A MODEL FOR SYNAPSIS IN FEMALES HETEROZYGOUS FOR THE CHERRY SUB-LOCUS DUPLICATION IN DROSOPHILA¹

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IN *Drosophila* the white-eye locus consists of five subloci in the fourth of which JUDD (1964) has reported a duplication (herein indicated as 4 4). The allele cherry (w^{ch}) is at this sublocus. The duplication ordinarily carries no mutant allele and by itself causes no change in eye color. It is detectible by virtue of the fact that it enhances zeste (z , an eye color mutation at the left end of the X). The identification and location of the duplication involved the employment of w^a (apricot at sublocus 3) and w^{ch} (cherry, at sublocus 4) as well as zeste and outside markers close to the white locus.

A testcross of a female heterozygous for the duplication in one X (red in expression) and $w^a w^{ch}$ in the other (a combination which is white) yields F_2 females which are predominantly either red or white. However, as a result of crossing over between w^a and w^{ch} , JUDD occasionally detected F_2 females that were either apricot or cherry. These are referred to as "exceptions." Some of the apricot exceptions had the duplication (five in a total of about 71,000 females) and some did not (21 in the total); none of the cherry exceptions (six in the total) had it. If we show all the elements at the white locus (1 to 5), then the above F_2 exceptions would be as listed in Table 1 (only the X derived from the female parent is shown, the X from the male is $w^a w^{ch}$).

In order to account for the above results, JUDD assumes that pairing in the heterozygous female may be of two kinds, as shown in Figure 1 (in which the arrow indicates the crossover point).

Crossing over between w^a and w^{ch} in type I pairing would give apricot with the duplication (w^a 4 4), and in type II, apricot with no duplication (w^a 4). The reciprocal crossover products would be formed in each case. In type I pairing they would be 3 w^{ch} , the cherry exceptions. In type II, they would be 3 4 w^{ch} . This

TABLE 1

Exceptions among 71,000 F_2 females from a cross of F_1 1 2 3 4 4 5/1 2 $w^a w^{ch}$ 5 female $\times$ 1 2 $w^a w^{ch}$ 5 male, as reported by JUDD

Exception	White locus	Number
Apricot with duplication	1 2 w^a 4 4 5	5
Apricot without duplication	1 2 w^a 4 5	21
Cherry (all without duplication)	1 2 3 w^{ch} 5	6

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	Pairing	Crossovers	Phenotypic Expression	No.
Type I		$1\ 2\ w^a\ 4\ 4\ 5$	apricot (with duplication)	5
		$1\ 2\ 3\ w^{ch}\ 5$	cherry (without duplication)	6
or				
Type II		$1\ 2\ w^a\ 4\ 5$	apricot (without duplication)	21
		$1\ 2\ 3\ 4\ w^{ch}\ 5$	red (not recognized as exceptions)	

FIGURE 1.—Chromosome pairing on JUDD's model in a female heterozygous for the cherry sublocus duplication, and the products of crossing over between w^a and w^{ch} as expected on the model.

class would appear red because it carries the normal allele of w^{ch} in the left element of the duplication. It is no different phenotypically from one of the non-crossover classes, and is therefore not recognized when the progeny are examined for exceptions. Presumably, however, there are the same number of them as the reciprocal crossover class (apricot without duplication), of which there were 21, making 42 crossovers from type II pairing. This is to be compared with 11 (5 + 6) from type I.

Although the above model accounts for the results of the cross, yet it makes unusual assumptions as regards synapsis in so far as in type I pairing the elements of the white locus to the right of the crossover point (indicated by the arrow) would be improperly paired; and in type II, those to the left.

It would seem that the results could more simply be accounted for on the assumption that all elements of the white locus are properly paired in the structural heterozygote except the left element of the duplication, and that this is unpaired as shown in Figure 2 (in which w^a would be in Element 3 of the structurally normal chromosome and w^{ch} in 4).

Crossing over might occur either between w^a and the first element of the duplication (Figure 3a), or between w^a and the second element (Figure 3b). In either event, no change would be required in the pairing of the elements.

It will be seen that on the present model the apricot exceptions might either have the duplication ($w^a\ 4\ 4$, Figure 3a) or not ($w^a\ 4$, Figure 3b) and that the cherry exceptions would not (3 w^{ch} , Figure 3a) as demanded by the results of the cross. The class reciprocal to the apricot, no duplication class would be the unrecognized reds (as before). On JUDD's model the greater frequency of the apricot exceptions without the duplication plus the presumed unrecognized reds (a total of 42) as compared with the other two crossover classes (11) would be due to a

FIGURE 2.—Proposed model for synapsis in a female heterozygous for a duplication (4 4) of the cherry sublocus in *Drosophila*.

FIGURE 3.—Proposed model for crossing over between w^a and w^{ch} in a female heterozygous for the cherry sublocus duplication. (a) Crossing over between w^a and the first element of the duplication; (b) between w^a and the second element.

difference in the frequency of the two pairing arrangements; on the present model, simply to a difference in the crossover rates between the elements involved in the two cases.

On a model of the present kind (involving correct pairing for the most part), the results would not be explained if the right element of the duplication was unpaired instead of the left, for in this event all of the apricot exceptions would have the duplication (instead of only five of the 26). This fact clearly indicates that chromosome pairing progresses from the proximal to the distal end of the chromosome, since then the right element would pair before the left, and as the structurally normal homologue has only one Element 4, the left one in the duplication would have no pairing partner.

Judd interprets type II pairing on his model as resulting from the pairing of the chromosomes from the proximal to the distal end, and as type II is more frequent than type I (which would require pairing in the opposite direction) he concludes that the pairing tends to be "polarized." On the present model, pairing would always be polarized. In any event, the genetic evidence for polarized pairing as derived from Judd's experiments is in accord with the classical account of chromosome pairing as cytologically observed at zygotene.

In the duplication heterozygote, the structurally normal chromosome is in a sense a deletion with respect to the homologue with the duplication, and in a salivary gland preparation of a deletion heterozygote, pairing is exact for all homologous elements outside the deletion. This fact would lend support to the model herein being proposed for the manner of synapsis in a female heterozygous for the cherry sublocus duplication. In general, salivary gland studies show that there is no disturbance in the exact pairing of allelic elements in a structural heterozygote, whether inversion, translocation or deletion heterozygote. It is unlikely that the present case should be an exception.

Crossing over between w^a and w^{ch} is much more frequent in a female hetero-

zygous for the duplication ($3\ 4\ 4/w^a\ w^{ch}$) than in a structurally normal one, but this increased frequency is due almost entirely, if not entirely, to crossovers involving breaks between the two elements of the duplication. Neither the present model nor Judd's explains the increased frequency in question. Whether or not an element of the duplicated sublocus participated in pairing would expectedly have little or no effect on the amount of crossing over between w^a and w^{ch} since the element in question is regarded as a subgene and so no crossing over would occur within it. All exchanges would occur between it and the neighboring elements and therefore such exchanges would not necessarily be prevented when the element in question was excluded from pairing, as shown in Figure 3.

The breakage rate between 3 and the first element of the duplicated sublocus is approximately the same as between 3 and 4 in the structurally normal female. Moreover, in a female of genotype $w^{bf}\ 3\ 4\ 4/2\ 3\ 4$ (w^{bf} , buff in sublocus 2), the total numbers of crossovers recovered by Judd in the interval between w^{bf} and the first element of $4\ 4$ (i.e., between subloci 2 and 3 plus those between 3 and $4\ 4$) was 25 in a total of 74,000 females. Assuming that the number between 3 and $4\ 4$ in this buff-duplication heterozygote is the same as in the $3\ 4\ 4/w^a\ w^{ch}$ female (11 in about the same total number of females), this would make about $25 - 11$, or 14 between w^{bf} and 3. This frequency of crossovers is not unusually low for the w^{bf} to 3 interval; neither is 11 for the 3 to $4\ 4$ interval (about the rate reported by GREEN [1959] between w^a and w^{ch} in the structurally normal female). The duplication is therefore probably having no effect on the crossover rate between the elements of the white locus to its left. This noneffect on the left is as expected on the present model, though on Judd's model a considerable reduction in the rate here would be expected because of the relatively high frequency of type II pairing on his model, involving improper pairing of the left elements.

The elegant design of Judd's experiments and the keen analysis of the results made possible the detection and location of the cherry sublocus duplication. It would seem, however, that the simple model herein proposed in explanation of the results of the testcross is worth considering, since it makes no unusual assumptions in regard to the nature of synapsis in the structural heterozygote. Undoubtedly, asymmetrical pairing sometimes occurs in *Drosophila*, but it is a rare event, comparable to mutation in frequency. As Judd has shown, the cherry sublocus duplication arose in this way, but it seems unlikely that it should now cause asymmetrical pairing as a regular occurrence in the heterozygote.

Asymmetrical pairing, in the sense of unequal crossing over, occurs when homozygous Bar gives rise to the normal allele of Bar and to double-Bar. But again, this is a relatively rare event. There is no evidence that structural heterozygosity in the Bar region regularly causes the chromosomes to undergo asymmetrical pairing either to the left or right of the Bar region. Similar considerations apply to Star and Beadex.

SUMMARY

A model is proposed to account for the "exceptional" types of F_2 females produced by a parent heterozygous for an X with a duplication of the cherry sub-

locus and a structurally normal X with apricot and cherry in *Drosophila*, as reported by JUDD (1964). This model is based on the assumption that all elements (subloci) of the white locus are properly paired in the heterozygote except the left element of the duplication, which would then be without a pairing partner. Pairing on the present model would be similar to that seen in a salivary gland preparation of a deletion heterozygote. The normal chromosome in the present instance would correspond to a deletion with respect to one of the elements of the duplication in the homologue. The left element of the duplication is assumed to be unpaired rather than the right because this arrangement accounts for the experimental results better than the alternate arrangement. An unpaired left element (rather than right) implies that at meiosis chromosome pairing proceeds in zipper-like manner from the proximal to the distal end of the pairing partners and is in accord with the classical account of synapsis as cytologically seen at zygotene.

LITERATURE CITED

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