Moriwaki, D. and Y. N. Tobari. Tokyo Metropolitan University, Japan. Unusual segregation of the four phenotypes in the dihybrid F_2 generation caused by male crossing over in D. ananassae.

In almost all species of Drosophila male crossing over does not occur spontaneously. Accordingly, an appearance of some flies of double recessive in the F_2 generation of the ordinary dihybrid experiment is liable to lead to the conclusion that the two loci are located on different chromosomes. However, if there exists a spontaneous crossing over in males, the appearance of double recessives does not necessarily mean their independence. In D. ananassae, as reported previously, male crossing over has been known to occur; thereupon it became necessary to reexamine some of the linkage data, concerning several mutant genes which were previously reported to be independent.

Let us take b (black) and se (sepia) for instance. Beginning with a cross of b x se, in the F_2 there appeared a considerable number of b se besides +, b, and se. The frequency of b se was different from the value of 1/16 expected under the condition of independent assortment. Nevertheless, it was concluded that b belonged to the 2nd chromosome and se to the 3rd (the previous conclusion to be corrected in this note). However, further tests by usual back cross technique using the double recessive flies, have shown that these two genes, b and se, must be linked in the same chromosome, although the loci are located fairly apart from each other. The data leading to the conclusion are as follows:

Region	Recombination value ♀♀	♂♂
	48.2% (1781 flies)	4.0% (1624 flies)
b ~ se	49.6% (2404 flies)	12.5% (319 flies)
	48.5% (610 flies)	12.2% (566 flies)

Concerning the estimation of recombination value between two genes, Mather (1938) has discussed the case where the recombination fraction differs in the male and female gametogenesis, representing the former by p_1 and the latter by p_2. The gamete series from the coupling case were expected as:

	AB	Ab	aB	ab
♂	$(1/2)(1 - p_1)$	$(1/2)p_1$	$(1/2)p_1$	$(1/2)(1 - p_1)$
♀	$(1/2)(1 - p_2)$	$(1/2)p_2$	$(1/2)p_2$	$(1/2)(1 - p_2)$

Writing P for $(1 - p_1)(1 - p_2)$, he maximized the logarithum likelihood expression obtained from the expectations of the four classes in the F_2, and arrived at the quadratic equation, $P^2(AB + Ab + aB + ab) - P(AB - ab - 2Ab - 2aB) - 2ab = 0$, where AB, Ab, aB, and ab represented the observed frequencies of the four classes indicated by the letters. Applying this formula to the present case, we reexamined almost every one of the unusual segregation cases. Two of them are sampled below.

(Example 1: repulsion) b^{65} (black-65, allelic to) x se > ♀ x ♂ >

AB(+)	Ab(se)	aB(b^{65})	ab(b^{65}se)	Total
400	126	156	7	689

$689P^2 + 171P - 14 = 0$ $P = (1 - p_1)(1 - p_2) = 0.065 \pm 0.018$

If we assume that $1 - p_2 = 0.5$, approximating to 48 ~ 50% (♀, R.V), we have $p_1 = 0.87$. As this is the repulsion case, the male recombination fraction is $1 - p_1 = 0.130$ (0.094~0.163).

(Example 2: repulsion) b x ma(maroon) > ♀ x ♂ >

AB(+)	Ab(ma)	aB(b)	ab(b ma)	Total
565	230	214	10	1019

$1019P^2 + 333P - 20 = 0$ $P = (1 - p_1)(1 - p_2) = 0.052 \pm 0.013$

If we assume that $1 - p_2 = 0.45$, approximating to 45~ 46% (♀ R.V.), we have $1 - p_1 = 0.115$ (0.086 ~ 0.140) as the male recombination fraction.

These results are at large consistent with the recombination values in the female and male obtained by the back cross technique: hence our revised conclusion seems to be verified. Thus, the mutant genes, st(→ cd, cardinal), se, and ba^{65}, which were once assigned

to the 3rd chromosome should be reassigned to the 2nd. Also the chromosome which bears M, px, and others must be the 3rd, not the 4th. At present no mutant gene is identified in the 4th chromosome. Here we correct our report in DIS 42:81 as follows:

The 16th line: "2-chromosome" for "3-chromosome"
The last line: "3-chromosome" for "2- and 4-chromosomes"
Several places: "cd(cardinal)" for "st(scarlet)".

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Control of chromosome pairing and the directed segregation of sex chromosomes in XYY males.

The existence of special sites (= collochores) in Xh for regular conjunction of the X and Y chromosomes in males has been demonstrated in spermatogenesis by Cooper (1964). The intercalation of Xe between collochores in In(1)Xh chromosomes with right break distal to NO apparently allows both collochores to pair simultaneously, which Cooper interprets to mean the loss of normally occurring intrachromosomal control over chromosome pairing. Does such behavior influence genetic segregation of the sex chromosomes in XYY males? From crosses of $In(1)w^{m4}/sc^{8}Y/sc^{8}Y$ males (single male/vial) to w^{m4} females we obtained 41 $w^{m4}w^{m4}$ (white eyes) daughters, 427 $w^{m4}w^{m4}Y$ (red eyes) daughters, 351 $w^{m4}Y$ (white eyes) sons and 24 $w^{m4}YY$ (red eyes) sons. Thus for XYY males carrying $In(1)w^{m4}$ segregation is nonrandom in that the Y's separate more often than the 67% expected for nonpreferential segregation (Grell, 1958, X International Congress of Genetics, Proceedings, Vol. II). Comparable crosses of $In(1)m^{m4}/B^{S}Y/y^{+}Y$ males and their $y/B^{S}Y/y^{+}Y$ brothers to y cv v f females yield results, given in Table 1, that each indicate directed segregation but the two sets of results are not significantly different from each other. Any role of the non-functional pole in spermatogenesis to account for the apparent non-randomness of segregation is difficult to evaluate and cannot entirely be ruled out. However, it may be noted for the three crosses that each of the three elements is recovered in 50% of the gametes and that complementary segregation classes are approximately equal, which suggests that the observed classes adequately reflect disjunction patterns in MI.

Table 1

Results of crosses of $y/B^{S}Y/sc^{8}Y$ ♂♂ and their $In(1)w^{m4}/B^{S}Y/sc^{8}Y$ brothers to y cv v f ♀♀

Fathers	Progeny Classes						
	y^{+}♀♀	y^{+} B^{S}♀♀	y ♀♀	y B^{S}♀♀	y^{+} cv v f♂♂	y cv v f B^{S}♂♂	y^{+} cv v f B^{S}♂♂
y	238	--	142	217	239	286	77
w^{m4}	294	158	--	--	215	232	41

Since $In(1)w^{m4}$ males present a different configuration in the first meiotic metaphase from males with a normal X but yield almost identical segregation classes, it may be asked whether the inferred intrachromosomal control over conjunction of collochores in spermatogenesis has any function in determining disjunctional patterns of conjoined chromosomes. Nonrandom assortment is consistent with the three sex chromosomes being associated at MI, as suggested by the trivalent formation observed cytologically. In this sense the role of collochores in chromosome conjunction is not questioned, although the simplest view of the cytological pictures predicts predominantly X - YY segregation, which is not observed. In(1)Xh chromosomes are also of interest because of their behavior when homozygous in oogenesis: X-chromosome exchange is reduced in XXY females relative to their XX sisters. Possibly a relation exists between such behavior in females and the loss of control hypothesized from cytological observations in spermatogenesis.