EFFECTS OF A COMPOUND DUPLICATION OF THE X CHROMOSOME OF DROSOPHILA MELANOGASTER

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INTRODUCTION

DOBZHANSKY (1934) has described effects on crossing over and disjunction of duplicating fragments of the X chromosome of *Drosophila melanogaster.* He has found that fragments partially suppress crossing over between the entire X's and that the effect is correlated with the length of the fragment. Some of the fragments were free and controlled by their own spindle fiber attachments and some others were attached to an entire X chromosome at the spindle fiber end.

Duplication 100 described here differs in length and in composition from those described in DOBZHANSKY'S study; the results are thus largely an extension of his results. The study was undertaken especially for a comparison of the effects of the same fragment in both states, when free and when attached to an entire X. Some effects of a Y chromosome in different combinations of two X's and the fragment have been observed.

MATERIAL

The duplication arose spontaneously in an apricot male which was mated to an attached-X yellow female. It was found, December, 1922, as a single not-yellow daughter, sister to the numerous yellow daughters. As in similar duplications, which have frequently been obtained later by irradiation of males, the X derived from the male was a deficient chromosome; it contained a distal and a proximal section and lacked the middle section of a normal X. In this case the deficient sperm had fertilized an $\underline{XX}$ egg in which the attached X's both carried the gene for yellow; the extra fragment, that is, the duplication, carried only wild type alleles, consequently the duplication female was not-yellow. The formula is $\underline{XX}X^{pd}$ (fig. 1 a). When the not-yellow female was crossed to an apricot male the duplication-bearing daughters received a Y chromosome from their father and were therefore $\underline{XX}X^{pd}Y$ (fig. 1 b).

One not-yellow daughter of the original duplication female differed from the others in that the fragment had become attached to one of the whole X chromosomes received from the mother; she had received her second X from her father. The formula is $X\underline{XX}^{pd}$ (fig. 1 c). A chromosome having a fragment attached to it would have resulted if crossing over had taken place between the proximal section of the fragment (X^p) and one of the attached X's. Such crossovers continued to occur rarely in the attached-X duplication stock ($\underline{XX}X^{pd}Y$), and the attached-duplication lines derived from them are known as Dp (1;1) 100. A small percentage of $X\underline{XX}^{pd}Y$ females (fig. 1 d) regularly occurs in these lines.

A fifth combination of the X homologues arose when an egg carrying the free duplicating fragment was fertilized by a rare type of non-disjunctional sperm carrying two paternal free X's. The formula is XXX^{pd} (fig. 1 e); the line is Dp (1;f) 100. The two X chromosomes in figure 1 e are marked with the symbols denoting mutant loci used in studying crossing over, to be described in detail below.

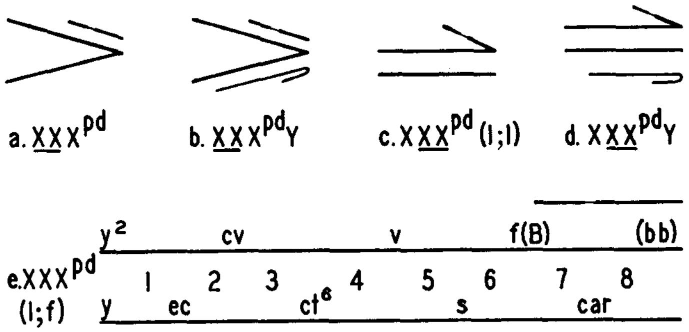

FIGURE 1.—Diagram representing the sex chromosomes (short line for X^{pd} or fragment, long line for X and hook for Y) in females of lines of Dp-100. Symbols for mutant characters used in crossover experiments and the numbers of the regions delimited by the mutant genes are entered in e.

From the Dp (1;f) line, in which the X's are not attached and the fragment also is free, it has been easy to determine genetically the extent of the deficiency of the fragment by observing the character of females carrying X's homozygous for mutant genes, and the wild type fragment. The distal section of the fragment (X^d) carries normal alleles of seven tested mutant characters (*y*, *ac*, *sc*, *svr*, *sta*, *br*, *pn*) from yellow to prune inclusive. The proximal section (X^p) carries normal alleles of fused (*fu*), carnation (*car*) and bobbed (*bb*). The fragment was found to be deficient for 16 tested loci in the middle of the chromosome including white to outstretched, vibrissae, small-eye and probably Beadex (*Bx*). There are exaggeration effects produced in achaete, facet and Beadex. Bar (*B*) eyes are narrower in duplication females whose X's are homozygous or heterozygous for Bar than they are in the respective non-duplication sisters, and also the eyes were very narrow in the few surviving duplication Bar males that have been observed.

The fragment is nearly always lethal in males. The rare survivors have been omitted from the tables. Females carrying the fragment show somatic effects of X chromosome duplication described by other authors such as narrow wings having straight outer margins and sometimes nicked or very serrated inner margins and tips. In extreme cases less than half of the wing remains, deeply indented. DOBZHANSKY and SCHULTZ (1931) found that intersexes carrying Dp-100 are of extreme female type, even breeding as female in one case of five that were tested.

Cytological preparations of oögonial cells have shown the duplication both in the attached, and in the free condition when the X's were free or attached. DOBZHANSKY (1932) measured the fragment in metaphase plates of oögonial divisions and found it to be about two-thirds of the length of an X, never as much as three-fourths. The measurements showed that the distal section of the fragment in metaphase plates comprises somewhat less than one-third of the length of the fragment. Measured by locations of genes on the salivary chromosome map, the proximal section of the fragment is about once and a half times as long as the distal section and the whole fragment is less than one-fourth of the length of the whole chromosome (fig. 2).

In an experiment (not used in this study) with a line of free X's and the fragment free (XXX^{pd}), two female mosaics and two gynandromorphs were observed, and in a line of attached X's and free fragment one female mosaic was observed. They can all be explained by somatic elimination; in one gynandromorph both an X and the fragment had been eliminated together or at two different divisions in the formation of the male region.

CROSSING OVER BETWEEN ENTIRE X CHROMOSOMES

Frequency of crossing over has been studied in the two forms of the duplication in which the two entire X's are not attached to each other, that is, in the XXX^{pd} line, Dp (1;f) 100, and in the $X\underline{XX}^{pd}$ line, Dp(1;1) 100, and also in the latter line when a Y was present ($X\underline{XX}^{pd}Y$), (tables 6–10, Appendix).

Females of the constitution Dp/y^2*cv v f*/*y ec* ct^6*s car* were mated to *y ec cv* ct^6 *v* s^2 *f car* bb^l (*y*X9) males, in alternated testcrosses, or were outcrossed to males marked by *B*; in experiment 7, one X was marked with *B* instead of *f*, and with *bb* to delimit the eighth region. Sisters of the duplication females were used as controls. In the (1;1) line the duplicating fragment was attached to the y^2 *cv v f* chromosome. In the crossover experiments and in all others to be reported the entire X's of the duplication females have carried yellow (or y^2); consequently when they were mated to males that were *y* or y^2 the character not-yellow was an indicator of the presence of the fragment, except when exchange between X and the distal section of the fragment (X^d) had taken place. Such X^d/X crossing over has been observed only in a few males and in two females (in experiment 7) which were not yellow but were carnation or bobbed showing that the fragment (X^p) was not present.

In testcrosses and in outcrosses of the line of the free fragment (XXX^{pd}) females that were y^2 but were wild type at other marked loci had been

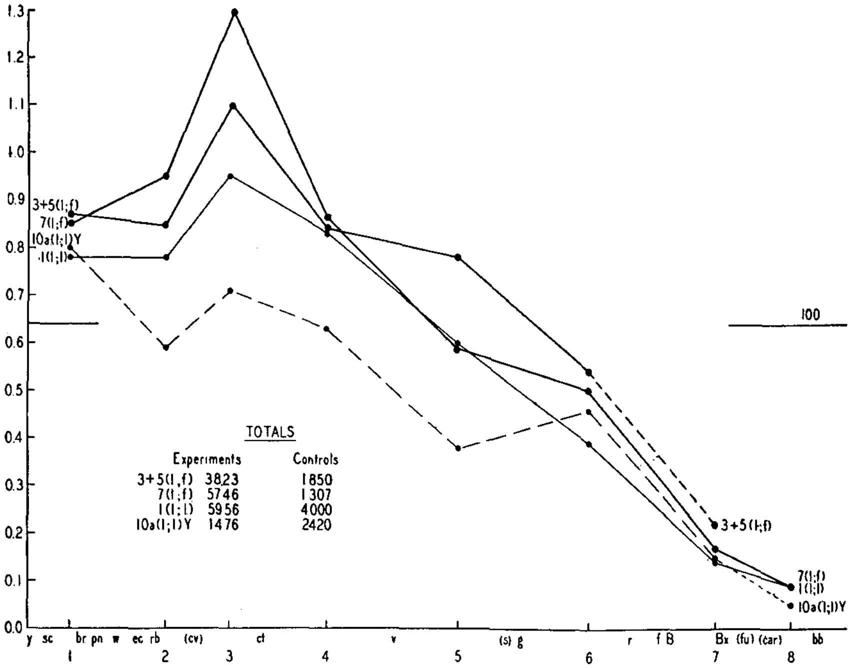

FIGURE 2.—Relation of percents of crossing over, in 8 regions between the two entire X chromosomes in Dp-100, to percents from controls (vertical axis) plotted against the salivary chromosome map (longitudinal axis). Relative positions of mutant genes on the chromosome (according to MACKENSON and BRIDGES) are marked by the symbols for the mutant characters (those in parenthesis have not been precisely located). The extent of the duplicating fragment is indicated by horizontal lines extending over the loci included in the distal and proximal components of the fragment. The fragment was free in experiments. 3+5 and 7 and was attached to the proximal end of an X in experiments 1 and 10a; a Y chromosome was also present in experiment 10a. In experiment 3+5, half of the crossovers between the proximal section of the fragment and X were included in region 7.

derived from XX eggs fertilized by Y sperm. In outcrosses of the line of attached fragment occurred wild type duplication females which were derived from $\underline{XX}X^{pd}$ eggs fertilized by Y sperm. These two types may for convenience be called "exceptional females." They occur regularly (as do "exceptions" from XXY females from which the term is borrowed) but they are exceptions in the sense that they form much smaller classes than the females from X, XX^{pd} or $\underline{XX}^{pd}$ eggs.

The term "percent of crossing over" is used to denote the percent of times that crossing over has occurred among total chromatids represented by observed zygotes, and not the percent obtained directly from observed regular zygotes. This method has been chosen because all of the chromatids are involved in the mechanism of crossing over. Hence the percents of crossing over have been reckoned as of a total that includes the chromatids of "exceptional" gametes (whether they produce viable or lethal zygotes) and of gametes of other smaller classes. Exceptional zygotes that survive in the line of the free fragment (XXX^{pd}), that is y^2 XXY females, represent four exceptional gametes (two containing the maternal X's and two containing the fragment, one of each fertilized by X or by Y sperm) since three of the four resulting zygotes, namely XXX, XX^{pd} and $X^{pd}Y$, are lethal. When the total counts include half of the zygotes (for example, non-duplication males and females) the exceptional females count as two chromatids, or as one chromatid when only males or females that do not carry the duplication are counted. The chromatids of the exceptions were in some cases crossovers and were rated accordingly.

In lines of the attached fragment ($X\underline{XX^{pd}}$ and $X\underline{XX^{pd}}Y$) y^2 females are crossovers between the proximal fragment and the free X; their X's are attached to each other and they represent two chromatids each, when the total includes non-duplication females and males (the lethal zygotes are pointed out in connection with X^p/X exchange). The exceptional females in these lines, from very infrequent $X\underline{XX^{pd}}$-O segregation, are wild type duplication females ($X\underline{XX^{pd}}Y$) and are treated as are exceptions in the line (1; f).

Table 1 shows the percents of crossing over from exchange between entire X's and the relation of those percents to the corresponding percents from controls. These are also shown graphically in figure 2.

The most noticeable result is the marked reduction in X/X crossing over in the presence of the fragment, especially in the region homologous to the proximal section of the fragment. When a Y was present as well as the fragment attached to an X, crossing over between the X's was still further reduced (experiment 10a). The results will be discussed later.

CROSSING OVER BETWEEN THE PROXIMAL AND DISTAL SECTIONS OF THE FRAGMENT AND AN ENTIRE X

Conclusions in regard to the frequency of X^p/X crossing over have been pieced together from the results obtained in different kinds of experiments and are summarized in table 3.

In the testcross experiment 7, in which the fragment was free and one maternal chromosome was marked with *bb*, there were three unique types that have been used to allocate the ambiguous

TABLE 1

Percents of crossing over between entire X's in Dp-100 in the presence of: experiments 3–7, the free fragment in XXX^{pd}*; experiment 1, the attached fragment in* $X\underline{XX}^{pd}$*; in experiment 10a, the attached fragment and Y in* $X\underline{XX}^{pd}Y$.

REGION	1 *y-ec*	2 *ec-cv*	3 *cv-ct*	4 *ct-v*	5 *v-s*	6 *s-f(B)*	7 *f(B)-car*	8 *car-bb*	TOTAL CHROMATIDS
exp. 3	7.3	8.9	8.6	12.3	7.3	7.4	1.36*	—	2225
control	7.9	10.4	8.8	15.2	8.7	13.2	5.8	—	1392
ratio	.93	.86	.98	.81	.84	.56	.22		
exp. 5	6.3	8.1	9.2	14.2	6.3	5.8	1.3*	—	1599
control	7.9	9.2	5.7	16.8	9.2	10.5	6.4	—	458
ratio	.80	.88	1.6	.85	.69	.55	.20		
exp. 7	6.2	8.6	10.7	13.9	5.5	7.4	1.13	0.55	5682
control	7.3	9.0	8.2	16.2	9.4	14.8	6.7	5.8	1307
ratio	.85	.95	1.3	.86	.59	.50	.17	.09	
exp. 1	4.7	7.6	8.1	13.0	6.5	5.4	1.0	0.54	5956
control	6.0	9.8	8.6	15.6	10.9	13.8	7.1		4000
ratio	.78	.78	.94	.83	.60	.39	.14	.09†	
exp 10a	4.8	5.8	6.1	9.8	4.2	6.4	1.1	0.27	1476
ratio	.80	.59	.71	.63	.38	.46	.15	.05†	

* Includes one half the quota of X^p/X crossovers at 7; the other half is included among noncrossovers for region 7.

† Based on control of experiment 7.

TABLE 2

Experiment 7, Dp (1;f)/y^2 *cv v B bb/*y^2 *ec* ct^6 *s car ♀ by yX9 ♂. Allocation of observed types of crossovers.*

	X/X CROSSOVERS						X^p CROSSOVERS				X^d/X CROSSOVERS			
REGION	—, 7		—, 8		—, 7, 8		7		8		Dp 1		non-Dp 1	
	·	·	·	·	·	·	·	·	·	·	y^2	*y*	·	*ec*
	·	·	·	·	·	·	·	·	·	·	*cv*	*ec*	*cv*	ct^6
	·	·	·	·	·	·	·	·	·	·	*v*	ct^6	*v*	*s*
	·	*s*	·	*s*	·	*s*	·	*s*	·	*s*		*s*		
	B	·	*B*	·	*B*		*B*		*B*		*B*		*B*	
	car	·		*car*	*car*					*car*				*car*
		bb		*bb*	*bb*									
♀ ♀ observed unique	37	27		11	0						1		1	1
ambiguous			27					5						
♀ ♀ observed and allocated†	37	27	**20**	11	0	**0**	**5**	**5**	**2**	**2**	1	**0**	1	1
♂ ♂ observed unique	46												2	1

† Allocations are printed in bold-faced type.

types of crossovers due to exchange in the region homologous to the proximal component of the fragment. Crossovers were determined in non-duplication female offspring.

Of the two complementary types of double crossovers between entire X's at 7 and 8, one, which is *B car bb*, is unique and none of this type was observed (table 2), as expected for so short a section (mutant characters to the left of *s* are disregarded since they varied with distal crossing over between the X's which is irrelevant to the present discussion). The complementary type (*s* not-*B* not-*car* not-*bb*) is ambiguous since it is also the type that would result (more often) from exchange at 7 between the fragment and the X carrying *s* and *car*. In the absence of the unique 7, 8 double crossover type, the 5 females of the sable type are all allocated to the class of X^p/X crossover at 7. The same *s* (*y* or y^2) type might also be a duplication female in which the fragment was yellow, from exchange between an X and the distal section of the fragment. X^d/X crossovers are rare, and none of the sable (*y* or y^2) females is allocated to this class. A y^2 *cv v B* female of the complementary type showed by somatic characteristics of duplication that she was of the class.

TABLE 3

Corrected percent of crossing over involving the fragments and entire X's in Dp-100, and in other duplications from the data of DOBZHANSKY *(1934) and* PHILIP *(1934). Percents for experiment 7 are based on allocations shown in table 2.*

KIND OF CROSSOVER		X/X		X^p/X				X^d/X
				X-EGGS		XX-EGGS		
	REGION	7	8	7	8	7	8	
No. of Exp.	Constitution of ♀							
7	XXX^{pd}	1.13	0.55	0.18	0.07	—	—	0.04
9d	XXX^{pd}			0.10	—	0.19	—	
9	XXX^{pd}			0.04		0.10		0.01
				X^p/X				
				with att. X		with free X		
1	$X\underline{X}X^{pd}$	1.0	0.54	—		0.02		none
1d	$X\underline{X}X^{pd}$			none		0.06		none
10a	$X\underline{X}X^{pd}Y$	1.09	0.27	0.15		0.15		none
10b	$X\underline{X}X^{pd}Y$			0.08		0.06		none
				X^p/X				
Dp-138	$X\underline{X}X^{p}$	1.24	0.15					
	$\underline{X}XX^{p}Y$			0.7				
Dp-B^S	$\underline{X}XX^{p;4}$			0.14				
	$X\underline{X}X^{p}$			0.20				
Dp-105	$\underline{X}XX^{pd}Y$							?*
	$X\underline{X}X^{pd}$							0.11
Dp-102	XXX^{pd}							0.23
Dp-T-3	$XXX^{d;3}$							0.21

* Frequency much lower than frequency of X^p/X in Dp-138.

Another unique type is one of the two complementary X/X crossovers at 8, namely, *s car bb* females. Eleven of these were observed and 27 of the complementary type which is *B* not-*car* not-*bb*. The latter is ambiguous, resulting also from exchange between the fragment and the X carrying *B*, at 7 or at 8. Five of the ambiguous *B* females are allocated to the class of X^p/X crossovers at 7 corresponding to the 5 of the complementary sable class described above. Finally, 2 of the 27 have been rated as X^p/X crossovers at 8 on the basis of the ratio of X/X crossovers at 8 to those at 7. This leaves 20 females that were Bar in the class of X/X crossovers at 8. Of the total of 27 *B* not-*car* not-*bb* females, 10 were tested and found not to be of the class carrying a duplication that was yellow, from X^d/X crossing over, and six others were examined and showed no somatic characters of duplication. The ratio of the 11 observed complementary unique type, *s car bb*, to the 20 *B* not-*car* not-*bb* flies that were rated as X/X crossovers at 8 is in fair agreement with the observed 0.65: 1 ratio of *bb* to not-*bb* among the non-duplication flies of the experiment. The rating of 2 of the *B* not-*car* not-*bb* females as X^p/X crossovers at 8 has led to allocation to the complementary X^p/X class (which shows *s* and *car*) of 2 females from the ambiguous non-crossover class (*y ec* ct^6 *s car*).

Percents of crossing over in X gametes between the free fragment and the X chromosomes have been obtained from the allocations of the observed types in experiment 7 (tables 2 and 3).

When the fragment is free, exchange between X^p and an X transfers the whole chromatid from its own spindle-fiber attachment to that of the fragment and vice versa (fig. 4). If the chromosomes separate after crossing over, an X chromatid and a fragment pass to each pole; if the other X segregates at random X and XX eggs containing the crossover chromosome are to be expected with equal frequency after exchange between X and the proximal component of the fragment.

In experiment 7 exchange was detectable only in X gametes. To test the presence of the crossover X in one-X and two-X eggs when X^p/X exchange had occurred, duplication females whose X's were marked by *car bb* or by $bb^l/car\ bb^l$ were mated to $y^2\ bb^l\ Y^{bb}$ males when the only source of not-*bb* was the fragment. Experiments 9 and 9d show that both kinds of eggs occurred (table 10 at (c), appendix). The Y^{bb} in experiment 9d had too slight an effect on bb^l for exchange to be detectable in region 8, but the distribution of *car* showed that crossover chromosomes from exchange between the fragment and X in region 7 were present in both kinds of gametes.

A different Y^{bb} (and bb^l in both maternal X's) was used in experiment 9. The values were lower than the corresponding values in experiments 7 and 9d, owing probably to the action of bb^l; heterozygous bb^l is known to reduce crossing over in XX females increasingly toward the proximal end, the amount of crossing over between *car* and *bb* being about half of normal.

In calculating the percents of X^p/X crossing over in X and XX gametes (table 3) corrections were made for lethal zygotes (XXX, XX^{pd} and $X^{pd}Y$). The differences between the frequencies of X and XX gametes containing X^p/X crossovers are not significant, though the XX gametes were consistently more frequent than the X gametes. Equal frequencies are (as shown above) to be expected if the fragment and X go to opposite poles after exchange between them, and distribution of the non-crossover X is random.

When the fragment is attached to an X, reciprocal exchange between them cannot be detected. In testcrosses (experiment 1) non-reciprocal (diagonal) exchange would produce attached-X females ($\underline{XX}Y$). They would be of the type of XX females that were crossovers between the X's, that is y^2 *cv v f* (if single crossovers) since the fragment was attached to the X so marked. The males that were *f* (and showed other recessive mutant characters) would have been derived from X/X exchange only, and are expected to be as frequent as the females of the same origin. The ratio of the apparent crossovers, at 8, is 14 females to 18 males, showing no excess of females attributable to exchange with the fragment.

In the outcrosses to males having Bar eyes (experiments 1d, 10a, 10b) diagonal crossovers would be attached-X females of a type that is not ambiguous (since the other class would be heterozygous for *B*); they would be y^2 *cv v f* (or *y w cv v f* in experiment 10b from the second kind of mating). If exchange had taken place also between the X's, the attached X females might be y^2 (*y* or *yw* in part of experiment 10b) and wild type in other distal regions. The percent of crossing over involving X^p and the attached X was obtained from the observed frequency of all such females (showing the proximal recessive characters). Each one represents eight chromatids, when correction is made for lethal classes of zygotes (from attached-X gametes fertilized by X sperm and from gametes carrying two fragments attached to each other) and correction for reciprocal X^p/X crossovers of an ambiguous type and the lethals that they represent.

Crossing over between X^p and the free X in both testcrosses and outcrosses would produce y^2 females that would be wild type for proximal loci but might from exchange between the X's show other distal recessive characters besides y^2. The percent of crossing over involving X^p and the free X was accordingly obtained from the observed frequency of proximally wild type attached-X females. Each one represents four chromatids when correction is made for lethals (zygotes from $\underline{XX}$ gametes fertilized by X sperm and zygotes from the complementary type of gamete containing a fragment).

To compare frequencies of exchange in the three combinations of the sex chromosome homologues, table 3, experiment 7 (in which bb^l was not used) can be considered for the XXX^{pd} line. It is assumed, from the results of the other experiments with the free fragment, that XX gametes after X^p/X exchange in experiment 7 were at least as frequent as X gametes. Frequency of X^p/X crossing over was then 0.5 percent.

The results are not entirely satisfactory, owing to complications incidental to the use of bb^l and of *bb* in X and Y, to the absence of some unique classes, and to the small sizes of the classes to be measured. They are however consistent, and appear to be sufficiently accurate to show an expected decrease in crossing over when bb^l is involved, which is correlated with an observed increase in non-disjunction of X's. If the classifications in the various experiments and the distribution shown in the table of allocations were correct, the results would indicate: that X^p/X crossing over occurs more frequently when the fragment is free than when it is attached to an X and a Y is not present; that Y increases X^p/X crossing over between an attached fragment and an X; and that when the fragment is attached, crossing over of the fragment is equally frequent with the attached X and with the free X (assuming that reciprocal exchange with the attached X and diagonal exchange are equally frequent).

Some of the X^p/X crossovers were at the same time crossovers in a more distal region between the entire X's. In experiment 7, with the line of the free fragment, 3 of the 5 observed X^p/X crossovers at 7 from X eggs were also crossovers in region 1 between the X's, (classified in table 8, appendix, as 7, 8 and 1, 7, 8 X/X crossovers, and allocated in table 2 to X^p/X crossovers). In the line of the attached fragment (with and without a Y) there were 10 (7 tested) X^p/X crossovers recovered in attached-X females. Of those 5 were also X/X crossovers in regions from 1 to 3 or 4 (experiments 1, 1d, 10a, 10b, tables 9 and 10). The second exchange (distal and between the X's) will be discussed in relation to disjunction.

Crossing over has not been studied between the Y and any of the X homologues.

There was a small class of yellow heterozygous bar extremely bobbed females in one of two experiments combined in experiment 9 (table 10, appendix). This type of female would be expected if an X gamete were fertilized by non-disjunctional XY sperm. Such sperm is frequent when bb^l is present. It is not clear why these females were more extremely bobbed than the regular so-called "exceptional" y bb^l Y^{bb} females. The work of STERN, NEUHAUS and others on different effects of bobbed and on the properties and crossing over of the Y chromosome show that the account of Dp-100 is not complete without more accurate study of the effects of bobbed and the role of Y.

Crossovers between the distal component of the fragment and an X are very rare. Among the flies on which percentages were based, in the six experiments in which the chromosomes were suitably marked, only two such crossover females were observed among 5682 females in experiment 7 (table 2).

DISJUNCTION

$\underline{XX}X^{pd}$

Offspring of the original Dp-100 female are shown in table 4. Two tested apricot males were sterile, as expected in the absence of a Y chromosome in the mother. The yellow male is accounted for if an egg containing an X chromatid, resulting from exchange between the proximal section of the fragment (X^p) and an X, had been fertilized by Y sperm. The complementary crossover is a chromatid having the fragment attached to it in place of the other X. One of the five not-yellow females carried such a chromosome. The only other fertile not-yellow female, and probably three that died, arose from non-disjunctional eggs carrying the attached X's and the fragment. Such females were expected to be as frequent as the apricot XO males (32) derived from nullo-X eggs. The marked deviation from equality may be accounted for by the relative inviability of the duplication females which, in the earlier generations of the line, was associated with marked exaggeration of some of the somatic disturbances characteristic of duplication.

TABLE 4

Offspring of the original $\underline{XX}X^{pd}$ *(wild type duplication) female and of* $\underline{XX}X^{pd}Y$ *(wild type duplication) female descendants (the entire X's were homozygous for yellow).*

	NOT X^p OR Y CROSSOVERS			X^p OR Y CROSSOVERS	
	FEMALES		MALES	FEMALES	MALES
PARENTAGE	*y*	NOT-YELLOW	w^a		*y*
NOT-YELLOW $\underline{XX}X^{pd}$ ♀	$\underline{XX}Y$		XO		XY
by w^a ♂	92	1 $\underline{XX}X^{pd}Y$ 1 $\underline{XX}X^{pd}$(Y?) 3 died	32		1

						FEMALES	
NOT-YELLOW	*y*	not-*y*	*w f B*	*w f B*	*f B*(±*yw*)	het. *B*	*y* het. *B*
$\underline{XX}X^{pd}Y$ ♀	$\underline{XX}Y$	$\underline{XX}X^{pd}Y$	XXX^{pd*}	XX^{pd*}	XY	$X\underline{XX}^{pd}$ or XXX^{pd}	XX
by *f B* ♂	111	274			442	1¶	
by *y w f B* ♂	428	859	1	2	1246	4†	3‡

* With or without a maternal Y chromosome

¶ Tested $X\underline{XX}^{pd}$.

† Not tested.

‡ 2 tested.

At disjunction the attached X's and the fragment went together to the same pole in 25.8 percent of the tetrads, the percent being represented by the ratio of non-duplication (XO) males to total non-duplication males and females (fig. 3b).

$\underline{XX}X^{pd}Y$

The $\underline{XX}X^{pd}Y$ line was derived from the non-disjunctional not-yellow daughter of the original $\underline{XX}X^{pd}$ female which had been mated to an XY w^a male. In this line there was a high percent of association at meiosis of attached-X's and fragment as shown by the high frequency of $\underline{XX}X^{pd}$ and

Y gametes which produced wild type duplication females and *f B* (±*yw*) males respectively when the fathers carried *f* and *B* (table 4).

The heterozygous *B* female whose father had been *f B* was shown by testing to have carried a maternal X with the fragment attached to it, the result of exchange between the fragment and an X. The two tested *y* heterozygous *B* females carried a single maternal X marked by *y*, presumably derived from exchange between the Y and an X, as observed by KAUFMANN (1933) in attached-X lines. From the matings to *y w f B* males at least two of the four not tested heterozygous *B* females showed somatic disturbances due to the presence of the fragment. The fragment may have been attached to an X (from X^p/X exchange) or it may have been present in the free state with a single maternal X which had resulted from exchange between the Y and an X.

The *w f B* female came from an egg containing the fragment (±Y) fertilized by non-disjunctional sperm carrying two X chromosomes. With this fly originated the line of two free X's and a free fragment (XXX^{pd}).

In the $\underline{XX}X^{pd}Y$ line the sex chromosome complement is composed of three partially homologous units. In this respect it is similar to XXY females. The classical theory of secondary non-disjunction suggested by BRIDGES (1916) to account for the types of segregation observed in such females has until recently been generally accepted. The theory postulates that when two of the three partially homologous chromosomes, X, X and Y, pass to the opposite poles of the meiotic spindle the third goes at random with one or the other. If p represents the proportion of tetrads in which the two X's segregate away from the Y, the limiting value of p is 0.5. STURTEVANT and BEADLE (1936) have found that the value of p is 0.63 in $XX^{In}Y$ females which are heterozygous for the delta-49 inversion in X, and STURTEVANT (1936) has found in triplo-IV flies that the frequency of one type of segregation of the fourth chromosomes may be as high as 70 percent. Likewise in some lines of attached X's with X-duplication, DOBZHANSKY (1934) and STURTEVANT (1936) have found a frequency of one type of segregation somewhat in excess of 50 percent.

The difference between this situation and the heretofore accepted theory of secondary non-disjunction in XXY is illustrated by STURTEVANT'S diagram of triplo-IV segregation; according to the older view when two chromosomes, such as X and Y in an XXY female (A, B fig. 3a), go to opposite poles of the meiotic spindle, segregations II and III will occur with equal frequency and it follows that neither can exceed 50 percent of total segregation; the higher values of certain segregations obtained in the cases cited show that frequency of segregation may be independent of a limiting random distribution of the third element.

This is shown also in the $\underline{XX}X^{pd}Y$ line of Dp-100. The frequency of segregation III (fig. 3c), by which the attached X's and the fragment go to the same pole, is represented by the ratio of non-duplication males, which are recovered from one fourth of the gametes from segregation III, to the total of non-duplication males and females, the latter being recovered from one fourth of the gametes from segregations I and II. The value is .76, corresponding to 76 percent of segregation III.

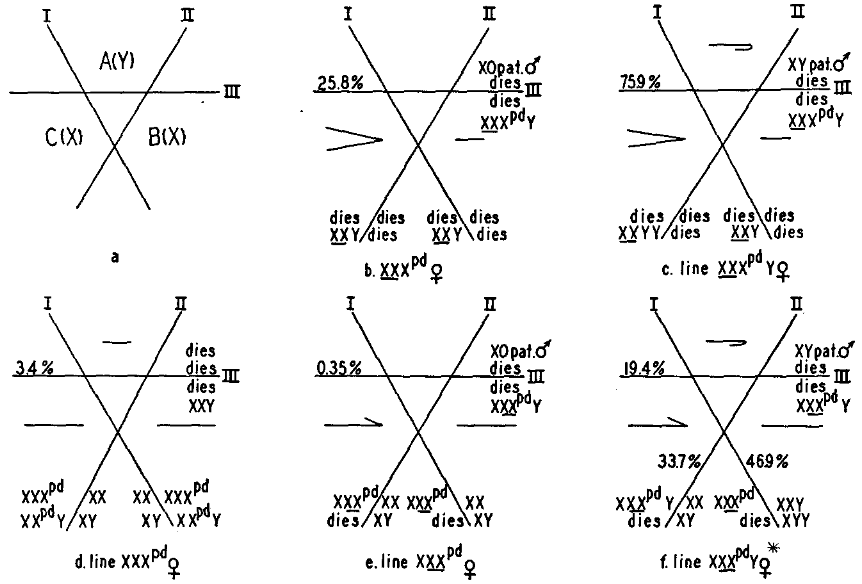

FIGURE 3.—Modeled after STURTEVANT'S diagram of triplo-IV segregation to show types of segregation in different lines of Dp-100. Chromatids that pass to opposite poles are represented by symbols (long line for X, short line for fragment and hook for Y) on opposite sides of the lines of segregation (I, II and III). Zygotes resulting from eggs that receive the chromatids indicated by the symbols are noted on the same side of the line of segregation, first those from eggs fertilized by X sperm, second by Y sperm. Crossovers involving the fragment or Y are disregarded. Percents refer to frequencies of segregations.

* Percents of segregations are recorded as found in experiment 10a and in agreement with those of experiment 10b. Other experiments showed a random segregation of Y with X and $\underline{XX}^{pd}$ (I and II).

Unpublished data of Dr. SCHULTZ obtained from experiments with a duplication similar to Dp-100 show 60.7 percent of segregation III, 35.0 percent of segregation I and 4.3 percent of segregation II. The duplication (known as Dp (1;f) eq) carries normal alleles of *y* to *pn* (inclusive) and *bb*; the proximal section is shorter than that of Dp-100.

XXX^{pd}, $X\underline{XX}^{pd}$ and $X\underline{XX}^{pd}Y$

In the other three lines, in which the entire X's are not attached to each other, the segregation by which the two X's go to the same pole of the meiotic spindle is called segregation III. The values obtained are given in table 5.

In the line XXX^{pd} (fig. 3 d) only one of the four gametes from segregation III is recovered (as an XXY female which is yellow). Hence each observed zygote from segregation III represents two gametes among the flies of the classes that were counted, when they were one half of the total (for example non-duplication males and females). In that case the formula for deducing the frequency of total exceptional gametes in XXY females from the frequency of observed exceptional zygotes can be used. The proportion of exceptional gametes ($=$ p) from XXY females is equal to $2q/1+q$, q representing the proportion of observed zygotes from XX and Y gametes. Applied to XXX^{pd} females this equation becomes $p=q$ when non-duplication males or females only are counted, that is one fourth of the zygotes (XX or XY) from $X\text{-}XX^{pd}$ segregations (I and II), with one fourth of the zygotes (XXY females) from $XX\text{-}X^{pd}$ segregation (III).

The same formula applies to the $X\underline{XX}^{pd}$ and $X\underline{XX}^{pd}Y$ lines. In these lines females from segregation III (fig. 3 e and f) are matroclinous duplication females and carry a Y. The males from segregation III can also be used if the paternal X is of good viability in XO or in XY individuals as was true in experiment 10a. Using both male and female exceptions with half of the other classes p equals q. Values thus obtained for segregation III (when two X's segregate together) have been compared with those from controls and from XXY females (table 5).

In the XX control of experiment 7 no females from XX gametes were observed. Two controls from the same stocks were experiments 4 and 6a (experiment 6 and additional matings); the difference between the values obtained from these is not significant.

Values used for comparison of XXY females have been computed from the data of BRIDGES (1916, table 2), from the published data of BRIDGES and OLBRYCHT (1926) (adding thereto the number of exceptional males (87) and females (159) and a correction for relative inviability of patroclinous males supplied by Dr. BRIDGES), and from experiment 5n in which non-disjunction was measured in F_1 XXY females of experiment 5a.

In the lines in which the X's were not attached to each other the percents of segregation of the entire X's to the same pole are of three orders (table 5).

When the X's are separate and the fragment is attached to one X ($X\underline{XX}^{pd}$) the frequency is slightly higher than the average of the more variable frequencies of primary non-disjunction in XX females of the control and other experiments. When a Y is also present ($X\underline{XX}^{pd}Y$) the X's (one carrying the fragment) segregate together in about 19 percent of tetrads (experiments 10a and b).

In the line of the free fragment the frequencies are of the order of the more variable frequencies of XX-Y segregation in XXY females; the similarity in frequency will be shown later to be superficial. When the X's carried *bb^l* non-disjunction was increased (experiment 9).

In the form of Dp-100 which consists of a fragment attached to X, a free X and a Y ($X\underline{XX}^{pd}Y$) frequencies of three segregations were measured and the percents are shown in figure 3f. Percents of segregations I and II were estimated from a sample of 170 F_1 females (of experiment 10a) with and without the attached fragment. These females were tested for a Y chromosome by outcrossing and observing the occurrence of exceptional offspring. The results agreed closely with those obtained from a sample of 171 F_1 females, in a similar experiment (10b), which were tested by outcrossing to Plum used as a detector of Y. Both tests seemed to show that Y segregates more often with X than with X and attached fragment, the ratios being about 1.4:1 and 1.7:1. However a subsequent test, in which $X\underline{XX}^{pd}Y$ females of the stock used in experiment 10b were mated directly to Plum, showed the presence of an extra Y in only about half of the F_1 non-duplication females and males. The same random distribution of Y has again been found. Non-duplication male and female offspring of $X\underline{XX}^{pd}Y$ females were mated to flies that were *y w* Dp w^{v} ^{cob}, another detector of Y. Of 217, tested in this way, one half of them (109) had received a Y chromosome from the mother, showing random distribution of Y with X, and with X and attached fragment in the $X\underline{XX}^{pd}Y$ females whose offspring were tested. The question then remains open as to whether

TABLE 5

Percents of types of segregation in Dp-100 (and derived lines) and controls.

SEGREGATION	XX-O		$X\underline{XX}^{pd}$-O		XX-Y	XX-X^{pd}	
Genetics of Drosophila (1925)	0.10	exp. 1d	0.40		8.2†		
exp. 2	0.30	exp. 1	0.30		6.0¶		
exp. 4	0.58					exp. 3*	3.50
exp. 6a	0.07			exp. 5n	2.8	exp. 5a*	4.30
exp. 8	0.0					exp. 7*	3.35
						exp. 9d	2.78
						exp. 9	5.37
	$\underline{XXX}^{pd}$-O	$\underline{XXX}^{pd}$-Y		$X\underline{XX}^{pd}$-Y	XY-$\underline{XX}^{pd}$	X-$\underline{XX}^{pd}$Y	
Dp-100	25.8	75.9	exp. 10a	19.4	46.9	33.7	
			exp. 10b	18.5	54.9	26.6	

* Includes XX gametes containing X^{p}/X crossovers.

† Bridges (1916) table 2.

¶ Bridges and Olbrycht (1926).

Y segregates less frequently with an X when a fragment is attached to the X.

Equational non-disjunction had occurred in possibly four instances in the lines both of the free and of the attached fragment (see table 10 for parentage). In experiment 9 with the (1;f) line, a y^2 *s car bb* female was tested and gave *y ec* ct^6 *s car* and y^2 *cv v s car* males (and crossovers), showing that the tested female had originated from non-disjunction of the proximal ends of the X's, one of the X's being a crossover in region 5. A y^2 *cv v f* female in experiment 5a had probably been derived from equational non-disjunction; or it may have come from reductional non-disjunction with X/X crossing over in region 7, that is, in a region nearer to the spindle-fiber attachment than in any other fly from reductional non-disjunction. In experiment 1d with the (1;1) line, a *y w* female was tested to determine whether she carried attached X's from X^p/X crossing over (with a second crossover between X's), but the test showed two separate X's and a Y chromosome. A *y w* female in experiment 10b was subject to the same explanation but was not tested.

Two patroclinous females were observed in experiment 10b. One was bred and the offspring showed that she had received two separate X's from her father and a Y from her mother. The females had developed from eggs of segregation III (figure 3f) but were of a class of zygotes so rarely to be expected that it has not been shown in the figure.

RELATIONS BETWEEN CROSSING OVER AND DISJUNCTION

The results of ANDERSON (1929), DOBZHANSKY (1933) and others have furnished abundant evidence that chromosomes that have exchanged segments usually pass to opposite poles of the meiotic spindle. Almost all of the recovered X/X crossovers in the experiments with Dp (1; f) 100 have been found in zygotes from X eggs. Very rarely flies derived from XX eggs, known not to contain a crossover with the fragment, were equational for recessive mutant characters. For example, in experiment 9 only one of 594 XXY females that were reductional exceptions and not X^p/X crossovers was equational for distal loci. She was y^2 *cv v bb*, which indicated crossing over in region 5 in one X. There were no reciprocal crossovers in 23 y^2 females that were tested.

In the line of attached fragment without Y ($X\underline{XX}^{pd}$, experiment 1, table 9) no equationals were observed among the very few females (9) derived from $X\underline{XX}^{pd}$ eggs.

In experiments 10a and 10b in which the mothers carried the attached fragment and Y, five females (namely two *w* and three *w cv*) among 1195 exceptions from $X\underline{XX}^{pd}$ eggs were equational for distal loci, and one was a reciprocal crossover between X's (table 10 at (c), appendix); 183 of the exceptional wild type duplication females were tested and were not reciprocal crossovers.

The effect on the distribution of the chromatids of a distal exchange between the X's accompanying X^p/X exchange was studied. When exchange occurs between the proximal section of a free fragment and an X it is assumed that the exchange will usually be followed by disjunction.

In the lines with the attached fragment ($X\underline{XX}^{pd}$ and $X\underline{XX}^{pd}Y$) exchange between the proximal section of the fragment and an X produces attached-X females (except in case of the undetectable exchange between the fragment and the X to which it attached). The distribution of the products of a second exchange between X's is determined by the attachment of the X's. Such double crossovers were found in about half of the attached-X females which were X^p/X crossovers.

By diagonal exchange between the fragment and X, sister strands are attached together and a resulting attached-X female shows the recessive characters of the X that is attached to the fragment and is detectable as an exceptional type in outcrosses. Sister strands being attached to each other a more distal exchange could take place only with the free X. There was one *y w cv v f* tested attached-X female (in experiment 10b) in which there had been no crossing over between X's. In two other such females a second exchange had occurred (in region 4 in one y^2 *v f* female in experiment 10a, and in region 1 or 2 in one y^2 *cv v f* female from the second type of female parent used in experiment 10b, table 10, appendix).

When X^p/X crossing over occurs between the fragment and the free X, the resulting attached-X female is y^2 and a second crossover might be reciprocal (detectable only by testing and none were found) or equational and detectable by homozygosis of distal recessive genes (except homozygosis of y^2). Of four y^2 females, two in experiment 1d and one in experiment 10a (table 10, appendix) were tested and were probably not crossovers for X, and one y^2 female in experiment 1 (table 9, appendix) was not tested. Three other crossovers between the fragment and the free X were also equationals for X; two y^2 *cv* females in experiment 10b were not tested but were of the type of attached-X females which are X/X crossovers in region 3 or 4, and one tested y^2 female in experiment 10a carried attached X's of which one was a crossover in region 2 (she was homozygous for y^2 and carried only normal alleles of *ec*).

It has been seen that when the X's and the fragment are free, crossover chromatids from exchange between the proximal section of the fragment and X are recovered in both X and XX eggs (table 3, experiment 9d, 9) and that three of the five females from X eggs found to be X^p/X crossovers, in experiment 7, were also X/X crossovers, indicating that about half of X^p/X crossovers were also crossovers between X's in the line of the free as in the line of the attached fragment.

The X^p/X crossing over is detectable only in females from X-gametes, in the experiments that show X/X crossing over, and is not detectable in XXY females from XX-gametes hence a calculation has been made of the frequency of distal X/X crossovers to be expected among XXY females when double crossing over (X^p/X and X/X) has occurred.

Assuming that, at the reductional (first) division, crossover proximal fragment and X pass to opposite poles, an X egg would receive a double crossover (X^p/X and X/X) chromatid only after three-strand double exchange and only when the crossover X's also disjoined and passed to opposite poles. The double crossover chromatid would go to the haplo-X pole, and after the equational division both daughter nuclei would receive a double crossover chromatid. The diplo-X pole of the first division is represented by figure 4, A1; after the second division one daughter nucleus would receive a crossover and a non-crossover chromatid, and one would receive two non-crossover chromatids (the possible combinations indicated in figure 4, A1). The females recovered from eggs containing one of the four reduced nuclei should be two double crossover XX females to one equational XXY female to one non-crossover XXY female. From four-strand double exchange the expectation is one XXY female that is equational to one non-crossover (figure 4, A2). Hence the total expectation when X crossovers pass to opposite poles is 2 XX double crossover females: 2 non-crossover XXY: 2 equational XXY. Random disjunction of crossover X chromatids after three and four strand double exchange includes all the distributions indicated in figure 4. It would result in 2 XX females, from X eggs containing a double crossover chromosome (derived from the nucleus of the haplo-X pole of the first division) to 8 XXY females from XX eggs which would be non-crossovers for X, equationals, and reciprocals in the ratio of 2:4:2.

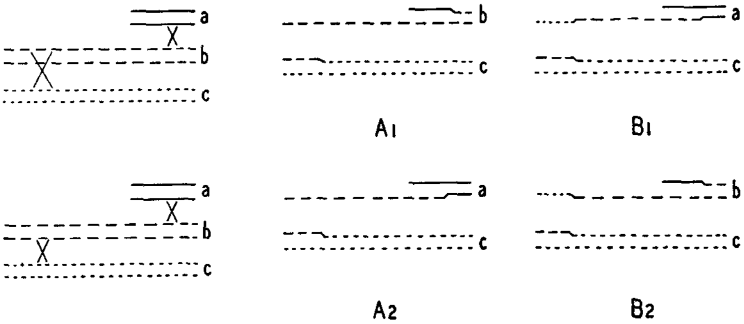

FIGURE 4.—Diagram of double crossing over in a duplication female XXX^{pd} (carrying free X's and fragment), when proximal crossing over occurs between the fragment and an X (X^p/X) and simultaneous distal crossing over between the entire X's (X/X). It is assumed that crossover fragment and X pass to opposite poles. The four chromatids that pass to the diplo-X pole after the first (reductional) division are represented by A1 and A2 it the X crossovers go to opposite poles, and by A1, A2, B1 and B2 if the X crossovers segregate at random. After the second (equational) division eggs which have received whole chromatids from a diplo-X pole will contain two X chromatids each, and if fertilized by Y sperm produce XXY females. If X crossovers always go to opposite poles at the reductional division the XXY females to be expected are 2 non crossovers: 2 equationals: 0 reciprocals, as shown by the possible combinations of chromatids at A1 and A2. If X crossovers segregate at random the expected XXY females are 2 non-crossovers: 4 equationals: 2 reciprocals.

The experiments yielded small numbers of these infrequent classes and show lack of agreement with either expectation; they show also inconsistencies which do not seem to be entirely due to the small number of observations. It has been noted that only five observed crossovers between the fragment and X (X^p/X) are available for determining the expectation of the frequencies of their own and of other classes in experiment 7. Three of the five were double crossovers (X^p/X and X/X). Allocations from ambiguous types make a total of 14 X^p/X crossover females from X-eggs. If the same proportion of these as of the X^p/X crossovers that were observed (that is about half) may be assumed to be also crossovers between the X's, then 7 at least of 190 observed XXY females would be expected to be equationals. This would be the expectation if the distal crossover X chromatids had disjoined, but twice as many equationals are expected and 7 reciprocals as well if segregation had been random. But of the 105 XXY tested females not one was either a reciprocal or an equational, and of the 85 not tested none was equational whereas only homozygosis for y^2 could not have been detected.

In 5a crossing over of the fragment was not detectable, but among 137 XXY females there were distal crossovers between the X's, table 10 at (b). There were three equationals (one *y* and two y^2 *cv*, showing crossing over in region 1 or 4 in one chromosome) and there were three reciprocals (involving regions 1, 2, or 4). These occurred among 108 that were tested and represent a total of four equationals (at most) and four reciprocals. The reciprocals show that non-disjunction of crossover X's had taken place in some of the nuclei. Assuming that X^p/X exchange had occurred with the same frequency as in experiment 7, there is an expectation of eight equationals and four reciprocals from random segregation. A y^2 *cv v f* female may have originated from equational non-disjunction. The entire absence of distal crossovers in XXY females in experiment 7 is not explained. Experiment 5a though not in close agreement comes nearer to expectation from random assortment.

In experiment 9, double exchange (X^p/X and X/X) could have been detected in females from XX eggs but none of the 11 XXY females that carried an X^p/X crossover chromatid was equational for recessive mutant characters.

Thus, the results from different experiments are at variance, for types found in some experiments have not been observed in others in which they would have been detectable. But the results show that almost all of the crossover X's observed in flies from XX eggs in the line of the free fragment may be accounted for as occurring in eggs that have been derived from proximal disjunction of crossover X and fragment as distinguished from reductional non-disjunction of X's; that few X/X crossovers occur in flies from $X\underline{XX}^{pd}$ gametes; and that whatever X/X exchange was observed in flies from either XX eggs or $X\underline{XX}^{pd}$ eggs had occurred in the distal region of the X.

DOBZHANSKY also found that in the lines of X-duplications crossovers are rare in gametes carrying two X's.

It has frequently been observed since first pointed out by BRIDGES (1916) that crossover X's do not occur in XXY females from secondary non-disjunction. GERSHENSON (1935) has found that 0.2 percent of exceptional gametes from $XX^{InClB}Y$ females were distal equationals but he found no reciprocal crossovers. This difference is to be expected if crossover chromosomes had disjoined and if proximal disjunction had been determined perhaps by a relation to the Y in a nucleus in which distal crossing over had taken place between the X's. It is consistent with the results of BRIDGES and ANDERSON (1925) in triploids in which they found (distal) equational but not reciprocal crossovers in XX gametes, and with the results of BEADLE (1934) in attached-X triploids in which disjunction is determined by the attachment, and reciprocal crossovers were found with the frequency expected in XX gametes if the second crossover is random.

The evidence from Dp-100 is in agreement with the view that crossover chromatids usually go to opposite poles of the spindle and suggests that in duplication females this holds more consistently for proximal crossovers than it does for distal crossovers, when one of the chromosomes involved has crossed over in a proximal region and disjoined from the third element. The converse question remains whether chromatids that are not crossovers stay together and to this end the distribution of the X homologues in no-exchange tetrads was studied.

The percent of tetrads in which there was no X/X crossing over has been approximately estimated; crossover and non-crossover strands represented by crossover zygotes have been subtracted from the total percents of corresponding strands in the proportions indicated by observed zygotes that were single, double and triple crossovers, on the basis of random exchange between non-sister strands in the four-strand stage. The final residue of non-crossovers is the estimated percent of tetrads containing no crossover strands.

In XXX^{pd} females (experiment 7) there were 11.0 percent no-exchange tetrads, of which 31.0 percent gave XX-X^{pd} segregation. In experiment 5 there were 13.4 percent no-exchange tetrads and (correcting for 5 percent of X/X crossing over in XXY females) it was found that 35.4 percent of these gave XX-X^{pd} segregation. Thus, in no-exchange tetrads containing the free fragment there is nearly random distribution of the X's and the fragment.

In $X\underline{XX}^{pd}$ females (experiment 1) there were 13.3 percent no-exchange tetrads; the total amount of $X\underline{XX}^{pd}$-O segregation was 0.30 percent which was only 2.3 percent of no-exchange tetrads, showing that disjunction of X from X with a fragment attached was nearly complete irrespective of crossing over. But when a Y chromosome was present there was 19.4 percent of $X\underline{XX}^{pd}$-Y segregation, which was 56 percent of no-exchange tetrads.

DISCUSSION

Crossing over. The relation of the percents of crossing over between entire X's in the presence of the duplicating fragment to percents from controls in the seven or eight regions that were studied have been plotted against the map of the salivary chromosome (fig. 2), on which are shown the relative positions of mutant genes as located by MACKENSEN (1935) and BRIDGES (1938). The graph shows that in Dp-100 when Y is not present the effect on crossing over is the same (except in one region) whether the fragment is controlled by its own spindle fiber or is attached to one of the entire X's. In both events the greatest reduction is at the spindle fiber end which is the region homologous to the proximal section of the fragment. The curves gradually increase to a maximum in the third region between *cv* and *ct* and then decrease to points somewhat below 1 (control) in the most distal first region which is homologous to the distal section of the fragment.

More detailed examination of the results shows that reduction in X/X crossing over is the same in the lines of the free fragment (1;f) and of the attached fragment (1;1) in regions 4, 6, 7 and 8; the relations are less regular in region 5. In region 3 the curves for the free lines (1;f) reach points higher than 1. The percent of crossing over in experiment 7 alone, or combined with the percents of experiments 3 and 5, is significantly higher than the percent in experiment 1 with the line of attached fragment (1;1). In the first region the results are again less different as between the free and the attached fragment.

The differences in region 1 between percents for the duplication and those for the control are so small as not to be significant in any one experiment but are so consistent as to indicate that there is in fact a slight reduction in crossing over.

For further comparison, results from DOBZHANSKY'S duplications of the X chromosome and those from experiments with the lines of free and attached fragment of Dp-100 are presented graphically in figure 5.

DOBZHANSKY (1934) has shown that in the duplications studied by him frequency of exchange between the entire X chromosomes is reduced in the presence of the duplication fragments, that the relatively greatest reduction is observed in the regions homologous to the fragments and in the adjacent regions, and that the degree of reduction is positively correlated with the length of the fragment.

Three of DOBZHANSKY'S duplications that are attached to chromosomes other than the X (T-3, T-7 at the ends of chromosomes III and II, and 126 attached to chromosome III at a point near to the spindle fiber attachment) very clearly show the reduction in the tested regions. So also does Dp-138 consisting of a proximal fragment attached to an X at the spindle fiber end.

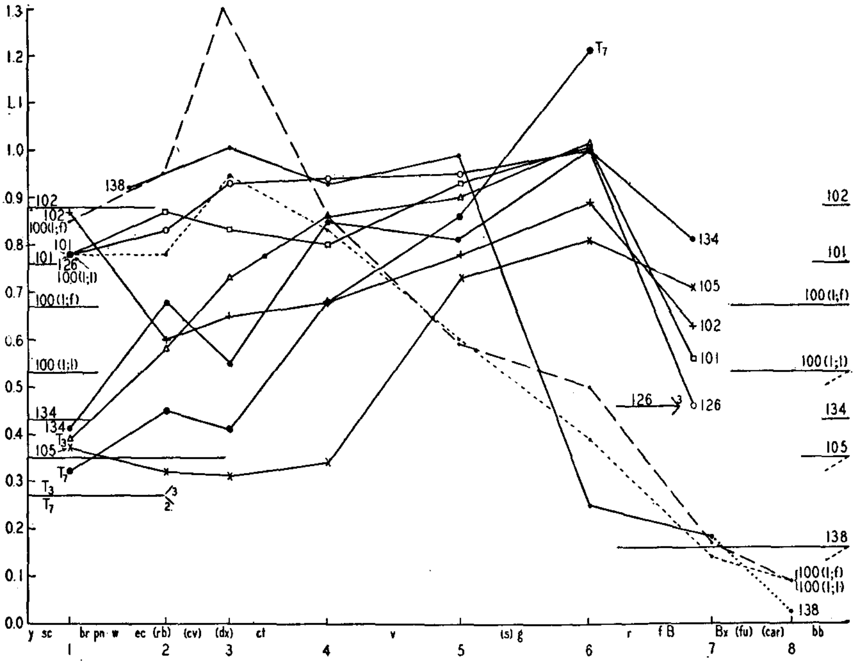

FIGURE 5.—Relation of percents of crossing over between entire X's to controls in experiment 7 (Dp (1;f)100), in experiment 1 (Dp (1;1)100) and in duplications studied by DOBZHANSKY. Axes, symbols, and lines denoting extents of fragments as in figure 2.

Four duplications (134, 101, 105, 102), consisting of distal fragments on spindle attachments of their own, give similar reductions, and in addition to the effect in the homologous distal region they show also a reduction in crossing over in the 7th region (there are no data for the 8th). These duplications contained some portion of the inert region, enough to include the locus of *bb* in Dp-101 and in Dp-105. In Dp-101 the reduction in the 7th region was even greater than the reduction in the distal region homologous to the short fragment which includes only the loci as far as *y* and *sc*. In Dp-105, which is the longest of the distal duplications and proximally contains the greatest length of inert region, crossing over was not as frequent as in the control in any region.

Dp-138 extends from the spindle attachment to a point distal to the locus of rudimentary and contains therefore an active section of X from *r* to *Bx* not included in Dp-100. The reduction in crossing over in the *f-car* region (7th) in Dp-100 is as great as in Dp-138. There was no control for Dp-138 in region 8, but using the control for experiment 7 (which is the same in regions 6 and 7 as the control for Dp-138) crossing over appears to be reduced more than in Dp-100 in region 8. Thus the effect of the proximal component of the fragment of Dp-100 is consistent with the results from the other duplications, including the reduction found in region 7 in duplications composed largely of a distal section.

But when the distal effect of Dp-100 is compared with that of largely distal duplications the result is quite different. The slight reduction indicated as probably occurring in the region homologous to the distal section of Dp-100 is by no means comparable, in relation to lengths of fragments, to the reductions found in the other "distal" duplications (only Dp-102 gives an inconsistent result in the 1st region and in the 7th but not in the 2nd which is homologous to the fragment). The distal effect of Dp-100 is like that of the much shorter Dp-101 and the effect is much less than that of the somewhat shorter Dp-134.

It is evident that the position of the components of the fragment may be a very important factor in their effects. In this connection it may be noted that the long proximal Dp-138 has a much greater effect on X/X crossing over than has the long distal section of Dp-105. Dp-100 has, in proportion to the length of its proximal component, an effect comparable to that of the simple proximal Dp-138, in the region of the X's homologous to the proximal component, and the distal effect also is not very different in spite of the presence of the distal component in Dp-100. Thus the results suggest an advantage in pairing at the proximal end of the chromosome over pairing at the distal end.

DUBININ et al (1935) showed that, in the salivary glands, short proximal sections of chromosomes pair rather than much longer distal sections.

PAINTER (1934 and 1935) had found the same kind of pairing in the salivary chromosomes in Mottled-5 and other translocations of the fourth chromosome. He found that in a heterozygote the normal fourth chromosome tends to pair with a very small segment of the fourth at the spindle fiber end rather than with the segment comprising almost the entire fourth chromosome attached to the X near its distal end, or to a point on a large autosome far removed from the spindle fiber attachment. He points out the importance of the telophase orientation in pairing and the possible application in the understanding of pairing at meiosis in forms in which there are aberrant elements.

DOBZHANSKY (1936) has shown that the chromosome pattern tends to persist through the interphase in spermatogonial divisions in *Drosophila pseudoobscura* and emphasizes the importance of taking into account the telophase orientation and spatial distribution of chromosomes in the study of crossing over variations in chromosomal aberrations.

With the telophase orientation as the key to the situation, the proximal component of the compound duplication is expected to be, at the time of pairing, in a position similar to that of a simple proximal fragment, and the proximal effects of Dp-100 are in fact comparable to the effects of the proximal Dp-138. In considering the effect of the distal component its position in the nucleus is a factor to be taken into account. In relatively simple "distal" duplications containing more or less of the inert region, the position of the proximal end of the distal fragment at telophase is near to the spindle fiber attachment or near to the locus of *bb* at the farthest; in Dp-100 its position is determined by its attachment to the distal end of the proximal fragment (near the locus of *fu*) which, due to the pairing of the proximal component, may be a relatively fixed point at about the middle of the X's. In this position the distal fragment has been shown to have scarcely any effect on the crossing over between the X's at their distal ends, whereas a shorter fragment in Dp-134 proximally attached to its own spindle fiber attachment and not including the locus of *bb* has a marked effect. In fact, in proportion to the lengths of the distal sections, Dp-134 has a relatively greater effect in the distal homologous region than have Dp-101 and Dp-105, both of which include the locus of *bb*; and Dp-134 has a lesser effect than either in region 7 (the most proximal region that was observed). Proximal sections are effective in proportion to their lengths; distal sections, attached to a proximal section, are effective directly in proportion to their lengths and inversely to the distances by which they are removed from the spindle fiber attachment.

The fact that the effect of the distal section of a compound duplication is conditioned by the extent of the proximal section is evidence that telophase orientation is important, and is consistent also with MATHER'S conclusion that in *D. melanogaster* pairing takes place first near the spindle attachment. His conclusion is based on a study of the relation of points of crossing over to the spindle attachment and to each other. It is also consistent with the relation found in inversions by STONE and THOMAS (1935) in agreement with observations of STURTEVANT and BEADLE (1936) who state "that an inversion is more effective in suppressing crossing over in segments distal to itself than in proximal segments." Since reduction in crossing over between the X's is the same whether the fragment is free or is attached, the telophase orientation appears to be in this regard as effective as a permanent attachment.

It has been seen that the effects of the compound Dp-100 are similar to those of the proximal Dp-138 in the regions that are homologous to both components of Dp-100; in the intermediate regions there are two differences. Proceeding distally from the region homologous to the fragment, in Dp-138 crossing over rises abruptly to the same frequency as the control in the region beyond the fragment whereas in Dp-100 the ratios increase gradually and in region 3 crossing over is more frequent than in the control, a peak only slightly shown in Dp-138 and not in the "distal" duplications. It is of interest to note that the peak occurs in a region which has a high coefficient of crossing over, the highest in fact of all regions of the complete chromosome complement (MORGAN, BRIDGES and SCHULTZ 1937).

The effects on crossing over in regions not homologous to the components of the fragment must in their turn be dependent upon spatial relations correlated with the peculiar pairing relations of the homologous regions. Furthermore the whole chromosome complement is involved in disturbances of crossing over in a given region, as shown by interarm effects and by interchromosomal effects (DOBZHANSKY and STURTEVANT 1931, DOBZHANSKY 1930, 1933, MORGAN, BRIDGES and SCHULTZ 1930, 1932, 1933, 1935, STEINBERG 1936 and MACKNIGHT 1937).

DOBZHANSKY has shown that the frequency of exchange between the fragment and an entire X is not at all commensurate with the reduction in crossing over between the X's in the homologous region. The two are however positively correlated and are correspondingly correlated with the length and position of the fragment.

Crossovers between a free fragment and one of two attached X's were observed by DOBZHANSKY in two duplications. In the long proximal Dp-138 he found crossing over between the proximal fragment and an X in 0.7 percent of gametes, and in the distal Dp-105 crossing over was apparently much less frequent. This relation corresponds to a greater reduction in crossing over between the X's in the regions homologous to the fragment in Dp-138 than in Dp-105, the ratios of percents of X/X crossovers in the duplications to control being 0.11:1 and 0.34:1 respectively (the smaller ratio representing the greater reduction).

The values for the duplicated regions of Dp-100 are consistent with these. For the proximal region, the values are nearly the same as those for Dp-138 and are intermediate between those for Dp-138 and Dp-105. In Dp (1;f)100, it is estimated that the frequency of X^p/X crossing over when the fragment is free is 0.5 percent and the ratio of X/X exchange to control (in the 7th and 8th regions) is 0.13:1. Exchange between the distal component and an X (X^d/X) takes place rarely and corresponds to a very slight distal reduction in X/X exchange, represented by the ratio 0.85:1.

Although the frequency of crossing over of the fragment increases as the reduction in crossing over between the X's increases, X^{Dp}/X crossing over is obviously only a small fraction of the total crossing over in the homologous regions, even with the longest of the fragments that have been studied. If exchange were random among the three homologues the expected ratio of X^{Dp}/X to X/X crossing over would be 2:1; in Dp-105, Dp(1;f)100 and Dp-138 the ratios are less than 0.13:1, 0.30:1 and 0.50:1 respectively. The three duplications are mentioned in the order of increase in X^p/X crossing over, and the ratios show further that increase of frequency of crossing over involving the fragment is positively correlated with increase in its proportion of total crossing over in the homologous region.

PHILIP (1934) studied crossing over in a duplication, known as Dp-B^S, in which the fragment is a proximal section of the X chromosome, (including the locus of *B* to the spindle-fiber attachment) to which most of the fourth chromosome is attached. Corrected data from females give 0.14 percent of crossing over between attached X's and the free fragment. The value is low compared to 0.7 percent for the somewhat longer proximal Dp-138 in the same form $(\underline{XX}X^p)$. When the fragment of Dp-B^S was attached to an X, the corrected data from females give 0.2 percent of X^p/X crossing over. This does not show the decrease in X^p/X crossing over, when the fragment is attached, which was found in Dp-100. An important factor in Dp-B^S is the attachment of the fourth chromosome at the distal end of the fragment which originated in a I, IV translocation.

DOBZHANSKY has compared two translocations T-3 and T-7 with the duplications derived from them and has reached conclusions that may be further analyzed. In each of the duplications the distal fragment of the X is attached at the end of an arm of one of the large autosomes and may pair with the two X chromosomes. In the corresponding translocations the only exchange in the distal region of the X is that which occurs between the fragment carried by the autosome and the single whole X. In a translocation, synapsis of the fragment is the condition for exchange in the region homologous to the fragment; in the corresponding region in a duplication the presence of the fragment is a factor in reduction of crossing over between the entire X's and of total crossing over in the region; the pairing of the autosomes involved is a factor affecting synapsis of the X's in both forms. DOBZHANSKY states that as a rule crossing over is more reduced in translocations than in duplications derived from them. His data show further that this relation holds for T-3 and T-7 only for the region homologous to the fragment, where crossing over between the fragment and the single entire X in the translocations was less frequent than crossing over between the entire X's in the corresponding duplications.

The regions not homologous to the fragment in T-3 and T-7 were present in the duplications in two chromosomes that were entire X's, and they were present in the translocations in one entire X and in a proximal fragment comprising a large portion of the X (from the spindle fiber attachment to a point proximal to ruby). The total frequency of crossovers in these regions between the partial X and the entire X in the translocations was the same as between the entire X's, in the corresponding duplications. The nature of the effect of a translocation on crossing over is perhaps more clearly shown in ANDERSON'S (1929) line of high non-disjunction. The X was broken near the locus of vermilion into two long segments and the distal fragment translocated onto chromosome III. The greatest reduction in crossing over between the X's was in the region of the break and the reduction decreased toward both ends of the X.

DOBZHANSKY'S data for T-3 show the relative frequencies with which the distal fragment crosses over when present in the heterozygous translocation and in the duplication. There were 0.42 percent crossovers between the distal fragment and the one entire X in the first region in the translocation (and some additional crossing over involving the fragment since it overlapped about half of the second region). In the duplication there were only 0.21 percent crossovers between the fragment and both of the X's.

Although the fragment in the duplication from T-3 was about three-fourths of the length of the distal section of Dp-105 and the reduction in crossing over between the X's was correspondingly not so great, still in Dp-T-3 the ratio of X^d/X to X/X crossing over (in the homologous region) was more than 0.13:1 as compared with a ratio much less than 0.12:1 in Dp-105 when the fragment was present with attached X's. This suggests that the fragment of Dp-T-3, in its position at the end of a large autosome, may have an advantage in crossing over, over a distal fragment attached to a short proximal region, without increase in its effect on crossing over between the entire X's. A similar advantage to a fragment in a free state rather than attached to an X has been shown in X^p of Dp-100. In Dp-105 the ratio of X^d/X to X/X crossing over was 0.02:1 when the fragment was attached to another X, and less than 0.12:1 when free and the X's were attached to each other.

DOBZHANSKY (1934) has pointed out that the effect of a fragment on crossing over in regions homologous to itself is opposite to that of a third X in a triploid. Total crossing over among X's in triploids is higher than in diploids, especially in the most proximal and distal regions (BEADLE 1934). DOBZHANSKY'S study and the present study of X-duplications show that the longer the fragment (in a given position) the greater the reduction in the total crossing over among the three units of the system and the greater the proportion of crossing over of the fragment. The limiting hypothetical situation is a system of three entire X's (the superfemale condition) in which crossing over should occur infrequently, and at random if at all.

Beadle and Ephrussi (1937) have recently found that the offspring from the ovary of a superfemale transplanted into a normal female show almost no crossing over among the three X's. But the authors' analysis of this and of other irregularities leads them to conclude that the chromosome unbalance characteristic of super females has a specific effect on the meiotic mechanism of all of the chromosomes.

In the conditions prevailing in triploids, in which crossing over is increased, Redfield (1930) has found that when crossover reducers are present in one of three homologues of a triploid "the remaining two chromosomes cross over as they do in triploids and not as they do in diploids."

DISJUNCTION

The diagram used by Sturtevant to show the disjunction relations that hold among three fourth chromosomes has been found convenient for representing the types of segregation of the sex chromosome homologues under discussion. Sturtevant, in estimating the frequency with which a fragment of the X chromosome will segregate with attached X's rather than with Y (in $\underline{XX}X^{pd}Y$ females) applied his results obtained for the fourth chromosome, but it appears from the present study that the relations of the chromosomes at disjunction established for the fourth chromosomes do not hold for the sex chromosomes. By use of the diagram and of certain definitions, Sturtevant illustrates a constant relation of disjunction between any two given fourth chromosomes of his series. He found that his results were verifiable if he assumed that, when two of three chromosomes go to opposite poles of the meiotic spindle, the proportion in which one of them goes to the diploid pole is a property of those two chromosomes and is independent of the nature of the third opposing chromosome.

This is found to be not true for X and Y when the third chromosome is another normal X or one which is altered in one way or another. For example, if an X and a Y chromosome are present with an X containing the inversion dl-49 then, when X separates from Y, the proportion of times in which X segregates with $X^{dl\text{-}49}$ is the frequency with which X passes to the diploid pole divided by the sum of the frequencies with which it passes to the diploid and to the haploid pole. Using this formula, which gives a constant value for any two fourth chromosomes, it is found that when X separates from Y the proportion in which it goes to the diploid pole is not constant when the third opposing chromosome is changed. The different values are 0.113, 0.726, 0.77 and 0.365 when the opposing elements are respectively normal X, In-ClB, In-dl-49 and an X with the fragment of Dp-100 attached to it. Obviously there are differences in the four examples in the crossover relations between the X (and the Y) and the various opposing X's. The effect of crossing over on disjunction probably enters into the problem. In XXY almost normal crossing over takes place between the X's. In $XX^{In}Y$ there is a reduction in crossing over due to the inversion in the opposing X. In the duplication an agent reducing crossing over is the fragment introduced by the third element, which is the fragment and X attached to each other. There may be other factors affecting disjunction due to the attached fragment. At the time of disjunction the proportion of tetrads containing only non-crossover chromatids varies in the four combinations.

STURTEVANT and BEADLE (1936) have studied the distribution of homologues in females heterozygous for X inversions and have found that the X's of nearly all tetrads in which no exchange has taken place segregate together when a Y chromosome is present. In XX females heterozygous for In-dl-49, in which exchange takes place in only about 30 percent of tetrads, disjunction of the X's occurs regularly. But when a Y chromosome is present, they have found that in 90 percent of no-exchange tetrads the X's pass together to one pole away from the Y.

In the line of attached fragment, Dp (1;1)100 (without Y), disjunction of the X's is nearly complete (there are about 0.30 percent of exceptions) although there are 13.3 percent no-exchange tetrads. The pairing relations concern three elements which in disjunction are reduced to two units. In the presence of Y there is 19 percent of non-disjunction of X's and the frequency with which the two X's segregate together in no exchange tetrads is 56 percent. Disjunction of the fragment is determined by its attachment to an X, and non-disjunction of X's in no-exchange tetrads is also in this combination increased by the presence of Y.

It has been seen that in Dp(1;f)100 with two normal X's and a free fragment 31 percent of no-exchange tetrads give non-disjunction of X's. This results in a total percent of exceptions which is nearly the same as the percent of secondary exceptions from XXY females in which crossing over is normal, but the analysis shows that the conditions leading to approximately the same result are different. The percent of exchange tetrads is greatly reduced by the presence of the fragment and disjunction in no-exchange tetrads is nearly random in the duplication female.

Observations have been made by STURTEVANT and BEADLE on disjunction in systems of three homologues when one of the X's carries an inversion and the third element is a Y or a short fragment, the length of the fragment being varied.

The Y chromosome has been found by them (STURTEVANT and BEADLE 1936) to be but slightly concerned with reduction in crossing over between the X's (for example in In-dl-49). They refer to a difference between the effect of Y and of a small fragment of X on the percent of exceptions in females heterozygous for In-ClB. Unpublished data from experiments done separately by the two authors show that the frequency of exceptional zygotes from ClB/+ is almost 0 (as in XX), from ClB/+/Y it is 40 percent and from ClB/+/X^{Dp} it is 5–10 percent, corresponding respectively to 57 percent and 9–18 percent of segregation of the X's to the same pole.

In XXX^{pd} females (Dp(1;f)100), non-disjunction of X's is nearly random in no-exchange tetrads, whereas in $XX^{dl\text{-}49}Y$ females, STURTEVANT and BEADLE found nearly complete non-disjunction of X's (90 percent) in no-exchange tetrads. If 57 percent of XX^{In}-Y segregation represents 90 percent of no-exchange tetrads in ClB and if fragments of X produce an effect similar to that of the fragment in Dp(1;f)100 then about one-third of 57 percent or 19 percent of XX^{ClB}-X^{p} segregation might be expected from duplication females heterozygous for ClB. The percent would vary with the length of the fragment since reduction in the amount of crossing over and probably the frequency of no-exchange tetrads are correlated with the length of the fragment.

The effect on disjunction of a fragment of X with the long arm of Y attached to it, described by PHILIP (1934), is in one combination of X homologues comparable to the effect of a Y chromosome. She found that in attached-X females carrying the proximal fragment of Dp-B^S the frequency of $\underline{XX}X^{p}$-O segregation was 8.7 percent; but, when the long arm of Y was attached to the fragment, there was nearly complete disjunction of this new unit from the attached X's (the frequency of $\underline{XX}\underline{X^{p}Y'}$-O segregation was only 0.33 percent). Complete disjunction occurs also in $\underline{XX}Y$ females.

The frequency of $\underline{XX}X^{pd}$-O segregation in the original female of Dp-100 was 25.8 percent and when a Y was present the frequency of segregation of the fragment with the attached X's away from Y ($\underline{XX}X^{pd}$-Y) was 75.9 percent. Comparison of duplications of DOBZHANSKY'S study shows opposite correlations of the frequencies of the two types of segregation with the length of the proximal section of the fragment. DOBZHANSKY observed a negative correlation between the length of fragment and the frequency of $\underline{XX}X^{Dp}$-O segregation. In the duplications studied by him that contained very short fragments of the distal region of X and more or less of the inert region, $\underline{XX}X^{Dp}$-O segregation was less frequent when the locus of *bb* was included, except in Dp-102 which has already been referred to as exceptional in crossover relations. The frequencies were 10–19 percent when the locus of *bb* was present and 24–27 percent in its absence. When a Y chromosome was present with the same fragments non-disjunction of the attached X's and fragment was increased but in such proportions that $\underline{XX}X^{Dp}$-Y segregation was more frequent when the locus of *bb* was included than when it was not present; non-disjunction was over 50 percent when the fragment covered *bb* and less than 50 percent when it was shorter. (One exception (Dp-106) which seemed when tested not to contain the locus of *bb* nevertheless gave frequencies of the two segregations similar to those of the other duplications covering *y svr* and *bb*; SIVERTZEV-DOBZHANSKY and DOBZHANSKY (1933) state that the tests were not altogether conclusive.) The relation of crossovers to disjunction in these combinations of attached-X's and fragment is not known.

A constant property of the Y chromosome is the effect of increasing non-disjunction of two other units of X homologues in combinations that have been described by others and in this study; non-disjunction is increased when Y is present with XX, XX^{In}, $\underline{XX}X^{Dp}$ and $X\underline{XX^{pd}}$.

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SUMMARY

1. The duplicating fragment of Dp-100 is an X chromosome deficient for the middle section. The fragment contains a distal component extending from the distal end of the chromosome (yellow) to a point between the loci of prune and white, and a proximal component extending from a point between the loci of Beadex and fused to the spindle fiber end. The fragment therefore contains the inert region, the section homologous to Y, and some of the active region of the middle and distal end of the X.

2. The fragment produces characteristic somatic effects and lowers viability in females. It is usually lethal in males. It may sometimes produce a fertile intersex when present with two entire X's in triploids (DOBZHANSKY and SCHULTZ 1931).

3. The homologues of X that are involved have been obtained in the combinations: (a) $\underline{XX}X^{pd}$, (b) $\underline{XX}X^{pd}Y$, (c) $X\underline{XX^{pd}}$, (d) $X\underline{XX^{pd}}Y$ and (e) XXX^{pd} (fig. 1).

4. Crossing over has been studied in the last three combinations (in which the X's are not attached to each other) in eight regions from yellow to bobbed, and a marked reduction in crossing over between the X's has been observed in the region homologous to the proximal component of the fragment (fig. 2). There is also a marked reduction in total crossing over in that region.

5. In the two lines with separate X's without Y, (e) and (c), reduction in crossing over between the entire X's is the same (except in region 3) whether the fragment is free (e) or is attached to one of the X's (c).

6. In lines (e) and (c) crossing over between X's is reduced to about one-tenth of the frequency of the control in the eighth region (nearest to the spindle fiber attachment). Toward the distal end of the chromosome, the curve representing ratios of duplication to control crossing over rises gradually to a maximum higher than control in the third region between *cv* and *ct*; it then falls but only to about 0.8 in the first region which is in part homologous to the distal component of the fragment (X^d).

7. When a Y chromosome is present and the fragment is attached to an X (d), crossing over is slightly lower throughout the length of the chromosome and still further reduced in the eighth region.

8. Crossing over takes place between the distal component of the fragment (X^d) and an entire X, with a very low frequency (0.01 to 0.04 percent).

9. Crossing over occurred between the proximal component of the fragment (X^p) and X. In the line of free X's and fragment (e) the frequency was estimated by allocations of ambiguous types from X eggs in experiment 7, or by marking the X's with bb^l which reduces exchange. The chromatids that are X^p/X crossovers seem to occur at least as frequently in XX as in X eggs. The frequency of X^p/X crossing over appears to be about 0.5 percent in the XXX^{pd} line (e).

10. Corrected frequency of crossing over between X^p and X in the line in which the fragment is attached to an X (c), as estimated from exchange between X^p and the free X, and diagonal exchange between X^p and attached X, was less than 0.1 percent.

11. When a Y was also present the frequency was 0.2 to 0.3 percent.

12. In the line of free X's and free fragment (e) crossovers between X's were rarely observed in zygotes from XX gametes known to be not crossovers between the proximal component of the fragment (X^p) and an X (1 equational in region 5 among 594 females). In experiment 7 half of the X^p/X crossovers from X eggs were also distal crossovers between the X's; but no X/X crossovers were observed in any of the females from XX eggs. In experiment 5a, a small percentage of both reciprocal and equational distal crossovers was observed in flies from XX eggs, showing that distal

X/X crossovers do not always disjoin. The frequency was not higher than was to be expected if the X/X crossovers were also X^p/X crossovers, which were not detectable.

13. In the lines with attached fragment, with a Y (d) or without (c), five distal equationals were observed among 1204 exceptional females. About half of the X^p/X crossovers which were recovered in attached-X females from $\underline{XX}$ eggs were also X/X crossovers in distal regions.

14. Crossing over between Y and the other X homologues was not studied and was observed only in the $X\underline{XX}^{pd}Y$ line (b).

15. Disjunction of the different partially homologous elements has been studied in the five lines of Dp-100:

a. The frequency of $\underline{XX}X^{pd}$-O type of segregation in the original female (a) was 25.8 percent.

b. With Y added, in the $\underline{XX}X^{pd}Y$ line (b), there was 75.9 percent of $\underline{XX}X^{pd}$-Y type of segregation, that is, more than the frequencies of both of the other types of segregation. This shows that in this combination of X homologues disjunction is not dependent on random distribution of one of the elements after separation of the other two. The result is similar to those obtained by Beadle and Sturtevant (1936) with X inversions, by Sturtevant (1936) with triplo-IV, and by Dobzhansky (1934) and Sturtevant (1936) with X duplications.

c. The frequency of segregation of two X's together (XX-X^{pd}) in experiment 7, with the line of free X's and free fragment (e), was 3.4 percent, that is, about one-third of the estimated percent of no-exchange tetrads, a nearly random distribution in no-exchange tetrads of the three homologues. Segregation in this combination is markedly different from that in $XX^{In}Y$ females, heterozygous for the dl-49 inversion, in which the X's segregate together in 90 percent of no-exchange tetrads (Sturtevant and Beadle 1936). These comparisons in connection with others show a distinct difference between the effects of Y and of even small fragments of X on disjunction of X's. Philip (1934) found that an element composed of the long arm of Y attached to a proximal fragment (extending to the locus of *B*) disjoins completely from attached X's. The effect is the same as that of Y in $\underline{XX}Y$ females but different from that of the fragment of Dp-100 (15a above) and of other duplications (Dobzhansky 1934).

d. Disjunction of the two X's, when the fragment is attached to one of the X's, in the $X\underline{XX}^{pd}$ line (c) of Dp-100 is almost complete as in XX or XX^{In} females; the frequency of $X\underline{XX}^{pd}$-O segregation was 0.3 percent which is about the same as in XX controls, and is only 2.3 percent of the frequency of no-exchange tetrads.

e. The presence of a Y with free X's and attached fragment (d) increases segregation together of the X's ($X\underline{XX}^{pd}$-Y) to about 19.0 percent. This is about 56 percent of the frequency of no-exchange tetrads.

16. The reductions in crossing over between X's in the region homologous to the proximal component of the fragment in Dp-100 and in the proximal Dp-138 studied by DOBZHANSKY (1934) are proportional to the respective lengths of the duplicating sections of chromosomes (shown graphically in figure 2). This is in agreement with the correlations shown by DOBZHANSKY in other duplications.

17. The slight reduction in crossing over between the X's in Dp-100, in the region homologous to the distal component of the fragment, is not as great, relative to the lengths of fragments, as the reductions found by DOBZHANSKY in distal duplications of varying lengths having their own spindle fibers and containing more or less of the inert region. The reduction in the distal region in Dp-100 is comparable to that found in a much shorter "distal" duplication (Dp-101), which includes the locus of *bb*.

18. The effect of Dp-100 is throughout the whole X very similar to the effect of the simple proximal Dp-138, some differences appearing in the regions not homologous to the fragments.

19. The results show that the proximal component of the fragment has more effect than the distal on crossing over of the X's in homologous regions relatively to their lengths. Other comparisons show correlation between the extent of effects of fragments and their position.

20. In the proximal region of Dp-100, the proportion of X^p/X crossing over to X/X crossing over, in experiment 7 with the line of free X's and free fragment (e), is about 0.30:1 whereas if exchange were random the ratio would be 2:1. Other duplications show a similar relation.

21. Comparison of Dp-100 with DOBZHANSKY'S proximal Dp-138 and mostly distal Dp-105 shows that increase in reduction of crossing over in the region homologous to the fragment is positively correlated with increase in reduction of total crossing over in that region, and with increase in the proportion of the total that involves the fragment. In some conditions, there appear to be factors that give an advantage in crossing over to the fragment without changing the extent of its effect on crossing over of the X's.

22. The persistence of the telophase relations of the chromosomes whereby the regions of spindle-fiber attachments are closely associated before the first meiotic division and whereby new relations are established in aberrations has been shown by DOBZHANSKY (1936) to be an important consideration in the study of crossing over in aberrations. By a comparison with other duplications a proportional effect on crossing over of the proximal component of Dp-100 is shown. The position of a distal section in a duplication is determined by its attachment to a long or short proximal

component or to another chromosome. On the relatively long proximal section of Dp-100 the distal component has less effect on X/X crossing over than have comparable distal fragments when attached to short proximal sections containing more or less of the inert region only, or when carried at the ends of the long autosomes.

LITERATURE CITED

Anderson, E. G., 1929 Studies on a case of high non-disjunction in *Drosophila melanogaster.* Z. i. A. V. **51**: 397–441.

Beadle, G. W., 1934 Crossing over in attached-X triploids of *Drosophila melanogaster.* J. Genet. **29**: 277–309.

Beadle, G. W., and Ephrussi, Boris, 1937 Ovary transplants in *Drosophila melanogaster*: meiosis and crossing over in superfemales. Proc. Nat. Acad. Sci. Wash. **23**: 356–360.

Bridges, C. B., 1916 Non-disjunction as proof of the chromosome theory of heredity. Genetics **1**: 1–52, 107–163.

1938 A revised map of the salivary gland X-chromosome of *Drosophila melanogaster.* J. Hered. **29**: 11–13.

Bridges, C. B., and Anderson, E. G., 1925 Crossing over in the X chromosomes of triploid females of *Drosophila melanogaster.* Genetics **10**: 418–441.

Bridges, C. B., and Olbrycht, T. M., 1926 The multiple stock "Xple" and its use. Genetics **11**: 41–56.

Dobzhansky, Th., 1930 Translocations involving the third and the fourth chromosomes of *Drosophila melanogaster.* Genetics **15**: 347–399.

1932a Cytological map of the X chromosome of *Drosophila melanogaster.* Biol. Zbl. **52**: 493–509.

1932b Deletion of a section of the X chromosome of *Drosophila melanogaster.* Bull. Lab. Genetics, Leningrad **9**: 193–216.

1933 Studies on chromosome conjugation II. The relation between crossing over and disjunction of chromosomes. Z. i. A. V. **64**: 269–309.

1934 Studies on chromosome conjugation III. Behavior of duplicating fragments. Z. i. A. V. **68**: 134–162.

1936 The persistence of the chromosome pattern in successive cell divisions in *Drosophila pseudoobscura.* J. Exp. Zool. **74**: 119–135.

Dobzhansky, Th., and Schultz, J., 1931 Evidence for multiple sex factors in the X chromosome of *Drosophila melanogaster.* Proc. Nat. Acad. Sci. Wash. **17**: 513–518.

Dobzhansky, Th., and Sturtevant, A. H., 1931 Translocations between the second and the third chromosomes of Drosophila and their bearing on Oenothera problems. Carnegie Instn. Wash. Publ. **421**: 29–59.

Dubinin, N. P., Sokolov, N. N., Tiniakov, G. G., and Sacharov, W. W., 1935 On the problems of chromosome conjugation. J. Biol. **4**: 175–204.

Gershenson, S., 1935 The mechanism of non-disjunction in the ClB stock of *Drosophila melanogaster.* J. Genet. **30**: 115–125.

Kaufmann, B. P., 1933 Interchange between X and Y chromosomes in attached-X females of *Drosophila melanogaster.* Proc. Nat. Acad. Sci. Wash. **19**: 830–838.

Mackensen, Otto, 1935 Locating genes on salivary chromosomes. J. Hered. **26**: 163–174.

MacKnight, R. H., 1937 Crossing over in the sex chromosome of racial hybrids of *Drosophila pseudoobscura.* Genetics **22**: 249–256.

Mather, K., 1936 The determination of position in crossing over. I. *Drosophila melanogaster.* J. Genet. **33**: 207–235.

Morgan, T. H., Bridges, C. B., and Schultz, Jack, 1930 The constitution of the germinal material in relation to heredity. Yearb. Carn. Instn. Wash. **29**: 352–359.

1932 Yearb. Carn. Instn. Wash. **31**: 303–307.

1933 Yearb. Carn. Instn. Wash. **32**: 298–302.

1937. Yearb. Carn. Instn. Wash. **36:** 298–305.

Painter, T. S., 1934 A new method for the study of chromosome aberrations and the plotting of chromosome maps in *Drosophila melanogaster*. Genetics **19:** 175–188.

1935 The morphology of the third chromosome in the salivary gland of *Drosophila melanogaster* and a new cytological map of this element. Genetics **20:** 301–326.

Philip, U., 1934 Die Paarung der Geschlechtschromosomen von *Drosophila melanogaster*. Z. i. A. V. **67:** 446–476.

Redfield, Helen 1933 Crossing over in triploid Drosophilas. Collecting Net **5:** 275–276.

Sivertzev-Dobzhansky, N. P., and Dobzhansky, Th., 1933 Deficiency and duplications for the gene bobbed in *Drosophila melanogaster*. Genetics **18:** 173–192.

Steinberg, A. G., 1936 The effect of autosomal inversions on crossing over in the X chromosome of *Drosophila melanogaster*. Genetics **21:** 615–624.

Stone, W., and Thomas, I., 1935 Crossover and disjunctional properties of X chromosome inversions in *Drosophila melanogaster*. Genetica **17:** 170–184.

Sturtevant, A. H., 1936 Preferential segregation in triplo-IV females of *Drosophila melanogaster*. Genetics **21:** 444–466

Sturtevant, A. H., and Beadle, G. W., 1936 The relations of inversions in the X chromosome of *Drosophila melanogaster* to crossing over and disjunction. Genetics **21:** 554–604.

APPENDIX

Tables 6–10. For each type of crossover the complementary class first recorded in the tables is that containing the distal end of the first entire

Table 6

Experiment 3. Offspring of Dp (1;f)/y^2 *cv v f/y ec* ct^6 *s car* ♀ *by yX9* ♂.

TYPE	NON-Dp (♂ ♀)		Dp (♀ ♀)		CONTROL (♂ ♀)		TYPE	NON-Dp (♂ ♀)		Dp (♀ ♀)		CONTROL (♂ ♀)	
0	512	567	238	146	295	267	3, 5	1	1	—	1	4	2
1	51	65	(with 0)		38	31	3, 6	3	4	—	2	3	7
2	87	74	10	15	44	48	3, 7	—	—	(with 3)		2	1
3	88	84	6	28	38	61	4, 5	1	3	2	1	4	5
4	119	117	31	41	81	74	4, 6	4	4	—	—	4	5
5	65	65	7	27	48	42	4, 7	—	1	(with 4)		3	6
6	45	78	17	8	60	62	5, 6	1	—	—	—	—	—
7	8	10	(with 0)		26	22	5, 7	2	1	(with 5)		1	3
1, 2	2	—	(with 2)		—	1	6, 7	1	1	(with 6)		1	—
1, 3	3	4	(with 3)		—	—	1, 2, 7	—	—	(with 2)		1	—
1, 4	5	5	(with 4)		7	5	1, 4, 5	—	1	—	—	—	—
1, 5	6	7	(with 5)		—	5	1, 4, 6	—	—	—	—	1	—
1, 6	4	7	(with 6)		7	6	1, 5, 6	1	—	—	—	—	—
1, 7	—	1	(with 0)		5	1	1, 5, 7	—	—	(with 5)		1	—
2, 3	1	—	—	—	—	—	1, 6, 7	—	—	(with 6)		1	—
2, 4	4	8	—	2	6	5	2, 3, 6	—	—	—	—	—	1
2, 5	2	5	1	—	3	3	2, 4, 7	—	—	(with 2, 4)		1	—
2, 6	7	5	—	2	16	10	3, 5, 7	1	—	(with 3, 5)		—	—
2, 7	2	—	(with 2)		5	1		1027	1118	312	274	708	676
3, 4	1	—	—	1	2	2	Total	2145*		586		1384	

* Class (a) from X-XX^{pd} segregation. Other classes: (b) 40 XXY females not equational (2 XXY females in control); (c) X^p/X crossovers included in (a) and (b); (d) X^d/X crossovers none.

Quota of chromatids used in determining percent of crossing over: 2145 from males and females of class (a), 80 represented by class (b).

chromosome to be described, namely, containing y^2, while the second entry is of the complementary class beginning with *y*. Numbering of regions follows the scheme: $y^2(y)$ 1 *ec* 2 *cv* 3 *ct* 4 *v* 5 *s* 6 *f*(*B*) 7 *car* 8 *bb*(bb^l) illustrated in figure 1 e. The tester male used in test crosses known as *y*X9 (*y ec cv* ct^6 *v* s^2 *car f* bb^l) carries a marker for every region.

Although in the actual experiments females and males were classified and totalled separately they have been combined in the following tables since careful inspection showed close agreement throughout. The duplication classes include only females, and since their viability is erratic, complementary crossovers may differ widely in value; they were not used in determining percent of crossing over.

TABLE 7

Experiment 5. Offspring of $Dp(1;f)/y^2\ cv\ v\ f/y\ ec\ ct^6\ s\ car$ ♀ *by f B* ♂, *and from XXY daughters by f B* ♂.

TYPE	XXX^{pd} NON-Dp (♂♂)		XX CONTROL (♂♂)		XXY		TYPE	XXX^{pd} NON-Dp (♂♂)		XX CONTROL (♂♂)		XXY	
0	386	379	129	73	430	304	3, 4	4	—	—	—	1	—
1	44	31	11	12	23	38	3, 5	3	—	—	—	6	5
2	63	49	19	8	72	56	3, 6	3	2	2	—	3	9
3	53	78	12	11	49	56	3, 7	—	3	—	1	4	2
4	105	98	25	30	114	104	4, 5	2	—	3	—	3	6
5	50	34	23	8	65	61	4, 6	3	1	2	—	10	10
6	33	36	19	16	53	63	4, 7	—	1	6	1	2	9
7	8	5	6	7	29	21	5, 6	—	—	—	1	—	—
1, 2	—	—	—	—	—	1	5, 7	—	1	1	—	—	2
1, 3	1	—	—	—	1	—	6, 7	—	—	—	—	—	—
1, 4	4	1	3	2	3	4	1, 3, 7	—	—	—	—	—	1
1, 5	5	2	1	—	4	2	1, 4, 5	—	—	—	—	—	1
1, 6	5	4	1	3	5	9	2, 4, 6	—	—	—	—	—	2
1, 7	1	2	2	1	2	3	3, 4, 6	—	—	—	—	—	1
2, 4	5	3	3	1	6	4	4, 5, 7	—	—	2	—	—	—
2, 5	2	2	4	—	12	7							
2, 6	4	2	3	1	8	12		784	734	278	178	907	794
2, 7	—	—	1	2	2	1	Total	1518*		456		1701	

* Class (a) from X-XX^{pd} segregation. Other classes: (b) 80 XXY females (1 XXY female in control); (c) X^p/X crossovers included in (a) and (b); (d) X^d/X crossovers none; (e) 1 matroclinous female. From XXY mothers there were 26 matroclinous females and 28 patroclinous males.

Quota of chromatids used in determining percent of crossing over: 1518 from males of class (a), 80 represented by class (b); 1 represented by class (e).

TABLE 8

Experiment 7. Offspring of $Dp(1;f)/y^2$ *cv v B bb/y ec* ct^6 *s car* ♀ *by yX9* ♂.

TYPE	NON-Dp (♀ ♀)		CONTROL		TYPE	NON-Dp (♀ ♀)		CONTROL		TYPE	NON-Dp (♀ ♀)		CONTROL	
0	1054	1653	206	285	2, 7	3	7	6	1	1, 4, 6	—	—	1	—
1	165	100	26	26	2, 8	1	—	2	2	1, 7, 8	3	—	—	—
2	229	170	32	39	3, 4	3	3	1	1	2, 3, 6	1	—	—	—
3	314	223	46	31	3, 5	7	9	1	2	2, 4, 6	—	1	1	—
4	399	299	77	67	3, 6	11	15	5	6	2, 5, 8	—	—	—	1
5	154	107	56	30	3, 7	2	4	—	3	2, 6, 8	—	—	1	—
6	186	113	68	58	3, 8	—	1	—	5	3, 4, 5	—	—	—	2
7	17	16	30	19	4, 5	2	2	2	3	3, 4, 6	—	—	1	—
8	20	10	23	9	4, 6	9	17	5	6	3, 4, 7	2	1	—	—
1, 2	—	1	—	—	4, 7	2	1	8	5	3, 5, 7	—	—	1	—
1, 3	2	1	—	—	4, 8	—	2	2	6	3, 6, 8	1	—	—	—
1, 4	12	12	6	3	5, 6	—	—	2	—	3, 7, 8	—	—	1	—
1, 5	3	9	—	2	5, 7	—	2	1	1	4, 5, 6	—	1	—	—
1, 6	7	25	3	13	5, 8	—	1	1	7	4, 5, 8	—	—	2	—
1, 7	3	2	6	3	6, 7	—	1	—	—	4, 6, 7	—	—	—	2
1, 8	—	—	3	1	6, 8	—	1	2	7	1, 4, 5, 8	—	1	—	—
2, 4	4	15	2	8	7, 8	—	2	—	—		2627	2863	637	670
2, 5	4	11	4	5	1, 2, 4	—	—	1	—	Total	**5490**		**1307**	
2, 6	7	24	1	11	1, 3, 8	—	—	1	—		(♂♂ = 6278)		(1484)	
										Total	**11768***			

* Class (a) from $X\text{-}XX^{pd}$ segregation. Other classes: (b) 190 XXY females not equational, 105 (tested) of these not reciprocal X/X crossovers (no XXY females in control); (c) X^p/X crossovers, from X-eggs, 5 apparent 7, 8 X/X crossovers, 3 of them also X/X crossovers at 1 (included in (a), (see table 2); X^p/X crossovers from XX-eggs included in (b); (d) X^d/X crossovers, 5 not-y non-Dp flies (2 females and 3 males) equally divided between complementary classes, and 1 Dp female carrying a y^2 (or y) fragment from X^d/X crossing over (see table 2).

Quota of chromatids used in determining percent of crossing over: 5490 from females of class (a), 190 of class (b) and 2 of class (d).

TABLE 9

Offspring in lines of Dp(1;1)100. Experiment 1. Dp(1;1), y^2 cv v f/y ec ct^6 s car ♀ by yX9 ♂. Experiment 10a. Dp(1;1), y^2 cv v f/y ec ct^6 s car/Y ♀ by y^2 f B bb^l ♂.

TYPE	$X\underline{XX}^{pd}$ NON-Dp (♂♀)	$X\underline{XX}^{pd}$ Dp (♀♀)	XX CONTROL (♂♀)		$X\underline{XX}^{pd}Y$ NON-Dp (♂♂)	TYPE	$X\underline{XX}^{pd}$ NON-Dp (♂♀)	$X\underline{XX}^{pd}$ Dp (♀♀)	XX CONTROL (♂♀)		$X\underline{XX}^{pd}Y$ NON-Dp (♂♂)
0	3279	1447	882	731	626	4, 6	18	3	24	20	5
1	253	(with 0)	76	71	59	4, 7	3	1	13	16	—
2	414	152	110	109	74	4, 8	3	(with 4, 7)	(with 4)		1
3	452	190	114	133	77	5, 6	—	—	2	1	—
4	720	260	228	225	126	5, 7	—	1	9	5	1
5	346	120	162	144	53	5, 8	1	(with 5)	(with 5)		—
6	273	66	180	190	76	6, 7	—	—	1	3	—
7	44	9	80	80	13	6, 8	1	(with 6, 7)	(with 6)		—
8	18	(with 7)	(with 0)		3	1, 2, 6	1	(with 2, 6)	—	—	—
1, 2	—	(with 2)	—	1	—	1, 2, 7	—	(with 2, 7)	1	—	—
1, 3	1	(with 3)	2	—	1	1, 4, 5	—	(with 4, 5)	1	—	—
1, 4	6	(with 4)	12	13	2	1, 4, 6	1	(with 4, 6)	1	—	—
1, 5	13	(with 5)	10	7	4	1, 5, 7	1	(with 5, 7)	2	—	—
1, 6	9	(with 6)	11	20	5	1, 6, 8	1	(with 6, 7)	(with 1, 6)		—
1, 7	1	(with 7)	9	4	—	2, 3, 7	—	—	—	1	—
1, 8	1	(with 7)	(with 1)		—	2, 4, 5	—	—	1	—	—
2, 3	—	—	1	—	—	2, 4, 6	—	1	1	—	—
2, 4	8	2	16	15	3	2, 4, 7	1	—	—	4	—
2, 5	8	4	25	13	2	2, 5, 7	—	—	—	2	—
2, 6	12	1	32	31	4	3, 4, 6	—	—	1	—	—
2, 7	6	2	15	12	2	3, 4, 7	—	—	1	1	—
2, 8	4	(with 2, 7)	(with 2)		—	3, 5, 6	—	—	—	1	—
3, 4	5	3	3	2	6	3, 6, 7	—	—	—	1	—
3, 5	12	5	20	9	2	4, 5, 7	—	1	2	1	—
3, 6	6	1	16	14	4	4, 6, 7	—	—	1	—	—
3, 7	5	2	13	10	—	2, 5, 7, 8	1	—	(with 2, 5, 7)		—
3, 8	2	(with 3, 7)	(with 3)		—				2090	1898	
4, 5	6	2	12	8	—	Total	5936*	2273	3988		1149†

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* Exp. 1, class (a) from X-$\underline{XX}^{pd}$ segregation. Other classes: (b) 9 $X\underline{XX}^{pd}Y$ females not equational (3 XXY females in control); (c) one y^2 X^p/X crossover involving the free X (not tested), presumably an $\underline{XX}$ female, not equational (homozygosis for y^2 was not detectable); (d) X^d/X crossovers none.

Quota of chromatids used in determining percents of crossing over: 5936 from males and females of class (a), 18 represented by class (b), 2 by class (c). Quota of control, 3988 males and females of class (a), 12 represented by class (b).

† Exp. 10a, class (a) from XY-$\underline{XX}^{pd}$ or X-$\underline{XX}^{pd}Y$ segregation. Other classes described in table 10.

Quota of chromatids used in determining percents of crossing over: 1149 from males of class (a) and (see table 10) 323 represented by class (b), 2 by diagonals of class (c) and 2 by crossovers with the free X of class (c).

TABLE 10

Experiment 9. Offspring of Dp(1;f)/y^2 *cv v f* bb^l/*y ec* ct^6 *s car* bb^l by y^2 *B* bb^l Y^{bb} ♂.

Experiment 9d. Offspring of Dp(1;f)/*y ec* ct^6 s^2 *car bb*/*y ec* ct^6 s^2 *car bb* ♀ by y^2 *B* bb^l(Y^{bb}?) ♂.

Experiment 1d. Offspring of Dp(1;1), y^2 *cv v f*/*y w* ♀ by y^2 *cv v B* ♂.

Experiment 10b. Offspring of Dp(1;1), y^2 *cv v f*/*y w*/Y ♀ or Dp(1, 1), *y w cv v f*/y^2/Y ♀ by y^2 *cv v B* ♂ and analysis of flies from two-X eggs in these experiments, in experiment 5a (including those from experiment 5, table 7, and additional matings) and in experiment 10a (table 9). For example, opposite (b), 2 =0:1, 4 is the record of two tested females, of class (b), whose X's were one non-crossover and one double crossover in regions 1 and 4; [1]=0:5 is the record of one not tested female, of class (b), whose X's were rated from the phenotype as one non-crossover and one crossover in region 5.

	OBSERVED ZYGOTES				CROSSOVER CONSTITUTION OF X'S (NUMBERS OF FLIES NOT TESTED IN BRACKETS)			
PARENT ♀	XXX^{pd}	XXX^{pd}	$X\underline{X}X^{pd}$	$X\underline{X}X^{pd}Y$	XXX^{pd}		$X\underline{X}X^{pd}Y$	
EXP.	9	9d	1d	10b	9	5a	10b	10a
Not X^p/X crossovers								
(a) X- or XY-eggs								
non-Dp ♀ ♀	15	1019	3149	4444				
non-Dp ♂♂	10476	1049	3058	4134		3084		1149
(b) XX-eggs	594	26			[570]=0:0 23 =0:0 [1]=0:5	[29] =0:0 102 =0:0 1 =0:1 2 =0:1, 4 or 1:4 [1]? =0:7 1 =1:1 1 =2:2 1 =4:4		
$\underline{XX}X^{pd}$-eggs			12	958			[800]=0:0 152 =0:0 2 =0:1 or 2 3 =0:3 or 4 1 =1 or 2:1 or 2	[206]=0:0 31 =0:0
O-eggs			16					
Y-eggs by								
X-sperm				1046				323
XX-sperm				2 pat. ♀ ♀				
(c) X^p/X crossovers						included in (a) and (b)		
X-eggs	4	1 ♂						
XX-eggs	11	2			[11]=0:0			
X^p/X c.o. with attached X (diagonal) $\underline{XX}$-eggs			0	2			1 =0:0 1 =0:1 or 2	1 =0:4
X^p/X c.o. with free X $\underline{XX}$-eggs			2*	2			[2]=0:3 or 4	1 =0:0 1 =0:2
(d) X^d/X crossovers	1 ♂	0	0	0		0		
(e) XXX^{pd}-eggs		1				1		
(f) XX-eggs, equational	1		1 (tested)	[1]?	1 =0:5	[1]? or =0:7 (see above)		

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* Tested not X/X crossovers.