CROSSING OVER IN THE THIRD CHROMOSOMES OF TRIPLOIDS OF *DROSOPHILA MELANOGASTER**

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INTRODUCTION

Upon *a priori* grounds it has long been assumed that any crossover involves at least two phenomena: (1) a rotation or overlapping of chromosomes or of their derivative strands, and (2) a breaking and reunion at one or more loci of these strands. (For a recent discussion see BELLING 1927.) It is known in Drosophila that the segmental exchange does not occur in males and that it takes place in diploid females at the four-strand stage (BRIDGES 1916, ANDERSON 1925, L. V. MORGAN 1925, STURTEVANT unpublished) and in triploid females at the corresponding six-strand stage (BRIDGES and ANDERSON 1925). Further evidence indicates that the process occurs in early oöcytes before the first maturation division (PLOUGH 1917, 1921; GOWEN 1929). The amount of double crossing over is dependent upon the distance between the loci involved and varies with the region of the chromosome under observation (BRIDGES and MORGAN 1923). Crossing over may be partially or completely inhibited by "crossover reducers" (STURTEVANT 1919, GOWEN 1928, etc.) some of

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which have been shown to be inverted sections of chromosome (STURTEVANT 1926).

A number of recent results indicate a correlation between the effects of various agents and the distance of the region involved from the spindle-fibre attachment. Using young females as contrasted with older females, or subjecting females to temperatures greater or less than about 25°C, or to X-rays, results in a considerable increase in crossing over in the region of spindle-fibre attachment (BRIDGES 1915, 1927; PLOUGH 1917, 1921; MAVOR 1923; MAVOR and SVENSON 1924; MULLER 1925, 1926; STERN 1926). This is undoubtedly true of the V-shaped second and third chromosomes in which the attachment is at the apex of the V, and is probably true also of the rod-shaped X chromosome in which the attachment is terminal and at the right end of the chromosome map. The fourth chromosome has not been tested.

Whatever the mechanical factors at work, it would seem that a substitution of six sets of crossover strands in the triploid for the four sets ordinarily present in the diploid might throw some light upon the process of crossing over. However, besides the mere substitution of a greater number of chromosome strands, triploidy involves changes in the general relationships within the cell, and, in particular, possible changes in the ratio of chromatin to cytoplasm as regards surface and volume. Such changes in themselves might be responsible for the crossover variations found. This question will be considered later.

One of the main difficulties encountered in the analysis of triploid data relates to the possibility of crossing over of sister strands (that is, the two strands resulting from the splitting of a single chromosome). Crossing over is ordinarily measured by the percentage of crossed-over chromosomes detected. But in both diploid and triploid, crossing over between sister strands, if it occurs, will remain undetected. If it is as likely to occur between sister strands as between non-sister strands, then in the diploid in any given region the undetected crossing over would be $\frac{1}{3}$ the actual total crossing over, that is, the ordinary "crossover" values would represent $\frac{2}{3}$ the actual physical crossing over. But in the triploid, since six strands are involved, only $\frac{1}{5}$ the total crossing over would be undetected—in other words, the detected "crossing over" would represent $\frac{4}{5}$ the total crossing over.

A simple correction may, of course, be made for sister-strand crossing over in comparing diploid with triploid, but it rests upon the assumption of free sister-strand interchange. It was expected, as a matter of fact,

that the possibility of such interchange could be investigated by means of data from triploids. Unfortunately, as BRIDGES and ANDERSON (1925) also found, the difference between triploid and diploid shows such great variation in different regions of the chromosome that any effect to which sister-strand interchange may give rise is completely masked. Corrected values will be tabulated whenever it seems advisable. These corrections are superfluous, if, as the recent paper of STURTEVANT (1928) indicates, there is no sister-strand crossing over. He finds that controlled cases of reversion of bar eye to round are always accompanied by detected crossing over. If sister-strand crossing over occurred at all in such crosses, it should have given many more apparent non-crossover reversions than can be explained on the basis of experimental error. On the other hand it is possible that bar reversion represents a special case, and if so there is no way of knowing at present whether or not sister-strand interchange takes place. However, as will be shown later (page 236), the conclusions of the present paper in regard to the differences between crossing over in triploid and diploid remain unaltered, even if sister strands cross over as freely as non-sister strands.

CROSSES IN WHICH THE THREE THIRD CHROMOSOMES WERE MARKED

Technically the study of crossing over in triploids is made difficult by a number of circumstances. Thus, relatively few offspring are obtained, and these offspring are of various types in regard to their chromosome balance. They include approximately: 3.9 percent triploid daughters, 46.8 percent diploid daughters, 6.0 percent diploid sons, 36.9 percent intersexes, 1.3 percent superfemales, and 5.2 percent supermales (see BRIDGES and ANDERSON 1925). The facts that some expected chromosome combinations do not appear at all (for example, individuals diploid except for the presence of three second or third chromosomes) and that the percentages of the types which do appear are very different from expectation, are believed to depend upon viability differences during development.

In the investigations of BRIDGES and ANDERSON on crossing over in the X chromosome advantage was taken of the fact that of the 46.8 percent diploid daughters produced, practically all (that is, 41.1 percent of the total offspring) represent exceptions which receive a Y chromosome from the father, the two X chromosomes coming from the triploid mother. Data on crossing over for this chromosome may then be obtained by genetic tests of the composition of the exceptional daughters.

But the corresponding exceptions for the two larger autosomes do not appear, and this technique is therefore not applicable in the study of chromosome III. The diploid sons and daughters have each received one third chromosome from the triploid mother and one from the diploid father. Crossing over is then measured directly by the relative proportions of the diploid types emerging from the cross.

In the crosses first successfully utilized all three third chromosomes were marked according to the scheme previously adopted by BRIDGES and ANDERSON. A series of mutant loci were chosen, such that very near each locus another favorable mutant gene is known for each of the points chosen; the two genes and the normal locus of the first were introduced into the triploid, one in each of the three chromosomes, and were treated virtually as a series of allelomorphs. Actually one is non-allelomorphic but is so close to the other locus that crossing over between them is relatively negligible. Because the characters which it seemed advisable to use interfere to a certain extent with each other, it was necessary, in covering the chromosome, to make use of two crosses instead of one. These crosses are as follows:

(1)
$$\begin{array}{|ccccc|}\hline + & D & m_a & S_b & + \\ \hline s_e & M_h & + & + & H \\ \hline h & + & c_u & b_x & e^s \\ \hline\end{array}\ \text{♀} \times s_e\ h\ m_a\ c_u\ b_x\ e^s\ \text{♂}.$$

(2)
$$\begin{array}{|ccc|}\hline + & H & + \\ \hline S_b & + & M \\ \hline b_x & e^s & c_a \\ \hline\end{array}\ \text{♀} \times b_x\ e^s\ c_a\ \text{♂}.$$

The symbols stand for the following third chromosome mutants, the genes having the positions indicated on the standard diploid map: s_e, sepia at 26.0 and h, hairy one-half unit to the right of sepia; M_h, minute-h at 40.1 and D, dichaete at 40.4; m_a, maroon at 49.7 and c_u, curled at 50.0; S_b, stubble at 58.2 and b_x, bithorax at 58.7; H, hairless at 69.5 and e^s, sooty at 70.7; c_a, claret at 100.7 and M, minute at 101.0.

Of the seven special stocks needed for the work, only hairless was already in existence; it was necessary therefore to synthesize the others. Each stock was derived from a single chromosome which was then (excepting $h\ c_u\ b_x\ e^s$ and $s_e\ h\ m_a\ c_u\ b_x\ e^s$) kept intact by being carried over the

$lC_L\ C_R$ combination which prevents crossing over. Each was then inbred for several generations before being used.

The appearance of the triploid with a single dose of the mutant genes involved is of some interest. As would be expected, the recessives do not become manifest. A dominant, on the other hand, may or may not have an observable effect. Thus minute and minute-h do not appear in single dose; hairless however has a distinct effect but is less extreme than in the diploid. And, finally, the manifestation of dichaete and stubble does not differ appreciably in triploid and diploid.

There are certain pronounced difficulties connected with the use of the stocks. In the first place it is impossible to distinguish between sepia and the sepia-maroon double recessive. This makes it necessary either to introduce a third eye color which behaves as a sensitizer and thus aids in the separation of the various eye-color types, or to test genetically all sepia-appearing diploid offspring (a third of all the diploids) for the presence of maroon. The genetic test was used until late in the work, when it was discovered that vermilion (a sex-linked recessive) behaves as a sensitizer. At this stage all the stocks were accordingly made homozygous for vermilion. But even in the presence of vermilion, the vermilion-sepia eye (a brassy orange color) and the vermilion-sepia-maroon eye (lemon yellow) become indistinguishable after the first half-day. It is necessary then to classify the flies before they are more than about ten hours old.

In the second place most of the dominants used are lethal in double dose in triploids and intersexes. This is true of minute, minute-h and dichaete; double hairless occasionally survives but is very extreme in appearance. Although double stubble was not detected in these experiments, it frequently survives, according to the unpublished data of SCHULTZ. In these crosses, due to the lethal effects, it is not possible to determine the position of the spindle-fibre attachment, for this determination depends upon the relative numbers of equational exceptions at the various loci (see page 245). There are further difficulties, in particular those connected with obtaining triploids of the proper composition to test, but these need not be discussed here.

The diploid controls include the following crosses from the same stocks used for the triploid crosses:

(1) $$\frac{s_e\ M_h\ +\ +\ H}{h\ +\ c_u\ b_x\ e^s}\ \text{♀} \times s_e\ h\ m_a\ c_u\ b_x\ e^s\ \text{♂}.$$

(2) $\frac{+ \quad D \quad m_a \quad S_b \quad +}{h \quad + \quad c_u \quad b_z \quad e^s} \varphi \times s_e\, h\, m_a\, c_u\, b_z\, e^s \sigma^{\prime}.$

(3) $\frac{+ \quad H \quad +}{b_z \quad e^s \quad c_a} \varphi \times b_z\, e^s\, c_a\, \sigma^{\prime}.$

(4) $\frac{+ \quad H \quad +}{S_b \quad + \quad M} \varphi \times b_z\, e^s\, c_a\, \sigma^{\prime}.$

The actual procedure was to isolate a diploid or triploid virgin of the required composition and to put her into a small vial with five males from the proper tester stock. These six flies were allowed to remain in the vial one day, after which they were transferred to the usual half-pint culture bottle provided with the cornmeal-molasses-agar medium. After five days in the first culture bottle they were transferred to a second new culture bottle and remained there five days. In the early stages of the work a transfer was then made to a third culture bottle, but it soon became obvious that triploid females give practically no offspring in these third cultures; and all females were thereafter discarded after the first eleven days of their life. These transfers were, of course, made in order to detect any gross variations with age. A more delicate test of the effect of age did not seem advisable.

The data for these triploid and diploid crosses appear in tables 1, 2, 3, and 4. In these tables the numerals "I" and "II" refer to the first and second cultures described above, that is "I" includes flies hatched in the first cultures from eggs laid on the second to the sixth days inclusive of the mother's life, and "II" includes flies from the second cultures from eggs laid on the seventh to the eleventh days.

The data from triploid mothers are given in full in tables 1 and 3. Since the control data (tables 2 and 4) are ordinary diploid data it was not considered necessary to present them in similar space-consuming form. The short laying period and the care taken of the culture bottles insured a reasonable equality of contrary classes; no viability differences appeared which were great enough to necessitate corrections.

In the data from triploids of the type $a_1a_2a_3 \cdots / b_1b_2b_3 \cdots / c_1c_2c_3 \cdots$ two types of double crossovers are to be distinguished. The first are the so-called "recurrent" doubles in which the same two chromosomes are involved in the two succeeding crossings over (for example $a_1b_2a_3$); the

TABLE 1

Offspring of the cross $\frac{+\ D\ m_a\ S_b\ +}{s_e\ M_h\ +\ +\ H}$ ♀ × $s_e\ h\ m_a\ c_u\ b_x\ e^s$♂. *R indicates recurrent double crossovers; P, progressive double crossovers.*

	I; 21 CULTURES	II; 18 CULTURES
Triploids	29	19
♀ Interxeses	186	129
♂ Intersexes	19	19
Superfemales	..	1
Supermales	..	2

Diploids

Type	Classes	♀	♂	Total	♀	♂	Total
0	$D\ m_a\ S_b$	103	15	340	68	18	225
	$s_e\ M_h\ H$	95	14		67	5	
	$h\ c_u\ b_x\ e^s$	93	20		62	5	
1	$s_e\ D\ m_a\ S_b$	9	..	47	7	..	37
	$M_h\ H$	7	..		5	..	
	$h\ D\ m_a\ S_b$	8	3		7	1	
	$c_u\ b_x\ e^s$	6	..		3	..	
	$s_e\ c_u\ b_x\ e^s$	9	..		6	2	
	$h\ M_h\ H$	5	..		6	..	
2	$D\ H$	12	1	110	8	2	61
	$s_e\ M_h\ m_a\ S_b$	9	3		4	..	
	$D\ c_u\ b_x\ e^s$	15	1		15	1	
	$h\ m_a\ S_b$	18	4		9	1	
	$h\ H$	24	..		12	..	
	$s_e\ M_h\ c_u\ b_x\ e^s$	22	1		7	2	

TABLE 1 (*continued*)

Diploids			I; 21 CULTURES			II; 18 CULTURES		
Type		Classes	♀	♂	Total	♀	♂	Total
3		$D\ m_a\ H$	8	1	40	7	1	29
		$s_c\ M_h\ S_b$	5	2		4	1	
		$D\ m_a\ b_x\ e^s$	7	2		2	..	
		$h\ c_u\ S_b$	6	1		6	1	
		$h\ c_u\ H$	4	1		3	..	
		$s_e\ M_h\ b_x\ e^s$	2	1		2	2	
4		$D\ m_a\ S_b\ H$	2	..	29	5	..	17
		$s_e\ M_h$	4	1		1	1	
		$D\ m_a\ S_b\ e^s$	7	1		1	..	
		$h\ c_u\ b_x$	2	..		4	..	
		$h\ c_u\ b_x\ H$	7	1		1	..	
		$s_e\ M_h\ e^s$	4	..		3	1	
1,2	R	$s_e\ D\ H$	2	..	16	1	..	5
		$M_h\ m_a\ S_b$	4	..		..	..	
		$m_a\ S_b$	2	..		..	..	
		$h\ D\ c_u\ b_x\ e^s$	..	..		..	..	
		$s_e\ H$	..	..		..	..	
		$h\ M_h\ c_u\ b_x\ e^s$	..	..		..	..	
	P	H	1	..		1	..	
		$M_h\ c_u\ b_x\ e^s$	2	..		..	..	
		$s_e\ m_a\ S_b$	1	..		1	..	
		$s_e\ D\ c_u\ b_x\ e^s$	..	..		..	..	
		$h\ D\ H$	3	..		1	..	
		$h\ M_h\ m_a\ S_b$	1	..		..	1	

TABLE 1 (*continued*)

Diploids			I; 21 CULTURES			II; 18 CULTURES		
Type	Classes		♀	♂	Total	♀	♂	Total
1,3	R	$s_e\ D\ m_a\ H$	1	..	7	..	..	4
		$M_h\ S_b$	1	..		..	..	
		$h\ D\ m_a\ b_x\ e^s$	..	..		..	..	
		$c_u\ S_b$	1	..		..	..	
		$s_e\ c_u\ H$	1	..		..	..	
		$h\ M_h\ b_x\ e^s$	..	..		..	..	
	P	$c_u\ H$	..	..		1	..	
		$M_h\ b_x\ e^s$	1	..		1	..	
		$s_e\ D\ m_a\ b_x\ e^s$	..	..		..	..	
		$s_e\ c_u\ S_b$	..	..		..	..	
		$h\ D\ m_a\ H$	1	..		..	1	
		$h\ M_h\ S_b$	1	..		1	..	
1,4	R	$s_e\ D\ m_a\ S\ H$	..	..	4	1	..	3
		M_h	..	..		..	..	
		$c_u\ b_x$	..	..		..	..	
		$h\ D\ m_a\ S_b\ e^s$	..	..		..	..	
		$s_e\ c_u\ b_x\ H$	..	..		..	..	
		$h\ M_h\ e^s$	..	..		..	..	
	P	$c_u\ b_x\ H$	1	..		..	..	
		$M_h\ e^s$	1	..		1	..	
		$s_e\ D\ m_a\ S_b\ e^s$	..	..		1	..	
		$s_e\ c_u\ b_x$	..	..		..	..	
		$h\ D\ m_a\ S_b\ H$	1	..		..	..	
		$h\ M_h$	1	..		..	..	

TABLE 1 (*continued*)

Diploids			I; 21 CULTURES			II; 18 CULTURES		
Type	Class		♀	♂	Total	♀	♂	Total
2,3	R	$D\ S_b$	3	1	22	1	..	5
		$s_e\ M_h\ m_a\ H$	1	..		..	..	
		$D\ c_u\ S_b$	2	..		..	..	
		$h\ m_a\ b_x\ e^s$	2	..		1	..	
		$h\ b_x\ e^s$	2	..		..	..	
		$s_e\ M_h\ c_u\ H$	1	..		..	..	
	P	$D\ b_x\ e^s$	3	..		..	..	
		$D\ c_u\ H$	..	1		..	..	
		$s_e\ M_h\ m_a\ b_x\ e^s$	..	..		1	..	
		$s_e\ M_h\ c_u\ S_b$	1	..		1	..	
		$h\ m_a\ H$	1	..		..	..	
		$h\ S_b$	3	1		1	..	
2,4	R	D	1	..	10	1	..	2
		$s_e\ M_h\ m_a\ S_b\ H$	..	..		..	..	
		$D\ c_u\ b_x$	..	..		..	..	
		$h\ m_a\ S_b\ e^s$	2	..		1	..	
		$h\ e^s$	1	..		..	..	
		$s_e\ M_h\ c_u\ b_x\ H$	..	..		..	..	
	P	$D\ e^s$	..	..		..	..	
		$D\ c_u\ b_x\ H$	2	..		..	..	
		$s_e\ M_h\ m_a\ S_b\ e^s$	2	..		..	..	
		$s_e\ M_h\ c_u\ b_x$	2	..		..	..	
		$h\ m_a\ S_b\ H$	..	..		..	..	
		h	..	..		..	..	

TABLE 1 (*continued*)

Diploids			I; 21 CULTURES			II; 18 CULTURES		
Type	Class		♀	♂	Total	♀	♂	Total
3,4	R	*D* m_a	..	..	5	..	..	1
		s_e M_h S_b *H*	..	..		..	..	
		D m_a b_x	..	..		..	..	
		h c_u S_b e^s	3	..		..	..	
		h c_u e^s	..	..		..	..	
		s_e M_h b_x *H*	..	..		..	..	
	P	*D* m_a e^s	..	..		..	..	
		D m_a b_x *H*	1	..		..	..	
		s_e M_h S_b e^s	..	..		..	..	
		s_e M_h b_x	..	..		..	1	
		h c_u S_b *H*	..	..		..	..	
		h c_u	1	..		..	..	
1,2,3		*h* M_h c_u S_b	..	..	..	1	..	1
1,2,4		s_e *D*	..	..	..	..	1	1
1,2,4		*h* M_h m_a S_b e^s	..	..	..	1	..	1
1,3,4		*h D* m_a	1	..	1	..	..	..
1		s_e *h* c_u b_x e^s	1	..	1	1	..	1
1		s_e M_h *D* m_a S_b	1	..	1	..	..	..
3		*D* m_a S_b b_x e^s	..	..	..	1	..	1
4		s_e M_h *H* e^s	1	..	1	..	..	..
1,2	P	s_e *D* m_a c_u b_x e^s	1	..	1	..	..	..
1,4	P	e^s	..	..	..	1	..	1
		Total	559	76	635	348	47	395

TABLE 2

Offspring from control diploid mothers of the composition indicated; the fathers were $s_e\ h\ m_a\ c_u\ b_x\ e^s$.

MOTHER	TYPE	0	1	2	3	4	1,2	1,3	1,4	2,3	2,4	3,4	1,2,3	1,2,4	1,3,4	2,3,4	TOTAL
$+\ D\ m_a\ S_b\ +$ / $h\ +\ c_u\ b_x\ e^s$	I; 15 cultures	1654	258	127	132	151	10	14	33	13	21	21	3	..	..	..	2437
	II; 14 cultures	1849	240	77	119	162	6	7	29	6	15	9	..	1	2	..	2522
$s_e\ M_h\ +\ +\ H$ / $h\ +\ c_u\ b_x\ e^s$	I; 13 cultures	1525	289	133	132	205	5	29	33	6	14	4	..	..	1	2	2378
	II; 12 cultures	1758	267	102	105	212	1	23	29	11	11	6	1	1	..	3	2530
Total	I; 28 cultures	3179	547	260	164	356	15	43	66	19	35	25	3	..	1	2	4815
	II; 26 cultures	3607	507	179	224	374	7	30	58	17	26	15	1	2	2	3	5052

TABLE 3

Offspring of the cross $\frac{+\ H\ +}{S_b\ +\ M}$ ♀ × $\frac{}{b_x\ e^s\ c_a}$ ♂.

	I; 28 CULTURES	II; 27 CULTURES
Triploids	80	75
♀ Intersexes	353	319
♂ Intersexes	84	107
Superfemales	..	..
Supermales	4	8

Diploids

Type	Class	♀	♂	Total	♀	♂	Total
0	*H*	215	40	649	189	38	574
	S_b M	158	28		141	32	
	b_x e^s c_a	180	28		152	22	
4	*S_b H*	9	2	69	8	2	58
	M	13	2		11	1	
	b_x H	7	..		9	..	
	e^s c_a	15	2		10	2	
	S_b e^s c_a	15	..		9	2	
	b_x M	3	1		4	..	
5	*S_b*	27	5	173	24	5	151
	H M	31	5		16	2	
	H c_a	24	7		31	4	
	b_x e^s	28	6		21	4	
	S_b c_a	27	3		29	3	
	b_x e^s M	8	2		11	1	

TABLE 3 (*continued*)

Diploids			I; 28 CULTURES			II; 27 CULTURES		
Type		Class	♀	♂	Total	♀	♂	Total
4,5	R	+	4	..	17	2	..	13
		S_b *H M*	1	..		1	..	
		b_x *H* c_a	..	..		1	..	
		e^s	1	..		1	..	
		S_b e^s *M*	..	..		1	..	
		b_x c_a	3	1		1	..	
	P	c_a	..	1		..	..	
		S_b *H* c_a	..	1		1	..	
		b_x *H M*	1	..		1	..	
		b_x	1	..		1	..	
		S_b e^s	..	..		2	..	
		e^s *M*	2	1		..	1	
4		*H* e^s c_a	2	..	2	..	..	..
4,5	R	S_b b_x e^s *M*	..	..	..	1	..	1
		Total	775	135	910	678	119	797

second are the "progressive" doubles in which all three chromosomes are involved two at a time (for example $c_1a_2b_3$). These are indicated in tables 1 and 3 by "R" and "P" respectively.

It will be seen that there is a certain expected amount of crossing over between the two mutant genes treated as markers of a given point (for example between *H* and e^s). In order to incorporate these crossovers the convention was followed that the first region includes the distance from sepia to dichaete; all other regions extend from the second gene of a given pair to the second gene of the succeeding pair. It is true that a very small amount of crossing over will remain undetected due to the fact that one of the markers of a given point is the normal allelomorph of one of the mutants, but this is insignificant.

TABLE 4

Offspring from control diploid mothers of the composition indicated; the fathers were $b_z\ e^s\ c_a$.

MOTHER	TYPE	0	4	5	4,5	TOTAL
$+\ H\ +$	I; 13 cultures	1684	270	843	64	2861
$b_z\ e^s\ c_a$	II; 12 cultures	1206	180	585	25	1996
$+\ H\ +$	I; 23 cultures	2455	433	1377	57	4322
$S_b\ +\ M$	II; 17 cultures	1640	237	766	23	2666
Total	I; 36 cultures	4139	703	2220	121	7183
	II; 29 cultures	2846	417	1351	48	4662

CROSSES IN WHICH ONE THIRD CHROMOSOME WAS MARKED

When the triploid data presented in the preceding section were analyzed the results were so unexpected that it was thought well to repeat the work with entirely different stocks. Accordingly the following triploid cross and its diploid control cross were used:

1) $\dfrac{\dfrac{r_u\ h\ t_h\ s_t\ c_u\ s_r\ e^s\ c_a}{+}}{+}$ ♀ × $r_u\ h\ t_h\ s_t\ c_u\ s_r\ e^s\ c_a$ ♂.

(2) $\frac{r_u\ h\ t_h\ s_t\ c_u\ s_r\ e^s\ c_a}{+}$ ♀ × $r_u\ h\ t_h\ s_t\ c_u\ s_r\ e^s\ c_a$ ♂.

The technique employed was quite similar to that described for the previous crosses except that ten males instead of five were used for every female in order to insure proper fertilization. The symbols represent the following mutant genes which have the loci indicated on the standard diploid map: r_u, roughoid at 0.0; h, hairy at 26.5; t_h, thread at 42.2; s_t, scarlet at 44.0; c_u, curled at 50.0; s_r, stripe at 62.0; e^s, sooty at 70.7; c_a, claret at 100.7.

In utilizing the data of cross (1) a correction must be made for undetected crossing over between the two similar wild-type chromosomes. If we consider any given region, for example region (4) between scarlet and curled, the amount of crossing over between the marked chromosome and the two wild-type chromosomes is known. But the amount of crossing over in region (4) between the two wild-type chromosomes is not known. If we assume this latter to be half the former (and, as will be seen, the results justify this assumption), then the crossing over for all three chromosomes will be $1\frac{1}{2}$ times the detected crossing over. (This correction, it should be noted, has nothing to do with a correction for sister-strand crossing over.)

A more explicit demonstration of this relationship is quite simple, but tedious. A brief resumé follows.

We may indicate the marked chromosome of the triploid by $a_1a_2a_3a_4a_5a_6a_7a_8$; and the wild-type chromosomes of this triploid by $b_1b_2b_3b_4b_5b_6b_7b_8$ and $b_1'b_2'b_3'b_4'b_5'b_6'b_7'b_8'$. We have then individuals of the following composition and appearance which are represented in the proportions indicated. That the various classes of a given type are equal for the first experiment is shown at once by a glance at table 1; it is assumed that the chromosomes of the present experiment behave similarly.

Crossover region	*Composition*	*Appearance*	*Proportion*	
0	$a_1a_2a_3a_4a_5a_6a_7a_8$	$a_1a_2a_3a_4a_5a_6a_7a_8$	s	3s
	$b_1b_2b_3b_4b_5b_6b_7b_8$	$b_1b_2b_3b_4b_5b_6b_7b_8$	*s*	
	$b_1'b_2'b_3'b_4'b_5'b_6'b_7'b_8'$	$b_1b_2b_3b_4b_5b_6b_7b_8$	s	

	$a_1b_2b_3b_4b_5b_6b_7b_8$	$a_1b_2b_3b_4b_5b_6b_7b_8$	t
	$b_1a_2a_3a_4a_5a_6a_7a_8$	$b_1a_2a_3a_4a_5a_6a_7a_8$	t
	$a_1b_2'b_3'b_4'b_5'b_6'b_7'b_8'$	$a_1b_2b_3b_4b_5b_6b_7b_8$	t
1	$b_1'a_2a_3a_4a_5a_6a_7a_8$	$b_1a_2a_3a_4a_5a_6a_7a_8$	t } 6t
	$b_1b_2'b_3'b_4'b_5'b_6'b_7'b_8'$	$b_1b_2b_3b_4b_5b_6b_7b_8$	t
	$b_1'b_2b_3b_4b_5b_6b_7b_8$	$b_1b_2b_3b_4b_5b_6b_7b_8$	t
2	6 classes	6 classes	6u
3	"	"	6v
4	"	"	6w
5	"	"	6x
6	"	"	6y
7	"	"	6z
1,2	12 classes	12 classes	$12c_1$
1,3	"	"	$12c_2$
.	.	.	.
.	.	.	.
.	.	.	.
.	.	.	.
5,7	12 classes	12 classes	$12c_{20}$
6,7	"	"	$12c_{21}$
1,2,3	24 classes	24 classes	$24d_1$
1,2,4	"	"	$24d_2$
.	.	.	.
.	.	.	.
4,6,7	24 classes	24 classes	$24d_{34}$
5,6,7	"	"	$24d_{35}$
1,2,3,4	48 classes	48 classes	$48e_1$
1,2,3,5	"	"	$48e_2$
.	.	.	.
.	.	.	.
3,5,6,7	48 classes	48 classes	$48e_{34}$
4,5,6,7	"	"	$48e_{35}$

We need not consider the possibility of further multiple crossovers since they do not occur. Their presence would not alter the expressions below except by the addition of terms.

Let us now consider the total amount of crossing over between any two

given loci, for example between loci 4 and 5. By collecting terms we obtain the following expressions:

The total crossing over $= 6w + 12(c_3 + c_8 + c_{12} + c_{16} + c_{17} + c_{18}) + 24(d_2 + d_6 + d_{10} + d_{11} + d_{12} + d_{16} + d_{20} + d_{21} + d_{22} + d_{26} + d_{27} + d_{28} + d_{32} + d_{33} + d_{34}) + 48(e_1 + e_5 + e_6 + e_7 + e_{11} + e_{12} + e_{13} + e_{17} + e_{18} + e_{19} + e_{21} + e_{22} + e_{23} + e_{27} + e_{28} + e_{29} + e_{31} + e_{32} + e_{33} + e_{35})$.

The detectable crossing over $= 4w + 8(c_3 + c_8 + c_{12} + c_{16} + c_{17} + c_{18}) + 16(d_2 + d_6 + d_{10} + d_{11} + d_{12} + d_{16} + d_{20} + d_{21} + d_{22} + d_{26} + d_{27} + d_{28} + d_{32} + d_{33} + d_{34}) + 32(e_1 + e_5 + e_6 + e_7 + e_{11} + e_{12} + e_{13} + e_{17} + e_{18} + e_{19} + e_{21} + e_{22} + e_{23} + e_{27} + e_{28} + e_{29} + e_{31} + e_{32} + e_{33} + e_{35})$.

That is, the crossing over between loci 4 and 5 is $1\frac{1}{2}$ times the detected crossing over. It may be similarly shown that no matter which two loci are chosen, the crossing over between them is $1\frac{1}{2}$ times the detected crossing over.

Up to this point the discussion has dealt with crossing over and with "crossover values," that is, with the number of crossovers that fall between two given loci for each hundred gametes. But this value cannot be obtained directly, for double crossing over may occur between two given loci without changing the combination of the genes in the loci. By experiments in which other loci between the two given loci are marked, the frequency of these doubles can be determined. These frequencies thus provide corrections by which the percentages of recombination of the genes of the given loci, which is the relation that is directly observed in an experiment, can be transformed into the desired crossover values. For the short intervals dealt with in this paper the amount of this correction is small (see page 241), and the recombination percents are used as indices of the conditions with respect to crossing over.

Table 5 gives the data in complete form for both triploid and diploid crosses in which one chromosome is marked. It should be noticed that the contrary classes of the diploid crosses are on the whole quite well balanced for viability. Indeed, for the type of cross made, the viability relations of the classes involved are unexpectedly good.

The "contrary" classes of the triploid crosses are not, of course, expected to be equal. The wild-type class, for example, includes not only the wild-type non-crossovers, but all the crossovers involving the two wild-type chromosomes alone. But that the viability in the classes of the triploid crosses is good is shown by the strict correspondence between the crossover

values obtained from these triploids and the values obtained from the triploids in which all three chromosomes were marked (see pages 234, 236).

THE RECOMBINATION VALUES

Table 6 presents the recombination values for the first experiment calculated from the data of tables 1, 2, 3, and 4. These figures represent the percentages of *detected* crossed-over chromosomes which emerge. They are not corrected for a possible sister-strand crossing over. The differences between the recombination values for triploid and for diploid, as well as the quotients of these values, are listed separately. It is clear that at the end of the chromosome included in this experiment (the right end) recombination for the triploid is almost half that for the diploid; and that there is a continuous increase in the relative amount of triploid crossing over as we pass from either end of the chromosome to the center. Thus, in the two regions from s_e, h to M_h, D and from S_b, b_x to H, e^s, triploid recombination is only slightly less than diploid recombination. But for the center of the chromosome, triploid recombination is over $3\frac{1}{2}$ times as great as diploid recombination. These relationships hold for both the first and the second sets of cultures. It should be noted that the quotients have relatively low probable errors.

TABLE 5

Offspring of triploids of the composition (r_u h t_h s_t c_u s_r e^s c_a/+/+) and of control diploids of the composition (r_u h t_h s_t c_u s_r e^s c_a/+); the fathers were r_u h t_h S_t c_u s_r e^s c_a. For the offspring from triploids the "types" indicate the apparent regions affected (see text).

	TRIPLOID						DIPLOID					
	I; 29 cultures			II; 25 cultures			I; 10 cultures			II; 10 cultures		
Triploids	91			73			..			..		
♀ Intersexes	339			251			..			..		
♂ Intersexes	202			142			..			..		
Superfemales	..			..			..			..		
Supermales	5			3			..			..		
Diploids												
"Type"	Class	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total
0	r_u h t_h s_t c_u s_r e^s c_a	64	7	462	55	6	309	177	162	754	113	115	617
	+	338	53		208	40		218	197		193	196	
1	r_u	27	6	58	26	3	43	96	68	293	67	80	234
	h t_h s_t c_u s_r e^s c_a	22	3		12	2		72	57		50	37	
2	r_u h	32	3	50	18	2	29	60	58	125	61	43	188
	t_h s_t c_u s_r e^s c_a	12	3		8	1		50	57		39	45	
3	r_u h t_h	..	..	1	..	..	1	2	..	8	..	..	2
	s_t c_u s_r e^s c_a	1	..		1	..		3	3		1	1	

TABLE 5 (*continued*)

4	$r_u\ h\ t_h\ s_t$	30	4	69	21	4	45	19	10	60	11	7	30
	$c_u\ s_r\ e^s\ c_a$	30	5		19	1		12	19		7	5	
5	$r_u\ h\ t_h\ s_t\ c_u$	19	1	57	14	1	35	31	33	168	20	15	91
	$s_r\ e^s\ c_a$	32	5		19	1		51	53		29	27	
6	$r_u\ h\ t_h\ s_t\ c_u\ s_r$	5	..	16	2	1	14	21	11	116	23	20	111
	$e^s\ c_a$	10	1		9	2		42	42		36	32	
7	$r_u\ h\ t_h\ s_t\ c_u\ s_r\ e^s$	12	1	50	8	..	29	103	85	419	79	65	381
	c_a	33	4		19	2		119	112		123	114	
1,2	$r_u\ t_h\ s_t\ c_u\ s_r\ e^s\ c_a$	1	..	8	3	..	5	1	..	13	..	..	5
	h	4	3		2	..		7	5		3	2	
1,3	$r_u\ s_t\ c_u\ s_r\ e^s\ c_a$	..	..	..	..	..	..	..	..	..	..	..	..
	$h\ t_h$	..	..		..	..		..	..		..	..	
1,4	$r_u\ c_u\ s_r\ e^s\ c_a$	4	..	18	..	..	9	3	3	12	4	2	11
	$h\ t_h\ s_t$	10	4		8	1		4	2		3	2	
1,5	$r_u\ s_r\ e^s\ c_a$	..	1	3	1	..	2	25	19	68	11	8	40
	$h\ t_h\ s_t\ c_u$	1	1		1	..		10	14		13	8	

TABLE 5 (*continued*)

Diploids		I; 29 CULTURES			II; 25 CULTURES			I; 10 CULTURES			II; 10 CULTURES		
"Type"	Class	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total
1,6	$r_u\ e^s\ c_a$	1	1	5	2	..	2	16	13	42	14	21	49
	$h\ t_h\ s_t\ c_u\ s_r$	2	1		..	..		6	7		9	5	
1,7	$r_u\ c_a$	3	..	11	2	..	6	60	44	195	47	42	140
	$h\ t_h\ s_t\ c_u\ s_r\ e^s$	7	1		4	..		53	38		20	31	
2,3	$r_u\ h\ s_t\ c_u\ s_r\ e^s\ c_a$	1	..	1	..	..	..	..	..	..	..	..	..
	t_h	..	..		..	..		..	..		..	..	
2,4	$r_u\ h\ c_u\ \ s_r\ e^s\ c_a$	1	1	3	3	..	8	2	2	9	2	2	7
	$t_h\ s_t$	1	..		5	..		4	1		1	2	
2,5	$r_u\ h\ s_r\ e^s\ c_a$	..	..	4	..	..	..	10	11	44	13	9	33
	$t_h\ s_t\ c_u$	4	..		..	..		12	11		7	4	

TABLE 5 (*continued*)

2,6	$r_u\ h\ e^s\ c_a$	1	..	3	..	..	..	5	9	29	6	9	25
	$t_h\ s_t\ c_u\ s_r$	2	..		..	..		9	6		4	6	
2,7	$r_u\ h\ c_a$	5	..	11	1	..	5	34	37	140	34	27	113
	$t_h\ s_t\ c_u\ s_r\ e^s$	4	2		3	1		39	30		21	21	
3,4	$r_u\ h\ t_h\ c_u\ s_r\ e^s\ c_a$	..	..	2	..	..	3	..	..	..	..	..	..
	s_t	..	2		..	3		..	..		..	..	
3,5	$r_u\ h\ t_h\ s_r\ e^s\ c_a$	..	..	..	..	..	..	..	..	..	..	..	..
	$s_t\ c_u$	..	..		..	..		..	..		..	..	
3,6	$r_u\ h\ t_h\ e^s\ c_a$	..	..	..	..	..	..	..	..	..	..	..	..
	$s_t\ c_u\ s_r$	..	..		..	..		..	..		..	..	
3,7	$r_u\ h\ t_h\ c_a$	..	..	..	..	..	..	..	..	1	..	..	2
	$s_t\ c_u\ s_r\ e^s$	..	..		..	..		..	1		..	2	
4,5	$r_u\ h\ t_h\ s_t\ s_r\ e^s\ c_a$	1	..	6	2	..	4	1	..	5	..	1	1
	c_u	5	..		2	..		2	2		..	..	
4,6	$r_u\ h\ t_h\ s_t\ e^s\ c_a$	1	..	4	..	..	..	2	4	11	1	..	1
	$c_u\ s_r$	2	1		..	..		4	1		..	..	

TABLE 5 (*continued*)

Diploids		I; 29 CULTURES			II; 25 CULTURES			I; 10 CULTURES			II; 10 CULTURES		
"Type"	Class	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total
4,7	$r_u\ h\ t_h\ s_t\ c_a$	4	1	14	3	..	6	9	5	29	4	7	27
	$c_u\ s_r\ e^s$	8	1		2	1		6	9		9	7	
5,6	$r_u\ h\ t_h\ s_t\ c_u\ e^s\ c_a$	..	..	..	..	..	..	..	..	2	..	..	2
	s_r	..	..		..	..		2	..		1	1	
5,7	$r_u\ h\ t_h\ s_t\ c_u\ c_a$	1	..	6	..	..	4	8	4	37	10	5	37
	$s_r\ e^s$	5	..		4	..		12	13		11	11	
6,7	$r_u\ h\ t_h\ s_t\ c_u\ s_r\ c_a$	2	..	4	..	..	3	..	..	18	..	..	10
	e^s	2	..		3	..		11	7		3	7	
1,2,4	$r_u\ t_h\ s_t$	2	..	2	..	..	..	..	1	1	..	1	2
	$h\ c_u\ s_r\ e^s\ c_a$	..	..		..	..		..	..		1	..	

TABLE 5 (*continued*)

1,2,5	$r_u\ t_h\ s_t\ c_u$	1	1	2	..	..	..	1	..	3	..	..	1
	$h\ s_r\ e^s\ c_a$	..	..		..	..		1	1		..	1	
1,2,6	$r_u\ t_h\ s_t\ c_u\ s_r$	..	..	1	..	..	..	..	..	2	..	..	3
	$h\ e^s\ c_a$	1	..		..	..		2	..		2	1	
1,2,7	$r_u\ t_h\ s_t\ c_u\ s_r\ e^s$	2	..	2	..	..	..	..	2	9	2	..	8
	$h\ c_a$	..	..		..	..		3	4		..	6	
1,4,5	$r_u\ c_u$	..	..	..	..	..	..	..	1	1	1	..	1
	$h\ t_h\ s_t\ s_r\ e^s\ c_a$	..	..		..	..		..	..		..	..	
1,4,6	$r_u\ c_u\ s_r$	..	..	..	1	..	1	..	1	1	..	1	1
	$h\ t_h\ s_t\ e^s\ c_a$	..	..		..	..		..	..		..	..	
1,4,7	$r_u\ c_u\ s_r\ e^s$	..	..	..	..	..	1	1	1	8	1	1	5
	$h\ t_h\ s_t\ c_a$	..	..		1	..		4	2		2	1	
1,5,6	$r_u\ s_r$	..	..	..	..	..	..	..	1	1	1	..	1
	$h\ t_h\ s_t\ c_u\ e^s\ c_a$	..	..		..	..		..	..		..	..	
1,5,7	$r_u\ s_r\ e^s$	2	..	3	..	..	..	7	7	23	3	4	11
	$h\ t_h\ s_t\ c_u\ c_a$	1	..		..	..		7	2		2	2	

TABLE 5 (*continued*)

Diploids		I; 29 CULTURES			II; 25 CULTURES			I; 10 CULTURES			II; 10 CULTURES		
"Type"	Class	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total
1,6,7	$r_u\ e^s$	1	..	1	..	..	..	1	2	5	2	4	8
	$h\ t_h\ s_t\ c_u\ s_r\ c_a$	..	..		..	..		..	2		2	..	
2,4,5	$r_u\ h\ c_u$	..	..	..	..	..	..	..	..	..	..	1	1
	$t_h\ s_t\ s_r\ e^s\ c_a$	..	..		..	..		..	..		..	..	
2,4,6	$r_u\ h\ c_u\ s_r$	..	..	..	..	..	..	1	..	1	..	1	1
	$t_h\ s_t\ e^s\ c_a$	..	..		..	..		..	..		..	..	
2,4,7	$r_u\ h\ c_u\ s_r\ e^s$	..	..	..	..	..	..	3	1	7	1	2	5
	$t_h\ s_t\ c_a$	..	..		..	..		..	3		1	1	
2,5,7	$r_u\ h\ s_r\ e^s$	..	..	..	..	..	1	4	8	21	2	2	12
	$t_h\ s_t\ c_u\ c_a$	..	..		1	..		4	5		4	4	

TABLE 5 (*continued*)

2,6,7	$r_u\ h\ e^s$	..	..	..	..	..	1	2	3	6	2	1	3
	$t_h\ s_t\ c_u\ s_r\ c_a$	..	..		1	..		1	..		..	..	
3,4,5	$r_u\ h\ t_h\ c_u$	..	..	2	..	..	..	..	..	..	..	..	..
	$s_t\ s_r\ e^s\ c_a$	..	2		..	..		..	..		..	..	
3,4,7	$r_u\ h\ t_h\ c_u\ s_r\ e^s$	..	..	1	..	..	..	..	..	..	..	..	..
	$s_t\ c_a$	..	1		..	..		..	..		..	..	
4,5,7	$r_u\ h\ t_h\ s_t\ s_r\ e^s$	..	..	1	..	..	..	..	..	..	..	..	..
	$c_u\ c_a$	1	..		..	..		2	1	3	..	..	
4,6,7	$r_u\ h\ t_h\ s_t\ e^s$	1	..	1	..	..	..	..	..	..	..	..	1
	$c_u\ s_r\ c_a$	..	..		..	..		..	..		..	1	
1,2,4,5	$r_u\ t_h\ s_t\ s_r\ e^s\ c_a$	..	..	1	..	..	..	..	..	..	..	..	..
	$h\ c_u$	1	..		..	..		..	..		..	..	
1,2,4,6	$r_u\ t_h\ s_t\ e^s\ c_a$	..	..	..	..	..	..	..	2	2	..	..	..
	$h\ c_u\ s_r$	..	..		..	..		..	..		..	..	
1,2,5,7	$r_u\ t_h\ s_t\ c_u\ c_a$	..	..	..	..	..	1	..	..	..	..	..	..
	$h\ s_r\ e^s$	..	..		1	..		..	..		..	,,	

TABLE 5 (*continued*)

Diploids		I; 29 CULTURES			II; 25 CULTURES			I; 10 CULTURES			II; 10 CULTURES		
'Type"	Class	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total
1,2,6,7	$r_u\ t_h\ s_t\ c_u\ s_r\ c_a$	..	..	..	..	..	..	..	..	..	..	..	2
	$h\ e^s$	..	..		..	..		..	..		1	1	
1,3,6,7	$r_u\ s_t\ c_u\ s_r\ c_a$	..	..	..	..	..	..	..	..	1	..	..	..
	$h\ t_h\ e^s$	..	..		..	..		..	1		..	..	
1,4,5,7	$r_u\ c_u\ c_a$	..	..	..	..	..	..	..	..	1	..	..	..
	$h\ t_h\ s_t\ s_r\ e^s$	..	..		..	..		1	..		..	..	
1,4,6,7	$r_u\ c_u\ s_r\ c_a$	..	..	..	..	..	..	..	..	1	..	..	..
	$h\ t_h\ s_t\ e^s$	..	..		..	..		1	..		..	..	

TABLE 5 (*continued*)

1,5,6,7	$r_u\ s_r\ c_a$	..	..	..	..	..	..	..	..	1	..	..	..	..	..
	$h\ t_h\ s_t\ c_u\ e^a$	..	..	..	..	..	..	..	..	..	1	..	..	..	..
2,3,4,5	$r_u\ h\ s_t\ s_r\ e^a\ c_a$	..	..	..	1	1	..	..	..	..	..	..	..	..	..
	$t_h\ c_u$	..	..	..	..		..	..	..	..	..	..	..	..	..
4,5,6,7	$r_u\ h\ t_h\ s_t\ s_r\ c_a$	..	..	1	..	..	..	..	..	..	..	..	..	..	..
	$c_u\ e^a$	1	..		..	..	..	..	..	..	..	..	..	..	..
	Total	764	120	884	495	73	568	1379	1317	2696	1143	1080	2223		

These facts are shown graphically by figure 1, which is from the recombination values for the first set of cultures. Ordinates represent the quotients of the recombination values, abscissae, the arrangement of genes along the chromosome as shown by the standard diploid map. The dotted lines give the respective probable errors for each region. This type of graphic treatment of crossing over data was previously used by MULLER

TABLE 6

Recombination values calculated from the data of tables 1, 2, 3, and 4.

REGION	TRIPLOID T	DIPLOID D	DIFFERENCE T-D	QUOTIENT T/D
CULTURES I				
s_e,h–M_h,D	12.3±0.88	14.0±0.34	− 1.7±0.94	0.88±0.07
M_h,D–m_a,c_u	25.0±1.16	6.9±0.25	18.1±1.19	3.62±0.21
m_a,c_u–S_b,b_x	11.8±0.86	7.4±0.25	4.4±0.90	1.59±0.13
S_b,b_x–H,e^s	8.9±0.49	10.9±0.19	− 2.0±0.52	0.82±0.05
H,e^s–M,c_a	20.9±0.91	32.6±0.37	−11.7±1.12	0.64±0.03
Total	78.9±1.98	71.8±1.19		
CULTURES II				
s_e,h–M_h,D	13.7±1.17	12.0±0.31	1.7±1.12	1.14±0.10
M_h,D–m_a,c_u	19.2±1.34	4.7±0.20	14.5±1.36	4.09±0.29
m_a,c_u–S_b,b_x	10.4±1.04	5.8±0.22	4.6±1.06	1.79±0.19
S_b,b_x–H,e^s	8.2±0.54	9.7±0.20	− 1.5±0.58	0.85±0.06
H,e^s–M,c_a	20.7±0.97	30.0±0.45	−19.3±1.07	0.69±0.03
Total	72.2±2.34	62.2±0.65		

(1925) in a study of the effects of X-rays. Since the quotients for cultures II are practically identical with those for cultures I (as is demonstrated by the table) it is unnecessary to publish graphs for the former.

Table 7 and figure 2 give the corresponding values for the second experiment. It is obvious that the results of the two experiments are in complete agreement. The effects observed are not, then, to be attributed

to crossover modifiers. This is shown also by the fact that standard values are obtained from the diploid controls.

It should be noted in passing that the strict correspondence between the two experiments is of some theoretical importance. In the first experiment all three chromosomes were marked; in the second experiment only one chromosome was marked, the other two being wild type. The fact

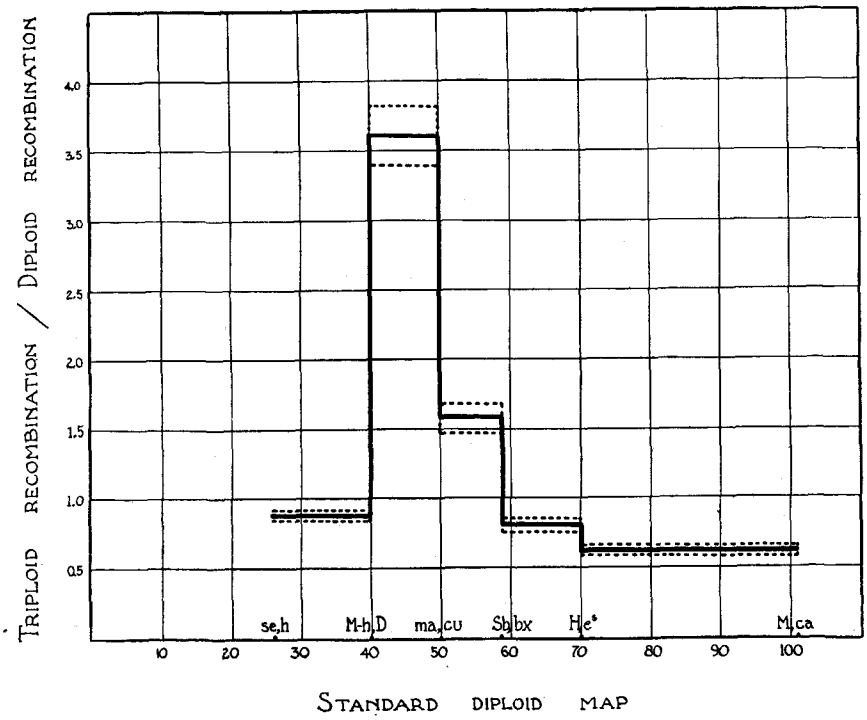

FIGURE 1.—The relation between triploid and diploid recombination along the chromosome. The data are from the first set of cultures of the first experiment. Ordinates represent the ratio of triploid recombination to diploid recombination; abscissae indicate the arrangement of the genes as shown by the standard diploid map. The dotted lines give the probable errors for the respective regions.

that the crossover behavior is the same in the two cases means, therefore, that the chromosomes cross over in the same manner whether they are marked or not. In other words, our assumption of page 220 is justified by the results, and we have definite evidence that crossing over is no more different between wild-type chromosomes than it is between two chromosomes one or both of which are marked. This has long been suspected, but has not previously been demonstrated.

If the assumption is made of free sister-strand interchange and the recombination values are corrected according to the discussion of page 206, we obtain the figures of table 8. A glance at this table will convince one that, although the recombination values are now somewhat different, their quotients still show the same regional differences and still have the same

TABLE 7

Recombination values calculated from the data of table 5.

CULTURES I

REGION	TRIPLOID T	DIPLOID D	DIFFERENCE T-D	QUOTIENT T/D
r_u–h	19.5±0.90	25.3±0.56	− 5.8±1.06	0.77±0.04
h–t_h	14.9±0.81	15.3±0.49	− 0.4±0.95	0.97±0.06
t_h–s_t	1.2±0.25	0.4±0.08	0.8±0.26	3.00±0.87
s_t–c_u	21.2±0.93	5.6±0.30	15.6±0.98	3.79±0.26
c_u–s_r	14.6±0.80	14.0±0.45	0.6±0.92	1.04±0.07
s_r–e^s	6.1±0.54	8.9±0.37	− 2.8±0.65	0.69±0.07
e^s–c_a	18.0±0.87	34.3±0.62	−16.3±1.07	0.52±0.03
Total	95.5±2.02	103.8±1.17		

CULTURES II

REGION	TRIPLOID T	DIPLOID D	DIFFERENCE T-D	QUOTIENT T/D
r_u–h	18.5±1.10	23.5±0.61	− 5.0±1.26	0.79±0.05
h–t_h	13.5±0.96	18.4±0.55	− 4.9±1.11	0.73±0.06
t_h–s_t	1.3±0.32	0.2±0.06	1.1±0.33	6.50±1.60
s_t–c_u	20.6±1.14	4.2±0.29	16.4±1.18	4.90±0.43
c_u–s_r	12.7±0.94	10.4±0.44	2.3±1.04	1.22±0.10
s_r–e^s	5.5±0.65	9.8±0.43	− 4.3±0.78	0.56±0.07
e^s–c_a	15.1±1.01	34.4±0.68	−19.3±1.22	0.44±0.03
Total	87.2±2.42	100.9±1.27		

general order of magnitude. The general conclusions remain unaltered, then, even if sister strands cross over as freely as non-sister strands.

An effect of age on crossing over might be expected to give significant differences between the recombination values for the first set of cultures and for the second set of cultures. Table 9 gives these differences listed separately for diploid and for triploid. The diploid mothers, especially of the first experiment, show a decrease of crossing over with age at central

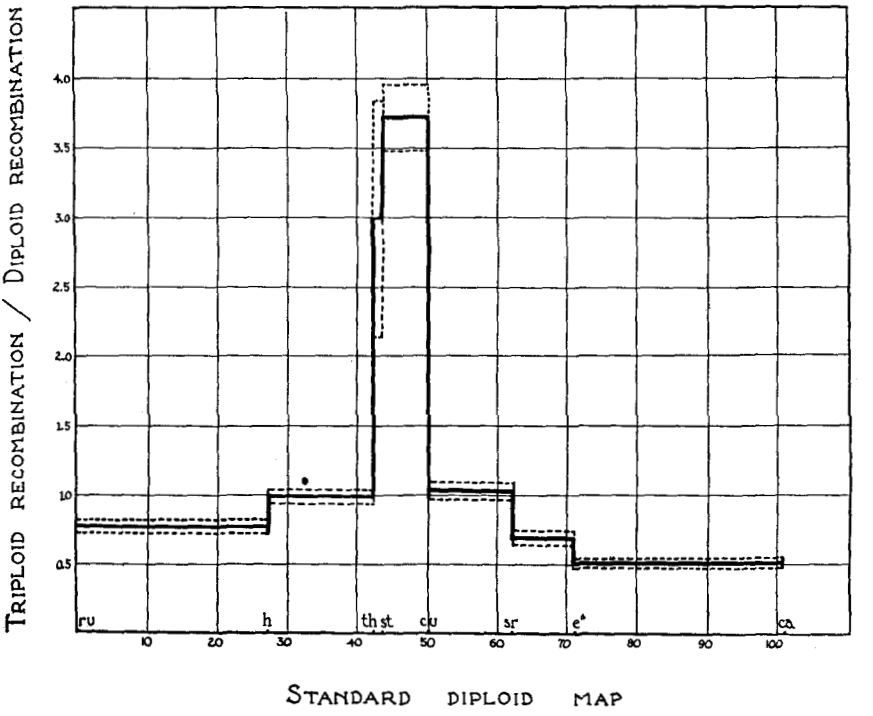

FIGURE 2.—The relations between triploid and diploid recombination along the chromosome. The data are from the first set of cultures of the second experiment. Ordinates and abscissae as in figure 1.

regions. These results are in agreement with those of PLOUGH (1921) and of BRIDGES (1927) for this chromosome. But there is no significant difference shown by the present data between the two sets of triploid cultures. This does not necessarily demonstrate the absence of an effect of age on crossing over in triploids. It is conceivable that such an effect exists, but that it is too delicate to be shown by the data, or that it does not coincide in its time relationships with that shown by diploids. At any rate it is obvious that there are differences between the age change in

diploids and in triploids. It is possible that this fact has some significant relation to the relative lengthening of the triploid chromosome in the center.

TABLE 8

Recombination values corrected on the basis of free sister-strand interchange.

CULTURES I

REGION	TRIPLOID	DIPLOID	REGION	TRIPLOID	DIPLOID
s_e, h–M_h, D	15.4±0.97	21.0±0.40	r_u–h	24.4±0.97	37.9±0.63
M_h, D–m_a, c_u	31.2±1.24	10.3±0.30	h–t_h	18.6±0.88	22.9±0.55
m_a, c_u–S_b, b_x	14.7±0.95	11.1±0.31	t_h–s_t	1.5±0.28	0.6±0.10
S_b, b_x–H, e^s	11.1±0.54	16.3±0.23	s_t–c_u	26.5±1.01	8.4±0.36
H, e^s–M, c_a	26.1±0.98	48.9±0.40	c_u–s_r	18.2±0.88	21.0±0.53
			s_r–e^s	7.6±0.60	13.3±0.44
			e^s–c_a	22.5±0.95	51.4±0.65
Total	98.5±2.15	107.6±0.75		119.3±2.20	155.5±1.32

CULTURES II

REGION	TRIPLOID	DIPLOID	REGION	TRIPLOID	DIPLOID
s_e, h–M_h, D	17.1±1.28	18.0±0.36	r_u–h	23.1±1.19	35.2±0.68
M_h, D–m_a, c_u	24.0±1.45	7.0±0.24	h–t_h	16.9±1.06	27.6±0.64
m_a, c_u–S_b, b_x	13.0±1.14	8.7±0.28	t_h–s_t	1.6±0.36	0.3±0.08
S_b, b_x–H, e^s	10.2±0.59	14.5±0.24	s_t–c_u	25.7±1.24	6.3±0.35
H, e^s–M, c_a	25.9±1.05	45.0±0.49	c_u–s_r	15.9±0.92	15.6±0.52
			s_r–e^s	6.9±0.72	14.7±0.51
			e^s–c_a	18.9±1.11	51.6±0.71
Total	90.2±2.55	93.2±0.75		109.0±2.61	151.3±1.43

It is the regional variation of crossing over along the chromosome with which we are primarily concerned. The regions of the third chromosome most affected by triploidy are the same regions most affected by temperature (PLOUGH 1921) and by X-rays (MULLER 1925). If the graphs of

figures 1 and 2 of the present paper are compared with the graphs for chromosome III of MULLER's paper, it will be seen that they are curiously alike. Indeed the only apparent difference is one of degree of effect; triploidy gives more extreme results than does the heavy X-ray dosage of MULLER. These similairites, as we shall see, have no direct significance. The results obtained by the subjection of diploids to temperature and to X-rays are correlated with the distance of the region involved from the spindle-fibre attachment. A comparison of recombination values for

TABLE 9

Age change in crossing over as shown by the recombination for cultures I minus the recombination for cultures II. From tables 6 and 7.

REGION	TRIPLOID	DIPLOID	REGION	TRIPLOID	DIPLOID
s_e,h–M_h,D	−1.4±1.46	2.0±0.46	r_u–h	1.0±1.42	1.8±0.83
M_h,D–m_a,c_u	5.8±1.77	2.2±0.32	h–t_h	1.4±1.26	−3.1±0.74
m_a,c_u–S_b,b_x	1.4±1.35	1.6±0.33	t_h–s_t	−0.1±0.41	0.2±0.10
S_b,b_x–H,e^s	0.7±0.73	1.2±0.28	s_t–c_u	0.6±1.47	1.4±0.42
H,e^s–M,c_a	0.2±1.33	2.6±0.58	c_u–s_r	1.9±1.23	3.6±0.63
			s_r–e^s	0.6±0.84	−0.9±0.57
			e^s–c_a	2.9±1.33	−0.1±0.92

chromosomes I, II, and III from such treated diploid females shows, so far as the data go, that the effect is greatest at the region of spindle-fibre attachment and decreases progressively from that region. This, as we have seen, is true also of chromosome III of triploids.

But when we consider chromosome I of triploids, and compare the data with those for chromosome III, we find that the results are exactly opposite in the two chromosomes with respect to distance from the spindle-fibre attachment. BRIDGES and ANDERSON (1925) found the following variation along chromosome I: crossing over in the extreme left end (from yellow, 0.0 to bifid, 6.9) was twice as high as in the diploid controls; but in regions to the right of bifid it was only about one-half as high. The right end of the chromosome is the region of spindle-fibre attachment. In the first chromosome, then, the increase is at the distal end of the chromosome with respect to the spindle-fibre attachment. If the data of BRIDGES and ANDERSON are plotted in the same manner as the data of the present paper

a curve is obtained similar in form to one-half the curve of figure 2. This would seem off-hand to correspond with the fact that the X-chromosome is rod shaped, whereas the third chromosome is V-shaped (that is, consists of two rods fastened together). But the maximum of the curve for chromosome III falls at the region of spindle-fibre attachment, and the maximum of the corresponding curve for chromosome I falls at the opposite end of the chromosome with respect to the attachment.

However, although the differences between triploid and diploid crossing over are not to be explained on the basis of a differential effect depending upon distance from the spindle-fibre attachment, it is a fact that a correlation exists between the lengthening or shortening of the triploid map and the spacing of the genes in the chromosomes as exhibited by the diploid map. Regions in which genes are clumped in the diploid, that is, in which there is relatively little crossing over between successive genes, are longer in the triploid; and, conversely, regions in which genes are far apart in the diploid, that is, in which there is relatively much crossing over between successive genes, are shorter in the triploid. This is true both for chromosome I and chromosome III. It seems reasonable to suppose, therefore, that triploid crossing over gives us a more dependable measure of the actual physical distance between genes than does diploid crossing over.

MULLER, ALTENBURG, and PAINTER (MULLER and ALTENBURG 1928, MULLER and PAINTER 1929) have recently reached conclusions of much interest in this connection from data of an entirely different nature. In a study of translocations produced in the diploid by exposure to X-rays these investigators find that regions in which genes are normally clumped are seen on translocation to be longer than the genetic results had previously indicated, whereas regions in which genes are normally sparse are seen to be shorter. That is, the scale of our diploid maps varies from region to region. If the contention of the present paper is justified, the scale of the triploid maps varies less than the scale of the diploid maps.

It may be stated incidentally that incomplete data upon crossing over in the second chromosome of triploids give results similar in direction but not so extreme in absolute value as those for the third chromosome of triploids.

The cytological studies of triploid Drosophilas by METZ (1925) led him to suggest that the peculiar genetic results obtained for the X-chromosome by BRIDGES and ANDERSON were a reflection of the observed anomalous behavior of the X-chromosomes. "The autosomes appear to associate uniformly throughout their length, but the X-chromosomes seem to behave differently. In most figures the latter are closely associated for about

half their length, and then diverge, finger-like as shown by the drawings. This may be due to a precocious separation of the homologues at one end, preceded by a state of close association throughout." The fact that chromosome III exhibits an even greater regional differentiation than the X would indicate that the correlation observed by METZ was of no direct causal significance.

CORRECTION CURVES AND MAPS

Correction curves may be constructed for the triploid data according to the method of BRIDGES (BRIDGES and MORGAN 1923) for the diploid, giving by a process of extrapolation the correction for double crossing over for the region between any two successive genes. The data of the first experiment are hardly amenable to such treatment since two crosses were necessary in covering the chromosome. Correction curves from the trip-

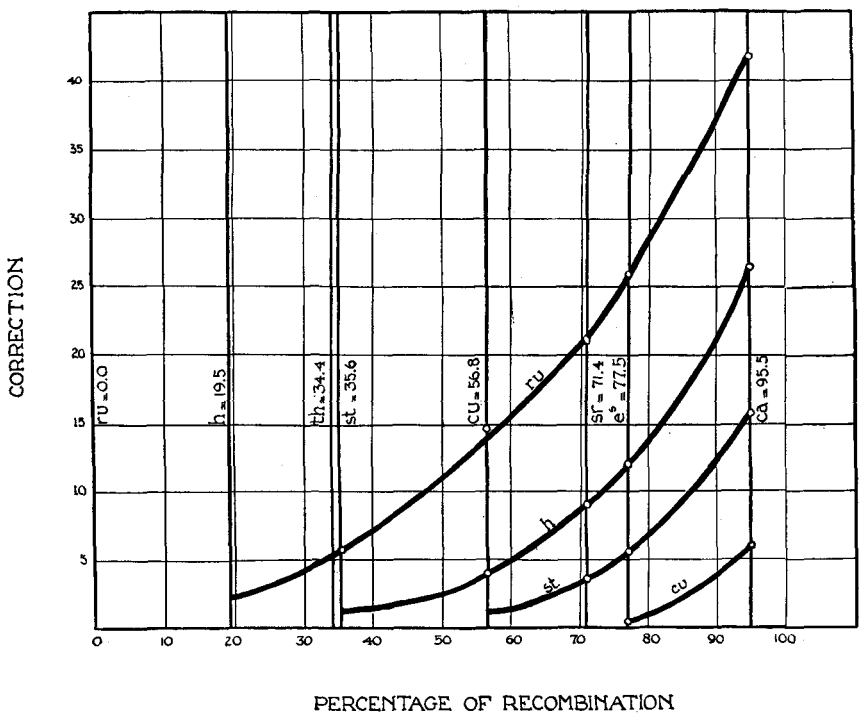

FIGURE 3.—Correction curves to give map distances for the third chromosome of triploids. The data used are from the first cultures of the second experiment. Ordinates represent the correction to be added to the respective recombination percentage to give the crossover value. The difference between the abscissae of two *succeeding* vertical lines represents the recombination value for the corresponding genes.

loid data of the second experiment are given in figure 3. Corresponding correction curves from the diploid data were practically identical with those published by BRIDGES and MORGAN (1923) and are therefore not given here. The ordinates of figure 3 represent the corrections to be added to the respective recombination percentages in order to give the correct crossover values, that is, the map distances. The difference between the abscissae of two succeeding vertical lines gives the recombination between the corresponding genes; this does not apply to genes separated by one or more mutant genes of the cross. The open circles of each curve show for the indicated gene the corrections calculated from the experimental data. These curves may be extended smoothly from the last circle toward the base line giving the approximate correction between successive loci. These corrections make no pretense to a high degree of accuracy. They will, however, facilitate somewhat the prediction of crossover values for chromosome III in triploid Drosophilas.

The one suggestive difference between these curves and those for the diploid depends upon the fact that the triploid curves begin with the first open circles at higher levels, at least for the ends of the chromosome. If this difference is significant it would indicate that double crossing over is higher in the triploid than in the diploid at the ends of the chromosome, in spite of the fact that the triploid recombination values are about half the diploid values. In other words, the reduction in crossing over at the ends of the triploid chromosome is dependent upon a considerable reduction in single crossing over, and exists in spite of a possible increase in double crossing over.

For the center of the chromosome there is no detectable difference between the corrections for triploid and for diploid. So far as the data go, therefore, they would indicate that there is a very marked increase in single crossing over in central regions of the triploid chromosome which entirely overshadows an apparent equality in double crossing over. These differences, however, should not be emphasized for it is not certain that they are significant.

Corrected maps for the triploid and diploid may be compared in figure 4. These maps are constructed similarly from the data of the first cultures of the second experiment. The values for the diploid are slightly higher than those of the standard diploid map, but this is to be expected since in the present experiments data from young and old females were segregated, which is not the case in ordinary crossover work. The genes used in the first experiment were omitted since the correction curves for these crosses are less accurate than are those of figure 3.

RECURRENT AND PROGRESSIVE DOUBLE CROSSOVERS

It is of interest to consider the relative occurrence of recurrent and progressive double crossovers. Obviously only the results of the first experiment are of value in this connection. When the proper data are selected

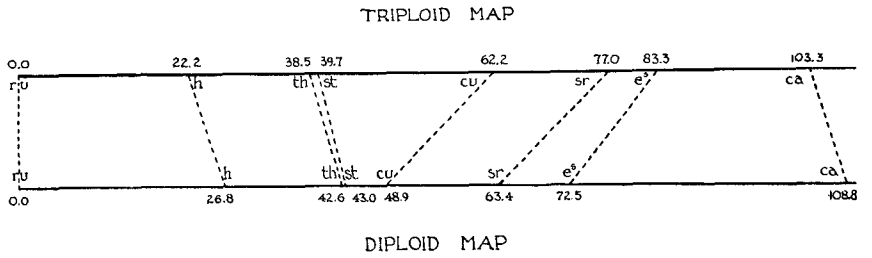

FIGURE 4.—A comparison of triploid and diploid maps for the third chromosome. The data are from the first cultures of the second experiment. Dotted lines connect the same genes.

from tables 1 and 3, table 10 is obtained. This table includes not only the simple double crossovers, but also the four triples of table 1, for a triple may be regarded as a succession of two double crossovers.

TABLE 10

A comparison of recurrent and progressive double crossovers. The data are taken from tables 1 and 3.

	RECURRENT	PROGRESSIVE	DIFFERENCE
Cultures I	43	43	0
Cultures II	20	26	6
Total	63=47.7%±2.9%	69=52.3%±2.9%	6=4.5%±4.1%

It is clear that the recurrent doubles and the progressive doubles are equal in number. It follows therefore that the chromosomes taking part in the first of two crossovers have no influence on the chromosomes taking part in the second. Or more accurately, when we recall that six crossover strands are present instead of three, one of the two strands which have crossed over at a first level crosses over at a second level as freely with a strand from the third chromosome as with a strand from the original two chromosomes. This would indicate that synapsis involves all three chromosomes equally. It would indicate further that the interference effects in triploids are not appreciably different for two successive crossovers in the same two strands than they are for two successive crossovers involving three strands. For if interference in the first case were greater, as one might

possibly be led to expect on *a priori* grounds, it would follow that progressive doubles would be more frequent than recurrent doubles. The equality of the two types of double crossovers observed here is quite in accord with the similar results of BRIDGES and ANDERSON (1925) for the X chromosome. These investigators record 15 recurrent and 10 progressive doubles. This would make a sum total of 78 recurrents and 79 progressives observed to date.

Coincidence values are not, strictly speaking, comparable in diploid and triploid. For coincidence is defined as the ratio of the actual percentage of doubles in two given regions to the expected percentage of doubles in these regions. Now the percentage of doubles expected as a matter of chance is obtained by multiplying together the crossover percentages of the two regions involved. It is obvious that this product represents the expectation of actual doubles (as exhibited by the emerging chromosomes) only in case two strands are in synapsis. It cannot be the expectation in four-strand crossing over, for the two separate crossings over do not necessarily involve the same single strand as central section. Still less is it the expectation in six-strand crossing over. Of course one may form the product irrespective of its significance and divide the observed percentage of doubles by it, thus obtaining an expression for "coincidence." This expression has no direct meaning in terms of the mechanism involved, but it is of some value in prediction and in comparison. "Coincidence" values are therefore given in table 11. Only data from the first experiment are

TABLE 11

"Coincidence" values for triploid and diploid derived from the data of the first experiment.

	CULTURES I		CULTURES II	
REGIONS	TRIPLOID	DIPLOID	TRIPLOID	DIPLOID
1,2	0.87	0.39	0.77	0.35
1,3	0.87	0.94	0.89	0.93
1,4	0.81	0.99	1.69	1.08
2,3	1.17	1.00	0.76	1.54
2,4	0.80	1.01	0.80	1.36
3,4	1.02	0.77	0.37	0.72
4,5	0.86	0.45	0.94	0.34

included here because the actual number of doubles cannot be directly observed in the second experiment.

It is immediately apparent that the values for the triploid are not uniformly higher than are those for the diploid. In this respect the results for the third chromosome are not in agreement with those of BRIDGES and ANDERSON (1925) for the X chromosome.

THE SPINDLE-FIBRE ATTACHMENT

The attachment of the spindle fibre to the third chromosome is seen in cytological preparations to be near the center of the chromosome at the apex of the V. Moreover the genetic evidence has long indicated that this point is somewhere between scarlet and curled near peach (48.0, standard diploid map). Evidence is now at hand from the recent paper of MULLER and PAINTER (1929), from the unpublished work of DOBZHANSKY, and from the data of the present paper to locate this attachment more accurately.

Certain individuals of the second experiment which were not classified in table 5 according to the characters which they displayed may now be considered. They include the so-called equational exceptions, that is, individuals which have received two third chromosomes from their mothers, these two chromosomes being derived wholly or in part from sister strands. Such exceptions will, of course, be detected only in case they are equational for one of the recessive mutant genes present in the mother in single dose. They will necessarily occur only among the triploid, intersex, and supermale offspring, since these alone have the requisite number of third chromosomes. Unfortunately the characters roughoid, hairy, and thread could not be classified with certainty in these experiments in intersexes; hence they were disregarded in formulating table 12.

If we count the number of times each gene is represented in this table we have the following graded series: s_t, 6; c_u, 6; s_r, 13; e^s, 16; c_a, 26. Now the number of representations of each gene expected as a matter of chance is 73.7. This figure is obtained as follows. If we consider any given locus, for example the scarlet locus, it is obvious that there are present in the six strand stage two scarlet sister genes and four normal allelomorphs. If in the formation of the diploid egg chance alone determines which two of these six allelomorphs pass to the given pole, 2/30, that is, 1/15, of the diploid eggs will contain two scarlet genes. Now the total number of eggs diploid for the third chromosome which are to be considered is represented by the sum of the total numbers of triploids, female intersexes, male intersexes, and super males; this sum is 1106. One fifteenth of this sum is, then, 73.7. The fact

that the representations fall much below expectation would indicate that the distribution is not a chance distribution. Another obvious relationship is that the genes form a graded series according to their distance from the center of the chromosome.

TABLE 12

Equational exceptions for the second experiment.

CLASS	TRIPLOIDS	♀ INTERSEXES	♂ INTERSEXES	SUPERMALES
s_t	1	2	1	1
$s_t\ e^s$	..	..	..	1
$c_u\ s_r\ e^s$	..	..	1	..
$c_u\ s_r\ e^s\ c_a$	..	2	3	..
s_r	..	..	1	..
$s_r\ e^s$	..	1	..	..
$s_r\ e^s\ c_a$	1	1	3	..
e^s	1	1	..	..
$e^s\ c_a$	..	1	..	..
c_a	1	10	5	..

A similar graded series of representations of genes in equational exceptions from triploids was found by BRIDGES and ANDERSON (1925) for the X chromosome. For this chromosome the number of equationals is lowest for the right end and increases progressively toward the left end. It is assumed by these investigators that separation of sister genes always occurs at the spindle fibre. Equational exceptions at loci not at the region of spindle-fibre attachment depend, then, upon crossing over and a resulting association of sister genes which would otherwise have been separated. The amount of crossing over would increase, obviously, with the distance of the locus from the spindle fibre. The attachment of the fibre to the X chromosome is therefore supposedly at the right end. The same conclusion had previously been reached by a similar consideration of the equational exceptions occurring in experiments with attached X chromosomes (ANDERSON 1925, L. V. MORGAN 1925 and unpublished work of STURTEVANT).

According to the same argument the spindle-fibre attachment to the third chromosome could not be to the right of curled. The fact that in no case do scarlet and curled appear in the same equational exception of table 12 would seem to demonstrate that the attachment is between these two genes. It may be stated that for those equational exceptions in which roughoid, hairy, and thread were readily classified, that is, in the triploids and supermales, the number of representations is as follows: r_u, 6; h, 4; t_h, 3; s_t, 3; Although these numbers are low they indicate, as expected, that the spindle fibre is not to the left of scarlet. The present data, therefore, place the attachment at the center of chromosome III between scarlet and curled. This location was previously suggested by the data of BRIDGES from preliminary crosses with triploid females designed to determine the attachment (MORGAN, STURTEVANT, and BRIDGES 1925).

These conclusions regarding spindle-fibre attachment are in complete agreement with those recently reached by MULLER and PAINTER (1929) and by DOBZHANSKY (unpublished) from a study of translocations. MULLER and PAINTER report a translocation in which slightly less than half of the third chromosome has broken away and has become attached to the end of the second chromosome. The cytological preparations demonstrate clearly that this break is just to the left of the spindle-fibre attachment. The genetic position of the break is, moreover, slightly to the left of the center of the linkage map half way between scarlet and pink—that is, at about 46 on the diploid map. This evidence, in conjunction with the evidence from triploids discussed above, would then place the attachment in a region limited by loci 46 and 50 of the standard diploid map.

The work of DOBZHANSKY offers further confirmation. In a study of translocations of pieces of the third chromosome to the fourth chromosome two cases were found in which the break occurred very near the spindle fibre, one just to the left of the fibre, and one to the right. These cases make possible the location of the spindle fibre with respect to the mutant genes marked. For from a study of the crossing over relationships it is clear that scarlet is to the right of the first break, and curled to the left of the second. The appearance of the chromosomes, as well as the crossover relations, gives DOBZHANSKY an opportunity to estimate the distances from these genes to the spindle fibre the attachment of which he accordingly places between loci 46 and 48.

DOBZHANSKY'S results are of further interest in connection with crossing over in triploids, for they show that, for central regions of the third chromosome, distances between genes are much longer than our standard diploid maps would indicate. This is obviously in agreement with the similar

results of MULLER and PAINTER (1929) and with the conclusions of the present paper (see page 240).

CELL SIZE AND CROSSING OVER

That there are marked differences between triploid and diploid crossing over cannot be questioned, and it would seem clear that triploid crossing over more nearly represents the actual distance between genes than does diploid crossing over, but the cause of the differences remains quite obscure. So far as we know, the crossing over system in triploid Drosophilas differs from that in the diploids in two respects. In the first place there are present six crossing over strands instead of four, and secondly the triploid cell is much larger than the diploid cell. The former follows from the data of BRIDGES and ANDERSON (1925), and the latter has been demonstrated by DOBZHANSKY (1929).

It is conceivable that the presence of six crossing over strands gives rise *per se* in some manner to the differences; they are not, however, as has been shown, the mere direct concomitant of sister-strand crossing over. On the other hand it seems plausible that marked alterations in the size of the cell-components might involve alterations in the relations of chromosomes to cytoplasm, and thus result in crossover variations.

There seem to be two immediate methods of attacking these problems. We may reduce the number of crossover strands in the triploid cell, and we may (possibly?) alter the size of the diploid cell. A reduction of the number of crossover strands is brought about readily by the proper use of crossover reducers. Crosses of this type are now well under way, but are not ready to report.

It was hoped, in the second place, that the diploid cell size of the mutant giant might be comparable to that of the normal triploid cell. The work of GABRITSCHEVSKY and BRIDGES (1928) had shown that giant and non-giant females from giant stock do not differ genetically and that the crossover values from these two types are normal and equal. It was known further from measurements of the chromosome plates published by these investigators that the chromosomes of giant females do not differ in length, and presumably also not in thickness, from ordinary diploid chromosomes. If giant cells proved to be larger than non-giant cells we should, therefore, have the altered diploid system desired.

Accordingly enough measurements were made of the cell size of giant and of non-giant females from giant-bobbed[11]-attached-X stock to detect any differences. These measurements were made with the assistance of Mr. IRWIN SPRITZER using the technique of DOBZHANSKY. Bristle counts

were made in three specific different regions of the wing. Since it is known that each cell of the wing is provided with a single bristle, it follows that the cell size is inversely proportional to the number of bristles per area. Table 13 gives these results as well as the results for normal female, normal male, and normal triploid taken from the paper of DOBZHANSKY.

TABLE 13

Number of bristles per 0.01 mm² in three given regions of the wing. The figures for 2N ♀, ♂, and 3N ♀ are from DOBZHANSKY. The giant females and non-giant females were from giant bobbed[11]-attached-X stock.

	REGION I	REGION II	REGION III
giant ♀	56.02±0.58	63.12±0.61	57.37±0.50
non-giant ♀	59.82±0.66	67.04±0.56	61.38±0.52
difference	3.80±0.88	3.92±0.83	4.01±0.72
2N ♀	50.76±0.22	61.01±0.31	55.67±0.29
♂	57.42±0.35	70.46±0.36	63.02±0.33
3N ♀	36.70±0.22	44.47±0.27	41.35±0.25

These figures demonstrate a difference which is just significant between the cell size of the giant female and that of the non-giant female; the two types are from the same culture and are presumably of identical composition. DR. BRIDGES informs me that preparations of the ovaries of giant females show rare cells diploid in composition and distinctly larger in size than the surrounding cells. It is possible that similar occasional large cells are present in the wing and account for the slightly larger average size of cells of the giant as compared with the non-giant, as shown in the table. The cells of the latter are somewhat different in size from those of the normal diploid female, but this is no doubt to be explained on the basis of the presence of different modifiers in the two stocks.

At any rate it is perfectly clear that the size of the triploid cell is of an entirely different order of magnitude from the size of cells of giant diploid females. It follows, then, that the counts from giant stock have no relation to the work on crossing over in triploids. They have been mentioned here because they have some incidental interest of their own. It would seem that, since the size of giant and of non-giant cells is not very different, the

distinctly greater size of the giant fly is dependent (at least partially) upon a greater number of cells. The rare presence of large cells in the ovaries, however, renders such a conclusion tentative until the matter is investigated further.

CONCLUSIONS

(1) In *Drosophila melanogaster* crossing over in the triploid shows marked regional differences along the third chromosome from crossing over in the diploid. Crossing over at the ends of the chromosome is slightly more than one-half as great in the triploid as in the diploid; and as we pass from either end of the chromosome to the center the relative amount of crossing over in the triploid increases continuously until we reach a maximum at the center, for which region triploid crossing over is more than three times as great as diploid crossing over.

(2) A comparison of these results with those of BRIDGES and ANDERSON for the X chromosome of triploids results in the conclusion that the variations are not correlated with the distance of the region from the spindle-fibre attachment.

(3) They are correlated, however, with the regional spacing of the genes as represented by the diploid maps. Regions in which genes are closely spaced on the diploid maps are lengthened in the triploid; and regions in which genes are far apart on the diploid maps are shortened in the triploid.

(4) It is probable, therefore, that the triploid maps represent more accurately than the diploid maps the actual spacing of the genes along the chromosomes.

(5) The data do not show any effect of age upon crossing over in the third chromosomes of triploids, although the usual effect is shown by the diploid controls.

(6) Crossing over takes place between two wild-type chromosomes to the same extent that it does between two chromosomes one or both of which are marked by mutants.

(7) For chromosome III the number of recurrent double crossovers is equal to the number of progressive double crossovers. It follows that the strands taking part in the first crossing over do not in any way determine which strands take part in the second.

(8) The data of the present paper, in conjunction with those of MULLER and PAINTER and of DOBZHANSKY, place the spindle-fibre attachment of chromosome III in the center of the chromosome at some point between loci 46 and about 48 of the standard diploid map.

(9) In attempts to determine the cause of the differences between diploid and triploid crossing over, measurements were made of the cells of females from giant stock. The average cell size of giant females is slightly greater than that of non-giant females from the same stock; it does not approach, however, the size of cells of triploid females.

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