A COMPARISON OF TRIPLOID AND DIPLOID CROSSING OVER FOR CHROMOSOME II OF *DROSOPHILA MELANOGASTER*[1]

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TABLE OF CONTENTS

	PAGE
INTRODUCTION	137
The measurement of crossing over in triploids	138
Data for chromosome II	138
Equational exceptions	144
DISCUSSION	147
CONCLUSIONS	151
LITERATURE CITED	151

INTRODUCTION

For *Drosophila melanogaster* crossing over is markedly different in triploid females and in diploid females, as has been shown by BRIDGES and ANDERSON (1925) for the X chromosome and by REDFIELD (1930) for chromosome III. Triploid crossing over may be greater or less than diploid crossing over; the sign of this difference and its absolute value depend upon the particular chromosome region involved.

Thus for the left end of the X chromosome crossing over in triploids is approximately twice that in diploids; at the right end of the X it is about half that in diploids. For the third chromosome triploid crossing over is about half diploid crossing over at either end; at the center it is more than three times as great. There is, moreover, a regular gradation in this ratio from the center of the chromosome to either end.

Regional differences had previously been found in crossing over as the result of a number of agents including age, temperature, and X-rays and it was suggested that these differences depend upon the distance of the region from the spindle-fibre attachment. The regional differences attendant upon triploidy, on the other hand, seem to be correlated with the physical spacing of the genes along the chromosome (REDFIELD 1930). It is possible that the differences caused by age, temperature, and X-rays are in the last analysis also correlated with the spacing of the genes, and

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that these results are therefore intimately related to the data from triploids; but this can only be determined by further work.

However these questions may be answered, the triploid genetic map for chromosome III corresponds more accurately with the cytological map than does the diploid genetic map. The present paper will show that this is true also for chromosome II, a result of interest since the spatial distribution of the genes for II differs from that for III (DOBZHANSKY 1930a).

THE MEASUREMENT OF CROSSING OVER IN TRIPLOIDS

Triploid crossing over was originally measured by BRIDGES and ANDERSON (1925) by marking all three X chromosomes at the same given loci ($A_1B_1C_1 \cdots / A_2B_2C_2 \cdots / A_3B_3C_3 \cdots$). The crossing over between two given loci is then the percentage of exchange between them. This technique is well adapted to the X chromosome, for a sufficient number of sets of genes are at hand which are actually or practically allelomorphic and which can be used in the same cross without difficulties in classification. The method can be used also for the third chromosome, but with difficulty; accordingly a second method was devised and used (REDFIELD 1930). This involves the marking of only one of the three homologous chromosomes; the other two chromosomes are alike and are wild-type ($A_1B_1C_1 \cdots / A_2B_2C_2 \cdots / A_2B_2C_2 \cdots$). Between any two loci, A and B, crossing over is detected between chromosome $A_1B_1C_1 \cdots$ and either of the chromosomes of the type $A_2B_2C_2 \cdots$, but it is not detected between $A_2B_2C_2 \cdots$ and $A_2B_2C_2 \cdots$. The actual crossing over between A and B is, then, 3/2 times the apparent crossing over; this is true no matter what loci are chosen. The values obtained from such crosses are in complete agreement with those from crosses in which all three chromosomes are marked (REDFIELD 1930).

For the second chromosome a sufficient number of sets of close and classifiable genes was not available for crosses in which all three chromosomes are marked; triploid crossing over for this chromosome was of necessity studied by means of the second of the methods outlined above.

DATA FOR CHROMOSOME II

The three triploid crosses used and their diploid controls are as follows:

(A)

$$\frac{a_1{}^2 d_p b p_r c p_x s_p}{+} \; ♀ \times a_1{}^2 d_p b p_r c p_x s_p \; ♂$$

$$+$$

$$\frac{a_1{}^2 d_p b p_r c p_x s_p}{+} \; ♀ \times a_1{}^2 d_p b p_r c p_x s_p \; ♂$$

$$+$$

(B) $$\frac{a_1^2 d_p b p_r}{+} \text{♀} \times a_1^2 d_p b p_r \text{♂}$$

$$\frac{a_1^2 d_p b p_r}{+} \text{♀} \times a_1^2 d_p b p_r \text{♂}$$

(C) $$\frac{p_r c p_x s_p}{+} \text{♀} \times p_r c p_x s_p \text{♂}$$

$$\frac{p_r c p_x s_p}{+} \text{♀} \times p_r c p_x s_p \text{♂}.$$

The symbols refer to the following mutant genes: a_1^2, aristaless-2, shortens the aristae and has its locus at 0.0 on the standard diploid map; d_p, dumpy wings, at 13.0; b, black body color, at 48.5; p_r, purple eyes, at 54.5; c, curved wings, at 75.5; p_x, plexus wing venation, at 100.5; s_p, speck at the root of the wing, at 107.0.

It was originally intended that the crosses of type A would give sufficient data for crossover determinations. Good care was taken of the cultures, and parents were transferred to subcultures to minimize larval competition. But when the data were tabulated it was found that the viability of a number of classes was quite poor. Accordingly the series of mutant genes was broken into two, and crosses B and C resulted. Viability relations for these crosses were satisfactory. Curiously the crossover values for A are very near those for B and C. It follows that the inviability of the poor classes of A is largely balanced, but this could hardly be predicted without the check afforded by the later crosses.

The offspring, classified according to sex, of the three triploid crosses are shown in table 1. The percentages of the various types are much like those ordinarily obtained. There is considerable variation in the ratio of male-like to female-like individuals within the intersex class, but this is not odd for it has previously been observed (DOBZHANSKY and BRIDGES 1928) that the type of sexual development of intersexes is very susceptible to genetic modifiers. It is interesting that crosses A and B which involve the same left end of II are alike in this respect, and are unlike cross C in which a new left end of II has been substituted (and possibly also other sections outside II).

The raw data for crosses A are given in table 2. This table includes the diploid offspring—that is, all individuals which have received one representative of each chromosome from each parent. Only in these (and in the

TABLE 1

Types of offspring produced by triploid mothers.

TYPE	CROSS A		CROSS B		CROSS C		TOTAL	
	NUMBER	PERCENT	NUMBER	PERCENT	NUMBER	PERCENT	NUMBER	PERCENT
Diploid ♀	3110	51.5	3232	48.2	3328	46.3	9670	48.4
Diploid ♂	473	7.8	484	7.2	576	8.0	1533	7.7
Triploid ♀	280	4.6	386	5.8	535	7.4	1201	5.5
Intersex ♀	1095	18.1	1303	19.6	2221	30.9	4619	23.2
Intersex ♂	1060	16.7	1269	18.9	512	7.1	2841	14.2
Super ♀	1	0.2	..	..	..	..	1	0.05
Super ♂	23	3.8	22	3.3	27	3.8	72	3.6

one superfemale found) can the type of chromosome II received from the triploid mother be directly observed. Each of the other offspring has received three representatives of II, including two from the mother; what the maternal representatives are would appear only as the result of genetic tests; these tests are not feasible, for intersexes and supermales are sterile and triploids frequently do not provide enough progeny to make their composition certain.

The condensed method of presentation of the data in table 2 was suggested by Dr. C. B. BRIDGES. The "type" gives the apparent regions of crossing over, 1 representing the first region from a_1^2 to d_p, 2 the second region from d_p to b, etc. For either cross, triploid or diploid, each type contains two contrary classes; the convention followed is that the class first mentioned is always that containing a_1^2. The same method is used in table 4 and in table 6. For table 6 the leftmost mutant used is p_r; the region from p_r to c is therefore region 1, and the class first mentioned of two contrary classes is that containing p_r.

As has been stated the diploid crosses do not show for all types the expected equality of contrary classes; this is obvious, for example, in single crossovers in regions 1 and 6 and in double crossovers in 1,5 and 2,5. For the triploid crosses, of course, contrary classes are not expected to be equal; this is because the apparent type of crossover is not always the true type. The class a_1^2, for example, includes not only single crossovers in region 1 between the marked chromosome and one of the two unmarked chromosomes, but also all multiples receiving a_1^2 whose points of crossing over, after the first, are between unmarked sections.

Crossover values computed from the data of table 2 are shown in table 3; the triploid values are computed as explained briefly on page 138 and in more detail in the previous paper (REDFIELD 1930). The differences be-

TABLE 2

Diploid offspring from backcrosses of triploid females of the composition $a_1^2d_pbp_rcp_xs_p/+/+$ and of control diploid females of the composition $a_1^2d_pbp_rcp_xs_p/+$. For each type the class first mentioned is that containing a_1^2.

APPARENT TYPE	TRIPLOID CROSS	DIPLOID CROSS	APPARENT TYPE	TRIPLOID CROSS	DIPLOID CROSS
0	414+1571	529+601	1, 2, 3	0+ 0	1+ 0
1	70+ 20	95+ 24	1, 2, 4	3+ 0	1+ 1
2	179+ 125	313+276	1, 2, 5	2+ 0	5+ 0
3	75+ 56	86+ 61	1, 2, 6	1+ 0	1+ 0
4	202+ 251	228+183	1, 3, 4	0+ 0	4+ 0
5	100+ 114	266+238	1, 3, 5	0+ 0	2+ 1
6	16+ 57	31+ 60	1, 4, 5	0+ 0	6+ 0
1, 2	6+ 5	10+ 3	1, 4, 6	0+ 0	4+ 1
1, 3	9+ 4	8+ 5	2, 3, 4	2+15	4+ 4
1, 4	14+ 13	28+ 11	2, 3, 5	1+ 2	6+15
1, 5	4+ 7	31+ 3	2, 3, 6	0+ 4	0+ 1
1, 6	2+ 0	11+ 1	2, 4, 5	0+ 3	7+19
2, 3	1+ 13	0+ 11	2, 4, 6	2+ 2	0+ 4
2, 4	12+ 49	22+ 98	2, 5, 6	0+ 2	0+ 1
2, 5	3+ 18	17+120	3, 4, 5	0+ 1	3+ 0
2, 6	5+ 8	51+ 27	3, 4, 6	0+ 0	2+ 4
3, 4	7+ 17	58+ 22	4, 5, 6	1+ 0	3+ 0
3, 5	3+ 5	14+ 22	1, 2, 3, 4	0+ 0	2+ 0
3, 6	9+ 5	79+ 7	1, 2, 3, 5	0+ 0	1+ 0
4, 5	2+ 36	4+ 25	1, 2, 4, 5	0+ 0	3+ 0
4, 6	13+ 14	18+ 10	..	..	..
5, 6	3+ 3	2+ 4	N	3583	3819

tween the triploid values and the diploid values are obvious. For region 1, from aristaless to dumpy, triploid and diploid crossing over are almost the same. For the second region from dumpy to black triploid crossing over is less than diploid crossing over, the ratio of the two being 0.72. From this region to the center of the chromosome, triploid crossing over increases relative to diploid crossing over, until for the section from purple to curved the triploid value is 1.35 times the diploid value. The next section to the right, namely from curved to plexus, again shows a decrease in triploid crossing over, the quotient falling to 0.61. At the right end of the chromosome from plexus to speck the ratio rises reaching a value of 0.74. Thus the second chromosome can be divided at the center into two limbs which behave similarly with regard to the relation of triploid crossing over to diploid crossing over. A like division into two limbs of chromosome III for triploids has previously been found (REDFIELD 1930). There are differences between the limbs of chromosome II and chromosome III and these differ-

ences, as will be shown, are correlated with corresponding differences in the spacing of the genes in these chromosomes.

It may be noted that the total crossing over from aristaless to speck for chromosome II is somewhat less (about 13 units less) in the triploid than in the diploid. In the crosses for chromosome III which involved the entire distance from roughoid to claret the total triploid crossing over was also appreciably less than the total diploid crossing over (REDFIELD 1930). Thus it would appear that the total frequency of crossing over is not necessarily the same in the triploid and in the diploid.

TABLE 3

Crossover values (with probable errors) computed from the data of table 2.

REGION	TRIPLOID T	DIPLOID D	DIFFERENCE T−D	QUOTIENT T/D
$a_1^2-d_p$	6.7±0.28	6.9±0.28	−0.2±0.39	0.97±0.06
d_p-b	19.4±0.45	26.8±0.48	−7.4±0.66	0.72±0.02
$b-p_r$	9.6±0.33	11.3±0.35	−1.7±0.48	0.85±0.04
p_r-c	27.6±0.50	20.4±0.44	+7.2±0.67	1.35±0.04
$c-p_x$	13.0±0.38	21.4±0.45	−8.4±0.59	0.61±0.02
p_x-s_p	6.2±0.27	8.4±0.30	−2.2±0.41	0.74±0.04
Total	82.5±0.93	95.2±0.96	−12.7±1.33	..

The data for crosses of type B are given in table 4 and the corresponding crossover values in table 5. The ratios of triploid to diploid crossing over are somewhat different than those for crosses of type A, but they are not more different than might be expected, and the change in the ratio along the chromosome is of the same nature as for crosses A. Thus the ratio is greater for $a_1^2-d_p$ than for d_p-b, and increases again for the region $b-p_r$ near the center of the chromosome.

TABLE 4

Diploid offspring from backcrosses of triploid females of the composition $a_1^2d_pbp_r/+/+$ and of control diploid females of the composition $a_1^2d_pbp_r/+$. For each type the class first mentioned is that containing a_1^2.

APPARENT TYPE	TRIPLOID CROSS	DIPLOID CROSS	APPARENT TYPE	TRIPLOID CROSS	DIPLOID CROSS
0	780+2199	2500+2874	1, 2	9+12	20+14
1	93+ 82	420+ 422	1, 3	6+ 4	25+15
2	192+ 166	1143+1273	2, 3	8+14	17+32
3	75+ 76	234+ 201	N	3716	9190

Similar data and crossover values for crosses of type C are given in tables 6 and 7. For the chromosome limb covered by these crosses, namely

TABLE 5

Crossover values (with probable errors) computed from the data of table 4.

REGION	TRIPLOID T	DIPLOID D	DIFFERENCE T−D	QUOTIENT T/D
$a_1^2-d_p$	8.3±0.31	10.0±0.21	−1.7±0.37	0.83±0.04
d_p-b	16.2±0.41	27.2±0.32	−11.0±0.52	0.59±0.02
$b-p_r$	7.4±0.29	5.7±0.16	+1.7±0.33	1.30±0.06

the right limb, the values of the ratio are practically the same as for crosses *A*. The quotient decreases as we pass from the end of the chromosome to intermediate regions; it increases as we pass from these intermediate regions to the center of the chromosome where it reaches a value of about 1.4.

TABLE 6

Diploid offspring from backcrosses of triploid females of the composition $p_rcp_xs_p/+/+$ and of control diploid females of the composition $p_rcp_xs_p/+$. For each type the class first mentioned is that containing p_r.

APPARENT TYPE	TRIPLOID CROSS	DIPLOID CROSS	APPARENT TYPE	TRIPLOID CROSS	DIPLOID CROSS
0	707+1948	2481+2871	1, 3	7+12	33+38
1	338+ 288	797+ 797	2, 3	4+ 0	1+ 4
2	129+ 147	993+ 946	1, 2, 3	1+ 0	3+ 0
3	39+ 51	203+ 261	..	..	..
1, 2	27+ 32	97+ 78	N	3904	9603

TABLE 7

Crossover values (with probable errors) computed from the data of table 6.

REGION	TRIPLOID T	DIPLOID D	DIFFERENCE T−D	QUOTIENT T/D
p_r-c	27.1±0.48	19.2±0.27	+7.9±0.55	1.41±0.02
$c-p_x$	13.0±0.36	22.1±0.29	−9.1±0.46	0.59±0.02
p_x-s_p	4.4±0.22	5.7±0.20	−1.3±0.30	0.77±0.06

The results of crosses *B* and *C* are shown graphically in figure 1; results from crosses *A* are not included since poorer viability relations make them less certain. The figure shows the relatively low value of the ratio at intermediate regions, its slight increase at the ends of the chromosome, and its definite and greater increase at the center of the chromosome. It should be noted that three of the regions concerned represent relatively long crossover sections, namely d_p-b, p_r-c, and $c-p_x$. For these regions a small

correction for undetected doubles would result if it had been possible to deal with shorter sections. In this case the general shape of the curve would have remained the same, but it would undoubtedly have shown minor changes.

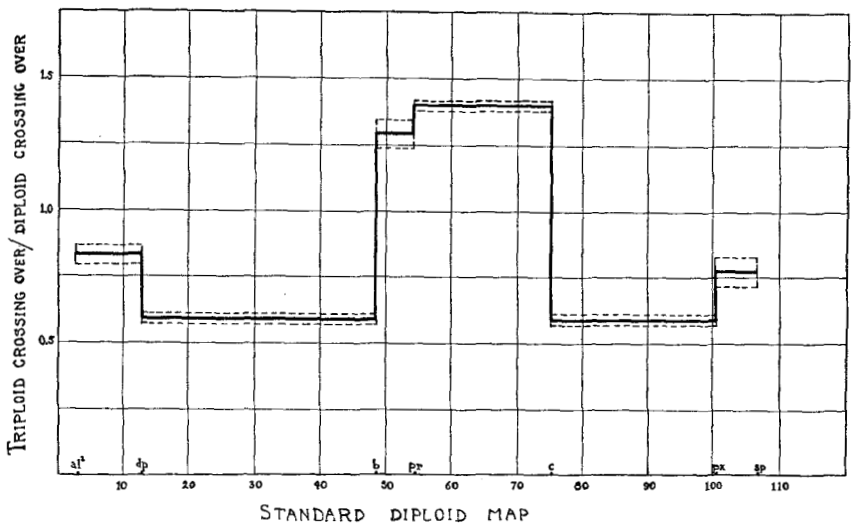

FIGURE 1.—The relation between triploid and diploid crossing over along the chromosome. Ordinates represent the ratio of triploid crossing over to diploid crossing over, abscissae the arrangement of the genes as shown by the standard diploid map. Dotted lines give the probable errors for the respective regions.

EQUATIONAL EXCEPTIONS

Triploid females containing a single dose of a given mutant gene produce occasional individuals which have received two maternal representatives of this gene. Since the diploid father contributes one chromosome II, such equational exceptions for II are found only among those types which have arisen from diploid eggs and which have three representatives of the locus in question, namely among the triploids, intersexes, and supermales.

If in the formation of the diploid eggs chance alone determined which two of six allelomorphic genes passed to a given pole, 1/15 or 6.66 percent of these eggs would contain two sister mutant genes. In other words, 6.66 percent of the triploids, intersexes, and supermales would in the present crosses show aristaless, or dumpy, or any other of the recessive mutant characters used. But it has been shown for the X chromosome of triploids (BRIDGES and ANDERSON 1925) and for chromosome III of triploids (REDFIELD 1930) that sister genes normally separate at the spindle-fibre

attachment, and that the tendency to separate becomes less the farther the locus is from the spindle fibre; the association does not become random, however, even for those genes which are farthest from the spindle-fibre attachment. Equational exceptions depend therefore upon crossing over between the locus and the spindle-fibre attachment resulting in an association of sister genes which would otherwise have been separated.

Thus the tendency in triploids of sister genes to separate may be used to place the spindle-fibre attachment. In this manner the attachment to the X has been shown to be at the right end of the chromosome, and to III at the center of the chromosome. These results are in agreement with previous determinations from studies of equational exceptions produced by attached-X diploids (ANDERSON 1925, L. V. MORGAN 1925, STURTEVANT 1931), from equational exceptions produced by a high non-disjunction line (ANDERSON 1929), and from studies of translocations (STERN 1926, MULLER and PAINTER 1929, DOBZHANSKY 1930b).

DOBZHANSKY'S examination (1930a) of translocations involving the second chromosome has shown that the spindle fibre is attached at the center of II slightly to the right of purple. This had long been suspected (BRIDGES and MORGAN 1923) and is in agreement with the results of the present paper.

Equational exceptions from triploid females of the composition $a_1^2\ d_p\ b\ p_r\ c\ p_x\ s_p/+/+$ are shown in table 8. The classification of curved in intersexes is not certain for intersexes often have their wings spread apart, but it was thought it would do no harm to attempt it, and the results of

TABLE 8

Equational exceptions from triploid females of the composition $a_1^2 d_p b p_r c p_x s_p/+/+$.

CLASS	TRIPLOID	♀ INTERSEX	♂ INTERSEX
a_1^2	1	6	9
$a_1^2 d_p$	..	4	2
$a_1^2 d_p b$	..	2	..
$a_1^2 c p_x s_p$	..	1	..
d_p	..	..	1
$b p_r c p_x s_p$	..	1	..
$b p_r p_x s_p$	..	..	1
$b c p_x s_p$	..	1	1
$b s_p$	..	1	..
p_r	..	1	..
$c p_x s_p$	..	12	5
$c p_x$	1	..	..
$p_x s_p$	4	8	4
s_p	2	3	6

table 11 show that it was not far wrong. Table 9 gives the equational exceptions for $a_1^2\ d_p\ b\ p_r/+/+$ triploids, and table 10 for $p_r\ c\ p_x\ s_p/+/+$ triploids. In the intersexes of the latter cross the classification of curved was very difficult and was omitted.

TABLE 9

Equational exceptions from triploid females of the composition $a_1^2 d_p b p_r/+/+$.

CLASS	TRIPLOID	♀ INTERSEX	♂ INTERSEX
a_1^2	5	3	3
$a_1^2 d_p$	..	5	7
$a_1^2 d_p b$	..	2	..
$a_1^2 d_p b p_r$	1	2	4
d_p	..	1	2
$d_p b$	..	1	..
$d_p b p_r$	..	1	..
b	2	1	..
$b p_r$	..	2	..
p_r	..	1	..

TABLE 10

Equational exceptions from triploid females of the composition $p_r c p_x s_p/+/+$. Curved could not be classified in the intersexes of these crosses and is therefore omitted.

CLASS	TRIPLOID	♀ INTERSEX	♂ INTERSEX
p_r	1	4	1
$p_r p_x s_p$	..	1	..
p_x	2	3	1
$p_x s_p$	6	32	9
s_p	3	5	..

Table 11 shows the numbers and percentages of representation of each gene in the equational exceptions for the three types of cross. In each case

TABLE 11

Representations of the genes in the equational exceptions. Chance expectation is 6.66 percent.

	CROSS A		CROSS B		CROSS C	
GENE	NUMBER	PERCENT	NUMBER	PERCENT	NUMBER	PERCENT
a_1^2	25	1.03	32	1.08	..	..
d_p	9	0.37	26	0.88	..	..
b	7	0.29	16	0.54	..	..
p_r	3	0.12	11	0.37	7	0.21
c	22	0.91	..	..	..	..
p_x	39	1.60	..	..	54	1.65
s_p	50	2.05	..	..	56	1.71

there is a regular gradation in the percentage of equational exceptions from the low value at the center of the chromosome to the relatively high value at either end. The lowest value reached for any of the loci is for purple, which means that the spindle-fibre attachment is nearest purple.

An examination of the classes of tables 8, 9, and 10 shows, moreover, that this attachment must be somewhat to the right of purple between purple and curved, rather than between black and purple. This is because purple tends to appear with genes to its left and not with those to its right. There are exceptions to this tendency, namely the $b\ p_r\ c\ p_x\ s_p$ female intersex and the $b\ p_r\ p_x\ s_p$ male intersex of table 8, and the $p_r\ p_x\ s_p$ female intersex of table 10. These, no doubt, are due to double crossing over, one point of crossing over being to the left of the spindle fibre but to the right of purple, the other to the right of the spindle fibre and either to the left or right of curved.

In no case does the percentage of representation approach that expected on the basis of random assortment (6.66 percent). In this respect the data are like those obtained for the X chromosome of triploids (BRIDGES and ANDERSON 1925) and for chromosome III of triploids (REDFIELD 1930). This may be due partially to low viability, but there is at least one other factor concerned. This is the fact that of the diploid eggs only those are available for equational exceptions which contain at least one chromosome representing recombination between the locus and the spindle-fibre attachment. It is of course an easy matter to calculate an approximation to the expected percentage of recombination between the spindle-fibre region and aristaless or speck near either end of the chromosome. When this is done the expected percentages of equational exceptions for the ends of the chromosome are higher than, but are not far from, the percentages actually obtained. However, these matters are undoubtedly further complicated by additional factors about which nothing is known so it seems advisable to postpone discussion.

DISCUSSION

Polyploid crossing over is not always markedly different from diploid crossing over. In the Drosophila triploid, as has been shown, there are regions for which the crossover values are the same as those in the diploid. The recent papers of SVERDRUP SÖMME (1930) and of DE WINTON and HALDANE (1931) have shown that crossover values are not far different in the tetraploid and in the diploid forms of *Primula sinensis*. It is, of course, possible that chromosome regions other than those with which they were able to deal will be found to give differing values. On the other hand, the

situation in Primula is somewhat different from that in Drosophila. So far as the number of strands involved is concerned, the tetraploid Primula may be regarded as a modified diploid type; for it is probable, as is pointed out by DE WINTON and HALDANE, that crossing over in these tetraploids involves only two of the four homologous chromosomes. In Drosophila it seems probable (ANDERSON 1925) that only two strands cross over at any one level, but the equality of recurrent and progressive double crossovers (BRIDGES and ANDERSON 1925, REDFIELD 1930) demonstrates that the chromosomes of the triploid of this form conjugate by threes and that the strands taking part in a first crossing over do not determine which strands take part in a second.

However it is well not to overemphasize this distinction. It would seem that a substitution of six sets of crossover strands in the triploid Drosophila (BRIDGES and ANDERSON 1925) for the four sets present in the diploid might in itself give rise to differences in crossing over, in particular as the result of sister-strand crossing over. Still there is evidence from the use of crossover reducers (REDFIELD unpublished) that when four strands alone of the six are allowed to cross over in the triploid cell the values obtained are triploid and not diploid. DOBZHANSKY has shown (1929a) that triploid cells in Drosophila differ from diploid cells not only in the number of crossing over strands but also in their general size relationships. It is conceivable that marked alterations in the relative size of the cell components might result in differences in crossing over.

From other considerations also it may be concluded that sister-strand crossing over cannot alone be held accountable for the differences in crossover values between triploid and diploid. If crossing over occurred between the two sister strands resulting from the splitting of a single chromosome its results would not be directly detected in either triploid or diploid. But if it occurred freely the net crossover values for the triploid would show a definite increase over the values for the diploid. For in this case the diploid values obtained would represent 2/3 the actual physical crossing over whereas the triploid values would represent 4/5 the actual total crossing over. It is clear, however, that the regional differences along the chromosome for the X, II, and III completely mask any constant difference due to sister-strand crossing over. Indeed, triploid crossing over may be considerably lower than diploid crossing over (the right end of the X, intermediate regions in II, and the ends of III). Thus the possibility of sister-strand interchange cannot be directly investigated by a comparison of triploid and diploid values, but it is believed it can be investigated, although with difficulty, by the use of crossover reducers in triploids; such crosses are now well under way.

Whatever may be the decision as to sister strand interchange (the very slight evidence we now have indicates that it does not occur, STURTEVANT 1928), the regional differences between triploid and diploid crossing over will still remain unexplained. And it is exactly these regional differences which are most striking in comparing diploid and triploid.

In an examination of the differences the first relation which occurs to one is the curious fact that chromosome regions in which crossing over in the triploid is increased are regions in which genes are clumped on the standard diploid maps. The converse statement also holds: regions in which crossing over in triploids is markedly decreased are regions in which genes are sparse on the diploid genetic maps. The former case is illustrated by the left end of the X, the center of II, and the center of III; the latter by the right end of the X, intermediate regions of II, and the ends of III. Thus there is a definite relationship between the spacing of the genes on the regular diploid maps and the differences between triploid and diploid crossing over.

Now it had long been suspected that there are differences between the spacing of the genes on the maps and their actual physical spacing along the chromosomes (BRIDGES and MORGAN 1923, MORGAN, BRIDGES, and STURTEVANT 1925). The studies of crossover reducers led to the suspicion that regions in which genes are clumped on the maps are regions in which crossing over is relatively lower per unit of physical distance between genes, that is, that the unit of crossing over varied from region to region. In most cases, then, the clumping of the genes was supposed to represent a genetic phenomenon rather than a physical condensation of genes.

The recent results from translocations (largely made possible by the introduction of X-rays into genetic studies) showed that this is indeed true. The first direct evidence of this type was presented by MULLER and PAINTER in a general preliminary paper (1929) reporting a number of different types of translocation. There followed the detailed studies of DOBZHANSKY (1929b, 1930b) on translocations involving the third and fourth chromosomes. He found on direct observation of the metaphase plates of these translocations and on genetic analysis of the points of breakage that for chromosome III "the distances between the loci of the breakages or of the genes lying in the middle part of the chromosome are longer cytologically than they might be expected to be on the basis of the genetical map. On the other hand, the distances between the loci lying near the ends of the chromosome are shorter cytologically than they might be expected to be on the basis of the genetical data. The genetical map represents the genes located in the middle part of the chromosome (near

the spindle fibre) relatively too close to each other, and the genes located at the ends of the chromosome relatively too far apart."

These results correspond well with those found by REDFIELD (1930) in a comparison of crossing over in the triploid and diploid Drosophila for the third chromosome. "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."

A subsequent study of translocations involving the second chromosome (1930a) led DOBZHANSKY to conclude for II: "The distances between the genes located at the middle of the chromosome are much longer cytologically than suggested by the genetic map. On the contrary, distances between the genes located to the right and to the left of the middle of the chromosome are relatively far shorter cytologically than the genetic map indicates. Finally, the distances between the genes located near the right end of the chromosome are again relatively longer cytologically than indicated by the genetic map. It is probable that the same is true in respect to the genes located at the extreme left end of the chromosome, though it is not certain."

It is immediately obvious that the present paper shows results of the same general nature. Triploid crossing over is about 1.4 times as great as diploid crossing over for central regions of II. The ratio decreases to about 0.6 for intermediate regions to the right and left of the central regions; it increases again for the terminal regions at either end of this chromosome although, curiously enough, it does not reach unity.

It should be emphasized that these statements are not intended to imply that triploid crossover values are directly proportional to distances on the cytological maps; it would be very surprising if such a simple relationship did hold, and indeed we are certain it does not. If it did we should expect, for example, that triploid values for the right end of II would be relatively much greater than they actually are.

It cannot yet be stated with certainty that the X chromosome fits into this scheme, although it would seem that the data suggest that it does. It has long been known that there is a definite clumping of genes at the left end of this chromosome and it has consequently been supposed that the left end is longer relative to the rest of the chromosome than the genetic map indicates. This fits very well with the results of BRIDGES and ANDERSON (1925) for the X chromosome of triploids which showed that crossing

over at the left end in triploids is approximately twice that in diploids, and that for the rest of the chromosome it is about half that in diploids. Other unpublished results (REDFIELD) give differences in the same direction and even more extreme for the ends of the chromosome and with a regular gradation from one end to the other.

But from a preliminary note published by PAINTER (1931) it would appear that these relations do not agree with his cytological map. Until this cytological question is definitely settled for the X, it is perhaps best not to discuss the matter further.

CONCLUSIONS

(1) For central regions of the second chromosome of *Drosophila melanogaster* triploid crossing over is greater than diploid crossing over (T/D is about 1.4); for the regions to the right and to the left of the center it it much less than diploid crossing over (T/D is about 0.6); and for regions at either end of the chromosome triploid crossing over again increases relative to diploid crossing over but does not become equal to it.

(2) The total crossing over from aristaless to speck is about 13 units less in the triploid than in the diploid.

(3) Triploid crossing over tends to increase relative to diploid crossing over in regions which are longer cytologically than the chromosome map indicates and tends to decrease relative to diploid crossing over in regions which are shorter cytologically than the chromosome map indicates. This conclusion is based upon a comparison of the present results with the cytological map of DOBZHANSKY for chromosome II. It is not implied that triploid crossover values are directly proportional to distances on the cytological maps.

(4) Triploid females containing a single dose of a given mutant gene produce occasional equational exceptions which have two maternal representatives of this mutant gene. The percentage of equational exceptions shows a regular gradation from the low value for genes at the center of chromosome II to the relatively high value for genes at either end. In no case does this percentage approach that expected on the basis of random assortment.

(5) These equational exceptions provide new and independent evidence that the spindle-fibre attachment is at the center of chromosome II slightly to the right of purple. This is in agreement with DOBZHANSKY'S previous evidence from a study of translocations.

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