles in trans-position has revealed a very mild forked phenotype expressed by one or two bristles in most of them. Claude Hinton (pers. communication) has noticed a similar relationship between a pair of *ananassae* forked alleles in his possession, one of them being f<sub>49</sub>.

The hybrid composition of this synthesized X-chromosome and estimates of the approximate physical locations of the three mutant genes have been determined by observing how the chromo-

some crosses over in a variety of genetic backgrounds. The chromosome which is identically submetacentric in both species has a left arm which is largely ananassae containing the mutant allele  $y^d$  and the standard ananassae gene sequence rather than the standard sequence of pallidosa with the fixed inversion  $ln(1) LA$ . The right arm is mainly pallidosa containing the two mutant alleles  $f$  and  $w$  from pallidosa.

Table 1. X-Chromosome Inversions

Inversion	Break points		Approximate proportion of chromosome arm
	Hinton's Map	Seecof's Map	
$ln(1) LA$	4A; 8C	5.7; 16.0	40%
$ln(1) LB$	9A; 11B	16.7; 20.3	25%
$ln(1) RA$	14B; 17A	8.5; 2.3	50%

Table 1 provides a description of three naturally occurring inversions in pallidosa and ananassae X-chromosomes.  $ln(1) A$  is a fixed sequence in pallidosa and two strains of ananassae from Papua, New Guinea (Futch 1966). Fig. 1 represents a photomicrograph of synapsed polytene salivary gland X-chromosomes from a female larva heterozygous for  $ln(1) LA$  and  $ln(1) RA$  and the standard ananassae gene sequence. Break points

Table 2.

Exp. No.	Structural karyotype of female parent			No. progeny	% Recombinant between	
<u>Chromosome</u>						
	X = 1	2	3		y - f	f - w
	L . R	L . R	L . R			
1	$\frac{+ . +}{+ . +}$	$\frac{+ . +}{+ . +}$	$\frac{+ . +}{+ . +}$	1992	42.8	20.4
2	$\frac{+ . +}{+ . +}$	$\frac{A . +}{+ . +}$	$\frac{A . +}{+ . +}$	2216	43.2	27.8
3	$\frac{A . +}{+ . +}$	$\frac{(C;D), B. (A;B)}{(C;D), B. (A;B)}$	$\frac{+ . B}{+ . B}$	2193	9.5	22.3
4	$\frac{A . +}{+ . +}$	$\frac{(C;D), B. (A;B)}{+ . +}$	$\frac{+ . B}{+ . +}$	1795	11.1	34.6
5	$\frac{A . A}{+ . +}$	$\frac{C, (E;B)F. (A;C), D}{+ . +}$	$\frac{C . (B;C)}{+ . +}$	1222	13.7	1.6
6	$\frac{A, B . A}{+ . +}$	$\frac{C, (E;B)F. (A;C), D}{+ . +}$	$\frac{C . +}{+ . +}$	1391	1.4	2.9

of each of the 3 X-chromosome inversions are given relative to two different cytological maps (Hinton from Hinton and Downs 1975, and Seecof from Stone et al. 1957). Approximate percentages of euchromatic portions of each arm occupied by each inversion as determined from polytene chromosomes are also given.

Table 2 presents recombination data for crossovers between  $y$  and  $f$  and between  $f$  and  $w$  involving the hybrid X-chromosome in combination with various

hybrid karyotypic conditions. The two major autosomes of both species are metacentric. The letter designations of autosomal inversions are from my earlier study (Futch 1966) as are the X-chromosome inversions; '+'s indicate standard ananassae arrangements. Centromere positions are indicated by dots. Parentheses surrounding two letters, e.g., (C/D) in chromosome 2L, identify instances of overlapping inversions; in this instance  $ln(2) LC$  and  $ln(2) LD$  occur together and overlap one another in this particular pallidosa chromosome.

The data in Table 2 clearly show the relationship of  $y$  with  $ln(1) LA$ . This agrees with Hinton's observation (pers. communication) that the locus of  $y$  is between the left and right break points of  $ln(1) LA$ . Crossing-over between  $y$  and  $f$  is even further reduced by the presence of  $ln(1) LB$  which has its right-hand break point very near to the right end (proximal end) of the euchromatic portion of XL. The effect of  $ln(1) RA$  on crossing over between  $f$  and  $w$  is also very clear showing that  $w$  is located in the medial to distal part of XR, very likely within the break points of  $ln(1) RA$ . The location of  $f$  is certainly very close to the centromere end and, based on these data, probably in the proximal part of XR.

Reductions in crossing over between genes located in an X-chromosome heterozygous for structural rearrangements are very obvious here. Also of significance are increases in crossing over associated with structural heterozygosity in other chromosomes. This interchromosomal, Schultz-Redfield effect (Schultz and Redfield 1951) is particularly apparent in Experiment No.



Fig. 1. Photomicrograph of synapsed polytene X-chromosome of a *D. ananassae* female larva heterozygous for *ln* (1) LA in the left arm (XL) and *ln* (1) RA in the right arm (XR).

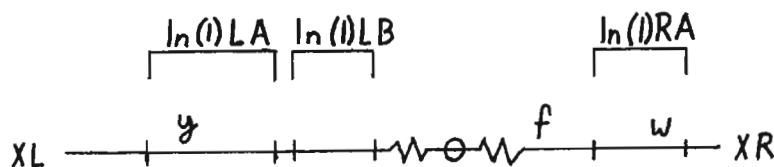


Fig. 2. Diagram of *ananassae-pallidosa* X-chromosome showing approximate locations of break points of three inversions and genes *y*, *f* and *w*.

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Galus, H.M., I.B. Perelle and L. Ehrman. SUNY College at Purchase, Purchase, New York. The heritability of egg length in *D. paulistorum*.

employed hatchability as the criterion of fitness and found that hatchability was higher from intermediate-sized eggs. Studies of artificial selection for egg length have also been undertaken utilizing this same species (Bell, Moore and Warren 1955; Parsons 1964). In these instances artificial selection for egg length resulted in the culling of both large- and small-sized lines diverging from unselected control lines. Maximum divergence occurred by the tenth generation of selection after which regression toward the unselected mean appeared to take place.

Research published by Perelle, Daniels and Ehrman (1980) indicates that egg length heritability is low in the Mesitas strain of *D. paulistorum*. A bimodal distribution resulted when

4 where the crossover frequency between *f* and *w* is 34.6% compared to 22.3% in Experiment No. 3, a highly significant difference ( $\chi^2 = 73.12$ ,  $p < .001$ ). A similar interchromosomal effect resulting in the enhancement of crossing over between *f* and *w* was found when Experiments 1 and 2 were compared ( $\chi^2 = 30.18$ ,  $p < .001$ ). The possibility of an interbrachial effect in the X-chromosome was also investigated but with no clear-cut results. The difference in crossing over between *y* and *f* in Experiments 4 and 5 ( $\chi^2 = 4.30$ ,  $p < .05$ ) is quite possibly due only to additional autosomal inversions while that between *f* and *w* in Experiments 5 and 6 ( $\chi^2 = 3.92$ ,  $p < .05$ ) could be interbrachial caused by the addition of *ln* (1) LB.

Fig. 2 presents a schematic representation of the X-chromosomes of *ananassae* and *pallidosa* showing the suggested locations of the three genes, *y*, *f* and *w*, and the three inversions, *ln* (1) LA, *ln* (1) LB, and *ln* (1) RA. The hybrid X-chromosome that it represents has been of considerable value to me since it has allowed me to examine aspects of chromosome behavior in two very closely related species using essentially the same chromosome in each species.

References: Futch, D.G. 1966, Univ. Texas Publ. 6615: 79-120; Hinton, C.W. and J.E. Downs 1975, J. Heredity 66: 353-361; Moriwaki, D. and Y.N. Tobari 1975, Handbook of Gene-

Research done by Curtsinger (1976a,b) indicates that egg length in the Oregon-R *D. melanogaster* strain is influenced by stabilizing selection. This is a type of natural selection in which intermediate phenotypes are favored. Curtsinger