TRANSLOCATIONS INVOLVING THE SECOND AND THE FOURTH CHROMOSOMES OF *DROSOPHILA MELANOGASTER*

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TABLE OF CONTENTS

THE PROBLEM

Five translocations involving the third and the fourth chromosomes have been described in previous papers (DOBZHANSKY 1929a, 1930a). In each of these translocations, a section of the third chromosome was found to be broken and reattached to the fourth chromosome. The lengths of the broken off sections of the third chromosome were determined by cytological observations and were found to be different in each of the translocations. The lengths of the same sections were determined also by genetic methods and expressed in units of the map-distance. A cytological map of the third chromosome was constructed. The cytological map indicates the location of the observed points of breakage as seen in the chromosome under the microscope. The comparison of the cytological map with the regular genetic map of the same chromosome revealed two facts. First, the linear order of the genes is the same in both maps, and, second, the relative distances between the genes on the cytological map are in some cases much longer, and in other cases much shorter than suggested by the genetic map. The genes located in the middle region of the third chromsome are represented by the genetic map as lying too close to each other, while the relative distances between the genes lying in the ends of the chromosome are exaggerated by the genetic map. This discrepancy is apparently due to the lower frequency of crossing over per unit of the absolute distance at the middle of the length of the chromosome, as compared with its frequency at the ends of the chromosome.

The main purpose of the present work was to secure data for the construction of a cytological map of the second chromosome of *Drosophila melanogaster*. Furthermore, the phenomenon of translocation presents unique opportunities for the study of the mechanism of conjugation, crossing over, and reduction of chromosomes. Accumulation of data bearing on these questions is very desirable. Attention is, therefore, paid also to this side of the problem.

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ORIGIN OF THE TRANSLOCATIONS

The first translocation described in the literature (BRIDGES 1923), and certain translocations found since then (STERN 1926, STURTEVANT and DOBZHANSKY 1930), appeared spontaneously. More recently it was discovered by MULLER (1928) that the frequency of translocations rises very considerably in the progeny of flies treated by X-rays. The discovery of MULLER has made it practicable to attempt to get at will translocations involving any two of the chromosomes.

Since the basic object of the present work was to secure information concerning the cytological map of the second chromosome of Drosophila, the experiment was planned primarily for obtaining translocations involving the second and the fourth chromosomes. For the purpose just stated such translocations are superior to those involving the second and any other chromosome. An attachment of even a very small section of the second chromosome to the very small fourth chromosome may be expected to produce cytologically visible changes in the length of the fourth chromosome. The addition of a section of the same size to any of the other chromosomes, which are much longer than the fourth, may be cytologically invisible.

The usual method of finding translocations is based on the appearance of an apparent linkage of genes located in chromosomes involved in translocations (this method is described in detail by MULLER and ALTENBURG 1930, and DOBZHANSKY 1930a). Young wild-type males (from the "Oregon" stock) were treated by X-rays. The dosage was as follows: 50 kv peak, 5 ma, duration 60 minutes, distance 16 cm from the anticathode, 1 mm aluminum filter. Irradiated males were crossed in individual cultures to untreated females having the constitution $\frac{e_y}{e_y} \cdot \frac{C_y\ p_r}{a_l\ d_p\ b\ p_r\ c\ p_x\ s_p}$[1]. In the

[1] These females are homozygous for the fourth-chromosome gene eyeless (e_y). One of their

F_1 generation wild-type males were selected, and backcrossed in individual cultures to $\frac{e_y}{e_y}\ \frac{C_y\ p_r}{a_l\ d_p\ b\ p_r\ c\ p_x\ s_p}$ females. These wild-type males, according to their pedigree, have the constitution $\frac{e_y}{+}\ \frac{a_l\ d_p\ b\ p_r\ c\ p_x\ s_p,}{+}$ that is, they received an untreated fourth chromosome carrying e_y, and an untreated second chromosome carrying $a_l\ d_p\ b\ p_r\ c\ p_x\ s_p$ from their mothers, and a treated fourth chromosome and a treated second chromosome carrying the wild-type allelomorphs of the genes just mentioned from their fathers.

In an experiment arranged in the fashion just described it is possible to discover only those translocations which involve the treated second, fourth, and Y-chromosomes. If no translocations involving these chromo-

TABLE 1

Cultures showing linkage of genes located in different chromosomes.

Progeny of the cross $\frac{+}{e_y}\ \frac{+\ +\ +\ +\ +\ +\ +\ +\ +}{a_l\ d_p\ b\ p_r\ c\ p_x\ s_p}$ ♂ × $\frac{e_y}{e_y}\ \frac{+\ +\ C_y\ +\ p_r\ +\ +\ +}{a_l\ d_p\ +\ b\ p_r\ c\ p_x\ s_p}$ ♀

CULTURE NUMBER	TRANSLOCATION	WILD-TYPE		e_y		$a_l\ d_p\ b\ p_r\ c\ p_x\ s_p$		$a_l\ d_p\ b\ p_r\ c\ p_x\ s_p\ e_y$		C_y		$C_y\ e_y$		$C_y\ p_r$		$C_y\ p_r\ e_y$		MINUTE p_r		$a_l\ d_p\ b\ c\ p_x\ s_p$	
		♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
6575	a	4	4	..	..	..	..	2	4	7	5	..	..	..	..	6	5	..	..	..	..
7781	b	13	9	..	..	..	..	4	2	18	14	..	..	..	..	15	8	..	..	..	..
7718	c	11	17	..	..	..	..	8	6	8	11	..	..	..	..	18	5	..	..	..	..
7691	d	12	9	..	..	..	..	4	3	7	12	..	..	..	..	16	5	..	..	..	..
6304	A	..	9	..	9	4	..	3	..	..	9	..	9	11	..	7	..	..	..	..	..
6370	B	..	6	..	4	6	..	5	..	..	7	..	2	4	..	1	..	..	..	..	..
7617	C	..	26	..	33	14	..	21	..	..	22	..	32	27	..	26	..	..	..	..	..
7573	D	..	22	..	16	7	..	13	..	..	11	..	17	14	..	11	..	..	..	..	..
7628	E	..	15	..	19	13	..	9	..	..	19	..	16	12	..	15	..	..	..	..	..
7681	F	..	16	..	11	9	..	7	..	..	25	..	12	17	..	13	..	..	..	..	..
7831	G	..	10	..	8	8	..	4	..	..	15	..	21	16	..	11	..	..	..	..	5
7810	H	..	9	..	8	6	..	6	..	..	29	..	20	8	..	11	..	2	..	..	13
7832	I	..	4	..	5	2	..	1	..	..	9	..	10	9	..	6	..	..	..	..	..
7748	J	..	29	..	27	19	..	11	..	..	22	..	16	23	..	23	..	..	..	..	..

second chromosomes carries the dominant gene Curly (C_y), the recessive purple (p_r), and the inverted sections $C_{II\ L}$ and $C_{II\ R}$ (not shown in the above given formula) which prevent most crossing over in the second chromosome. The other second chromosome carries the recessive genes aristaless (a_l), dumpy (d_p), black (b), purple (p_r), curved (c), plexus (p_x) and speck (s_p).

I am greatly obliged to Doctor H. J. MULLER who kindly placed this stock at my disposal.

somes occur, sixteen classes of offspring are expected in the next generation (the first sixteen classes shown in table 1). If a translocation involving the second and the fourth chromosomes takes place, only eight classes of offspring appear, since the other eight classes, representing the recombinations of the second- and the fourth-chromosome characters, must be either inviable or possess visible external abnormalities. Likewise, if a translocation involving the second and the Y-chromosome occurs (that is, if a section of the second chromosome becomes attached to the Y-chromosome), eight classes of offspring representing the recombinations of sex and the second-chromosome characters may be expected to be missing or visibly abnormal.

Out of 551 cultures, 412 cultures gave the normal result (that is, free recombination of sex, the second- and the fourth-chromosome characters), 125 cultures were sterile, 4 cultures (numbers 6575, 7781, 7718, 7691, see table 1) gave no recombination of the fourth-chromosome and the second chromosome characters, and 10 cultures (the rest of the cultures shown in table 1) gave no recombination of sex and the second-chromosome characters.

Wild-type males from each of the four cultures, which gave no recombination of e_y and the second-chromosome characters, were crossed separately to $\frac{e_y}{e_y} \frac{C_y \; p_r}{a_l \; d_p \; b \; p_r \; c \; p_z \; s_p}$ females. The apparent linkage of the fourth-chromosome and the second-chromosome characters persisted in the next generation, confirming the presence of translocations involving chromosomes II and IV. By repeating this mating in each generation, four lines were established, which were designated as translocation II-IVa, II-IVb, II-IVc, and II-IVd respectively (see table 1).

Wild-type males from each of the ten cultures which gave no recombination of sex and the second-chromosome characters were crossed to homozygous $a_l \; b \; c \; s_p$ females. Mostly wild-type males and $a_l \; b \; c \; s_p$ females were produced. Translocations involving chromosomes II and Y are, therefore, present in these cultures. By mating wild-type males to $a_l \; b \; c \; s_p$ females in each generation, ten separate strains were established, which were designated as translocation II—Y A, B, C, D, E, F, G, H, I, J respectively (see table 1).

The present paper gives an account of the results of the investigation of the translocations involving chromosomes II and IV. Those involving chromosomes II and Y have been briefly described (DOBZHANSKY 1930b) and will be described in more detail later.

LOCI AT WHICH THE SECOND CHROMOSOME IS BROKEN IN TRANSLOCATIONS

The apparent linkage of genes located in the second and in the fourth chromosomes may be explained on four different assumptions. First, both chromosomes involved in a translocation may fuse together to form one compound chromosome. Second, a section of the second chromosome may become broken off, and reattached to the fourth chromosome. Third, a section of the fourth chromosome may be broken off, and attached to the second chromosome. Fourth, both the second and the fourth chromosomes may be broken each into two fragments, and the four resulting fragments may reunite in a new way, to form two "new" chromosomes. If the first assumption is true, the genes of the second and of the fourth linkage groups lie in the same chromosome, and the linkage observed in translocations is a real linkage. If the second, the third, or the fourth assumption is true, we are dealing with an apparent linkage; for in these cases gametes carrying recombinations of the genes belonging to the second and to the fourth linkage groups may be formed, but these gametes must carry either a duplication or a deficiency for a section of one of the chromosomes involved in the translocation, and may, therefore, give rise to inviable zygotes.

The first assumption may be considered very improbable. The fusion of the second and the fourth chromosomes would result in the formation of a chromosome having two spindle-fibre attachments (each of the chromosomes fused contributing one attachment). No translocations leading to formation of chromosomes having none or more than one spindle-fibre attachment are described in the literature, and one may suppose that, at least in Drosophila, such chromosomes are unable to behave normally at mitosis, and are, therefore, eliminated.

The third assumption is also improbable. If a section of the fourth chromosome is attached to the second chromosome, some gametes carrying a duplication or a deficiency for this section must be formed in flies carrying translocations. Since individuals having a deficiency or a duplication for the whole fourth chromosome are known to be viable and distinct in appearance from normal flies (BRIDGES 1921), one may suppose that gametes carrying a duplication or a deficiency for a part of the fourth chromosome will give rise to viable zygotes. Hence, some recombination of the second- and the fourth-chromosome characters would appear in the progeny of such translocations. No such recombination-classes are, however, found. This evidence is, of course, not entirely conclusive, because hypo- or hyperploidy for a section of a chromosome may in some cases be more del-

eterious than hypo- or hyperploidy for the whole of this chromosome (intrachromosomal unbalance, MULLER 1930a).

There remain, therefore, the second and the fourth assumptions, the former being apparently more probable than the latter since a breakage of the fourth chromosome has never been demonstrated.

The locus of attachment of the fourth chromosome to the second (which is also the locus at which the second chromosome was broken) may be determined by a linkage experiment. Indeed, if a female fly carrying a translocation is heterozygous for a second-chromosome gene *a*, and for a fourth-chromosome gene *b*, the frequency of recombination of *a* and *b* indicates the distance between *a* and the locus of breakage. (For a more detailed discussion of this method of determination of the locus of breakage see DOBZHANSKY 1930a).

Wild-type males from each of the cultures in which II-IV translocations were found (see table 1) were crossed to homozygous $e_y\ a_l\ d_p\ b\text{-}p_r\ c\ p_x\ s_p$ females. In F_1 wild-type females were selected and backcrossed to $e_y\ a_l\ d_p\ b\ p_r\ c\ p_x\ s_p$ males. These wild-type females have the constitution $\frac{+\ \ +^{e_y}}{e_y\ \ a_l\ d_p\ b\ p_r\ c\ \ p_x\ s_p}$, that is, they are heterozygous for the translocation and for the recessive genes indicated (the second chromosome involved in the translocation is represented by a broken line). The results of this backcross are presented in tables 5–8 (see Appendix). The calculated crossing-over values for each of the four translocations studied are presented in table 2.

As shown in table 2, in each of the four translocations the fourth-chromosome gene e_y seems to occupy a different locus among the second-chromosome genes. That is to say, in each of the translocations the second chromosome has been broken at a different locus. In b-translocation the breakage took place in the a_l-d_p interval, in c-translocation in the d_p-b interval, in a-translocation in the p_r-c interval, and in d-translocation in the $c-p_x$ interval. The position of these genes, as well as of the breakage points, on the genetic map of the second chromosome is shown in diagram 2.

An examination of table 2 shows, furthermore, that the frequency of crossing over in the same interval may be very different in different translocations. In order to get a standard of comparison for the crossing-over values observed in the translocations, a control experiment was undertaken. Wild-type "Oregon" males were crossed to $e_y\ a_l\ d_p\ b\ p_r\ c\ p_x\ s_p$ females, and wild-type females which appeared in F_1 were backcrossed to $e_y\ a_l\ d_p\ b\ p_r\ c\ p_x\ s_p$ males. Two thousand one hundred ten flies were ob-

tained in the next generation; the crossing-over values observed in these counts are presented in table 2.

TABLE 2

Crossing-over values for the intervals studied in the second chromosome.

			Translocation a				
Interval	a_l–d_p	d_p–b	b–p_r	p_r–e_y	e_y–c	c–p_x	p_x–s_p
Value	10.6	30.75	8.6	1.75	0.1	4.8	3.75
			Translocation b				
Interval	a_l–e_y	e_y–d_p	d_p–b	b–p_r	p_r–c	c–p_x	p_x–s_p
Value	0.2	0.06	0.8	0.5	19.4	26.6	8.4
			Translocation c				
Interval	a_l–d_p	d_p–e_y	e_y–b	b–p_r	p_r–c	c–p_x	p_x–s_p
Value	0.3	0.1	9.5	6.1	26.4	30.3	6.9
			Translocation d				
Interval	a_l–d_p	d_p–b	b–p_r	p_r–c	c–e_y	e_y–p_x	p_x–s_p
Value	13.7	32.5	9.2	13.7	9.3	0.7	2.6
			Control experiment				
Interval	a_l–d_p	d_p–b	b–p_r	p_r–c	c–p_x	p_x–s_p	
Value	13.6	31.0	8.5	21.3	23.8	7.1	

In a- and in d-translocation the frequency of crossing over is strongly reduced in all intervals lying to the right of the gene p_r (see table 3), and is normal, or even slightly increased, in all intervals lying to the left of p_r. In

TABLE 3

Differences between the crossing-over values observed in the translocations and those observed in the control experiment.

INTERVAL	TRANSLOCATION				LIMB OF THE CHROMOSOME
	a	b	c	d	
a_l–d_p	−3.0	−13.3	−13.3	+0.1	
d_p–b	−0.2	−30.2	−21.4	+1.5	Left
b–p_r	+0.1	−8.0	−2.4	+0.7	
p_r–c	−19.5	−1.9	+5.1	−7.6	
c–p_x	−19.0	+2.8	+6.5	−13.8	Right
p_x–s_p	−3.3	+1.3	−0.2	−4.5	

b- and in c-translocation crossing over is scarce to the left of p_r, but it is normal to the right of p_r. It is known, however, that in a- and in d-translocation the second chromosome is broken to the right of p_r, and in b- and

in c-translocations the breakage occured to the left of p_r. That is to say, the reduction of the frequency of crossing over to the right or to the left of the p_r-locus is a function of the location of the breakage-point in respect to this gene. The strongest relative reduction of crossing over takes place in or at the interval in which the breakage-point lies (in the p_r-c interval in a-translocation, in the c-p_x interval in d-translocation). However in all four cases studied, the reduction of crossing over extends to the locus of p_r, but not beyond that locus. One may suppose that some point lying at or close to the p_r-locus is responsible for this phenomenon.

The behavior of the translocations under discussion is quite parallel to that of the III-IV translocations (DOBZHANSKY 1929a, 1930a). It has been shown there that crossing over is reduced in the whole limb of the V-shaped third chromosome in which the locus of breakage lies, but remains normal in the opposite limb. The point dividing the two limbs is the locus of the spindle-fibre attachment. One may suppose by analogy that the locus of p_r, dividing the second chromosome into two genetical "limbs" of approximately equal length (see diagram 2), lies at or close to the spindle-fibre attachment. This supposition is substantiated by independent evidence from several sources. BRIDGES and MORGAN (1923), studying the distribution of the double crossovers in the second chromosome, came to the conclusion that the attachment of the spindle fibre is located in the region of the genes black or purple. STURTEVANT (in press) came to the same conclusion on the basis of the study of the effects of the inverted sections of the second chromosome. STURTEVANT and DOBZHANSKY (1930, in press) found that the spindle fibre is probably attached at a point lying about 0.2 of a map-unit to the right of the gene Bristle (which is located 0.2 of a map-unit to the right of p_r). Finally, this was demonstrated genetically and cytologically on the basis of the study of II-Y translocations (a preliminary account, DOBZHANSKY 1930b). One may conclude that the genes p_r and B_1 are located in the chromosome close to the attachment of the spindle fibre.

The results of the study of crossing over in the second chromosome of the translocations (tables 2, 5–8) show that in all four cases studied the broken-off fragment of the second chromosome is attached to the fourth chromosome by its broken end, and not by its free end. The following reasoning shows how this conclusion is arrived at. Suppose the chromosome *abcdefgh*, having the spindle fibre attached at *h*, is broken between the loci of the genes *c* and *d*. The fragment *abc* is attached to another chromosome (symbolized by *M*, and, of course, having its own spindle fibre) by

its free end (the *a* end). An individual heterozygous for this translocation must be represented thus:

$$\frac{\overline{M}}{\overline{M}} \quad \frac{\underline{M\ a\ b\ c} \quad \underline{d\ e\ f\ g\ h}}{a'\ b'\ c'\ d'\ e'\ f'\ g'\ h'}$$

Simple crossing over between the fragment *abc* and the normal chromosome *a' b' c' d' e' f' g' h'* leads to formation of chromosomes having two spindle fibres (chromosome *M a b c' d' e' f' g' h'*) and having no spindle fibre (chromosome a' *b' c*). Such chromosomes presumably are inviable, and, therefore, no simple crossing over between the fragment *abc* and the normal chromosome can be recovered. If, however, the fragment *abc* is attached by its broken end, so that an *abcM* chromosome is formed, simple crossing over between the fragment and the normal chromosome gives gametes which must produce viable zygotes. As shown in tables 5–8, simple crossing over occurs between the breakage point and both ends of the second chromosome in all translocations.

HOMOZYGOUS TRANSLOCATIONS

The above description dealt with the behavior of translocations in heterozygous form. Individuals heterozygous for the translocations must have, and, as will be shown below, do have, one normal second chromosome, one normal free fourth chromosome, and one second chromosome broken into two fragments, the shorter of which is attached to the other fourth chromosome. Individuals homozygous for the translocations must have no normal second or fourth chromosomes, but must have two pairs of "new" chromosomes. One of the "new" ones represents a fragment of the chromosome II attached to IV, and the other represents the remaining fragment of II retaining its spindle fibre.

As shown by MULLER and ALTENBURG (1930) and by DOBZHANSKY (1929b, 1930a), most of the translocations are, for some not yet exactly known reason, lethal when homozygous, or individuals homozygous for translocations are abnormal in appearance, sterile, and have low viability. Individuals heterozygous for translocations are in most cases quite normal in appearance and fully viable.

Flies were obtained which were heterozygous for the a-, b-, c,- and d-translocations respectively, and which carried in their normal (unbroken) second chromosome the dominant genes Curly and Lobe (*L*), and the crossover suppressors $C_{\text{II L}}$ and $C_{\text{II R}}$. Such flies, heterozygous for the same translocation, were mated to each other. Any wild-type individual appearing in the next generation must be homozygous for the respective

translocation. In case the homozygous translocation is fully viable, a ratio 2 C_y L:1 wild-type must be expected.

It was shown by this method that a-translocation apparently is always lethal when homozygous. In c- and in d-translocation homozygous individuals appear very rarely (less than 3 percent of the expected frequency). They are very weak, their wings usually do not unfold (in c-translocation) or are filled with liquid (in d-translocation), and they die soon after emergence. Both sexes presumably are completely sterile, although it is difficult to ascertain this point since they usually die before they mate. Only b-translocation is viable when homozygous, normal in appearance, and fully fertile in both sexes. It is, however, less vigorous than wild-type flies, since instead of the expected ratio 2 C_y L:1 wild-type a ratio approaching 3:1 is obtained.

The death of the individuals homozygous for c- and, especially, d-translocation takes place mostly in later stages of development. This is shown by the fact that the cytological study of the fully grown larvae from the mating translocation×translocation revealed the presence of many individuals homozygous for the translocations (see below).

NON-DISJUNCTION OF THE SECTIONS OF THE SECOND CHROMOSOME

A convincing proof of the presence of breakage in the second chromosome in translocations is provided by the phenomenon of non-disjunction of sections of this chromosome.

Individuals were obtained (see table 8) which were heterozygous for d-translocation, and which carried the genes p_x and s_p in the fragment of the second chromosome attached to the fourth, and the genes a_l and d_p in the other fragment of the second chromosome remaining free. The constitution of these individuals is represented in the upper part of diagram 1. At gametogenesis such individuals may produce six kinds of gametes, shown in diagram 1. At the reduction division, both fragments of the second chromosome involved in the translocation may pass to the same pole, the normal second chromosome going to the opposite pole. Gametes 1 and 2 (diagram 1) are formed in this way. Either fragment of the second chromosome may pass, however, to the same pole of the spindle together with the normal second chromosome. Gametes 3 to 6 are formed in this case.

If an individual of the constitution represented in diagram 1 is crossed to flies free from translocations, only gametes 1 and 2 give rise to viable zygotes. Gametes 4 and 6 produce zygotes carrying a duplication for a section of the second chromosome, while gametes 3 and 5 give rise to zy-

gotes deficient for a section of the same chromosome. Individuals possessing a deficiency or a duplication for a section of a chromosome are usually abnormal in appearance, and may be identified. No such individuals were, however, found in the progeny of d-translocation crossed to wild-type flies. Hence, these gametes either are not produced at all, or else give rise to inviable zygotes.

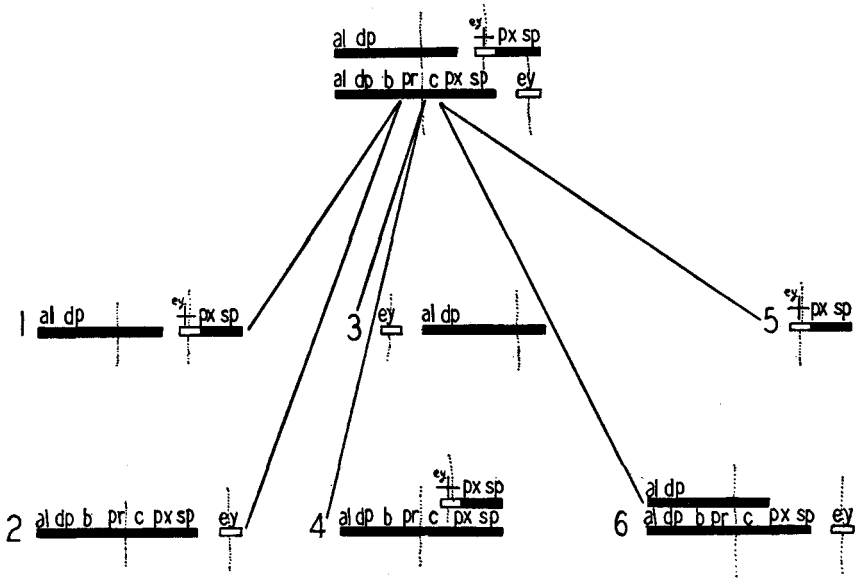

DIAGRAM 1.—Six kinds of gametes which may be produced in a fly heterozygous for d-translocation. Second chromosome—black, fourth chromosome white. Spindle fibres are indicated by dotted lines. 1 and 2—regular gametes, 3–6 non-disjunctional gametes. 3 and 5 gametes carrying a deficiency for a section of the second chromosome, 4 and 6—gametes carrying a duplication for a section of the second chromosome.

This alternative may be decided by mating two individuals heterozygous for the same translocation to each other. Each parent in this case may be supposed to produce the six kinds of gametes shown in diagram 1. If gamete 3 from one parent meets gamete 4 from the other parent, a viable zygote is produced, since these gametes are complementary to each other (deficiency is neutralized by the corresponding duplication). A viable zygote is also produced if gamete 5 meets gamete 6. As shown in table 4 the results of mating two individuals heterozygous for the translocation and having the constitution

$$\frac{a_l\ d_p}{a_l\ d_p\ b\ p_r\ c\ p_x\ s_p}\ \frac{+^{e_y}\ p_x\ s_p}{e_y} \times \frac{}{C_y\ p_r}\ \frac{+^{e_y}}{e_y}$$

must be the following: 1 wild-type: 3 C_y: 1 $C_y\ p_r\ e_y$: 1 $p_x\ s_p$: 1 $a_l\ e_y$ (pro-

vided all six kinds of gametes are produced in equal number). If the fragment of the second chromosome retaining its own spindle fibre (the $a_l\ d_p$

TABLE 4

Mating	(1) $a_l\ d_p$ / $+^{e_y}\ p_x\ s_p$	(2) e_y / $a_l\ d_p\ b\ p_r\ c\ p_x\ s_p$	(3) e_y / e_y	(4) $a_l\ d_p\ b\ p_r\ c\ p_x\ s_p$ / $+^{e_y}\ p_x\ s_p$	(5) $+^{e_y}\ p_x\ s_p$ / $C_y\ p_r$	(6) e_y / $a_l\ d_p$ / $a_l\ d_p\ b\ p_r\ c\ p_x\ s_p$
(1) $+^{e_y}$	Homozygous translocation (1)	Wild-type (2)	dies (3)	dies (4)	dies (5)	dies (6)
(2) $C_y\ p_r$ / e_y	C_y (7)	$C_y\ p_r\ e_y$ (8)	dies (9)	dies (10)	dies (11)	dies (12)
(3) e_y / —	dies (13)	dies (14)	dies (15)	$p_x\ s_p$ (16)	dies (17)	dies (18)
(4) $+^{e_y}$ / $C_y\ p_r$	dies (19)	dies (20)	C_y (21)	dies (22)	dies (23)	dies (24)
(5) $+^{e_y}$	dies (25)	dies (26)	dies (27)	dies (28)	dies (29)	$a_l\ d_p$ (30)
(6) / $C_y\ p_r$ / e_y	dies (31)	dies (32)	dies (33)	dies (34)	C_y (35)	dies (36)

fragment, diagram 1) always passes to the opposite pole from the normal second chromosome at the reduction division, no gametes 5 and 6 will be produced. In this case the expected ratio is L wild-type:2 C_y:1 $C_y\ p_r\ e_y$:1

$p_x\ s_p$. If no non-disjunction takes place the expected ratio is 1 wild-type: 1 C_y:1 $C_y\ p_r\ e_y$ (compare table 4). The results obtained in the experiment are:

	Wild-type	C_y	$C_y\ p_r\ e_y$	$p_x\ s_p$	$a_l\ d_p$	Homozygous translocation
Observed	225	459	182	236	..	3
Expected (*1:2:1:1*)	*220.4*	*440.8*	*220.4*	*220.4*	..	..

It may be concluded that in d-translocation gametes 1, 2, 3 and 4 are formed in approximately equal numbers, and gametes 5 and 6 are very seldom if ever formed. That is to say, the fragment of the second chromosome attached to the fourth is distributed at random with respect to the normal second chromosome at the reduction division. The deviation from the expected ratio is due, probably, to the lower viability of the e_y-carrying class.

Similar experiments were performed also for a-, b- and c-translocation. Individuals heterozygous for a-translocation and having the constitution:

$$\frac{a_l\ d_p \quad +^{e_y}}{a_l\ d_p\ b\ p_r\ c\ p_x\ s_p} \quad \frac{\quad}{e_y} \times \frac{\quad +^{e_y}}{C_y\ p_r} \quad \frac{\quad}{e_y}$$

were mated together. The expected ratios in this case are (compare table 4) 2 wild-type:3C_y:1 $C_y\ p_r\ e_y$:1 $a_l\ d_p$ (in case all six kinds of gametes are produced), or 2 wild-type:2 C_y:1 $C_y\ p_r\ e_y$ (in case gametes 5 and 6 are not produced), or 1 wild-type:1C_y:1 $C_y\ p_r\ e_y$ (in case no non-disjunction takes place). The results obtained are:

	Wild-type	C_y	$C_y\ p_r\ e_y$	$a_l\ d_p$
Observed	891	863	375	..
Expected (*2:2:1*)	*851.6*	*851.6*	*425.8*	..

One may conclude that in a-translocation the fragment of the second chromosome attached to the fourth is independent of the normal second chromosome at the reduction division, but no non-disjunction of the fragment of the second chromosome retaining its own spindle fibre takes place.

Individuals heterozygous for c-translocation and having the constitution

$$\frac{+^{e_y} \quad b\ p_r\ c\ p_x\ s_p}{a_l\ d_p\ b\ p_r\ c\ p_x\ s_p} \quad \frac{\quad}{e_y} \times \frac{+^{e_y}}{} \quad \frac{\quad}{e_y}$$

were crossed to each other. Here the expected ratio is 5 wild-type:1e_y:1 *b*-

$p_r\ c\ p_x\ s_p$ (in case all six kinds of gametes are formed), or 4 wild-type:1 e_y (in case the fragment of the second chromosome retaining its own spindle fibre undergoes no non-disjunction), or 2 wild-type:1 e_y (if no non-disjunction takes place). The observed ratio is:

	Wild-type-	e_y	$b\ p_r\ c\ p_x\ s_p$	Homozygous translocation
Observed	975	224	..	5
Expected (*4:1*)	*959.2*	*239.8*	..	..

It follows that in c-translocation the fragment of the second chromosome attached to the fourth is independent of the normal second chromosome at the reduction division, but the fragment of the second chromosome retaining its spindle fibre does not undergo non-disjunction.

In b-translocation, individuals carrying a duplication for a section of the second chromosome survive under certain conditions. If a male heterozygous for b-translocation and heterozygous for $e_y\ a_l\ d_p\ b\ p_r\ c\ p_x\ s_p$ is crossed to $e_y\ a_l\ d_p\ b\ p_r\ c\ p_x\ s_p$ females (free from translocation) only wild-type and $e_y\ a_l\ d_p\ b\ p_r\ c\ p_x\ s_p$ offspring are produced. Here individuals carrying the duplication do not survive, presumably because of the decrease of viability produced by the second-chromosome recessive genes just indicated. If, however, the same males are crossed to $a_l b\ s_p$ females (free from translocations), some individuals carrying a duplication survive. In a cross of the nature just indicated there were obtained:

Wild-type	$a_l\ b\ s_p$	$b\ s_p$ (duplication)
768	713	315

The $b\ s_p$ individuals are, evidently, carrying a duplication for a section of the second chromosome including the gene aristaless (they have two doses of a_l, but the manifestation of a_l is nearly completely suppressed by its normal allelomorph). These individuals are different in appearance from normal flies. They have short and plump bodies, the dorsal surface of the abdomen is flattened, the eyes are strongly convex, the wings are expanded and curved (sometimes resembling the mutation curved), the scutellar bristles are often erect (this character is, probably, due to incomplete suppression of a_l), their development is slow, they have low viability, and are sterile in both sexes. As shown above, in b-translocation the second chromosome is broken between the genes a_l and d_p, and the fragment carrying a_l is attached to the fourth chromosome. The $b\ s_p$ individuals just described carry, therefore, a duplication for a section of the second chromosome in-

cluding a_l, but not including d_p or any other second-chromosome gene located to the right of d_p.

Individuals heterozygous for b-translocation and having the constitution

$$\frac{+^{e_y} \quad c\ p_x\ s_p}{a_l\ d_p\ b\ p_r\ c\ p_x\ s_p} \quad \frac{}{e_y} \times \frac{+^{e_y}}{C_y\ p_r} \quad \frac{}{e_y}$$

were mated together. This cross may give the following results. The ratio 3 wild-type:3 C_y:1 $C_y\ p_r\ e_y$:1 $c\ p_x\ s_p$ must be produced if both fragments of the second chromosome involved in the translocation are distributed at random (it has to be taken into account that in b-translocation the individuals homozygous for the translocation survive, compare table 4). If only the fragment of the second chromosome attached to the fourth undergoes non-disjunction, a ratio 3 wild-type:2 C_y:1 $C_y\ p_r\ e_y$ is expected. If no non-disjunction takes place the ratio 2 wild-type:1 C_y:1 $C_y\ p_r\ e_y$ is expected. The results of the experiment are:

	Wild-type	C_y	$C_y\ p_r\ e_y$	$c\ p_x\ s_p$	Duplication
Observed	976	761	448	..	83
Expected (3:2:1)	*1092*	*729*	*364*	..	..

The agreement of the observed results with the expectation here is less close than was obtained in other translocations. This may be due, first, to the lower viability of the homozygous translocation as compared with heterozygous (this produces a decrease of the wild-type class), and, second, to the not quite random distribution of the fragment of the second chromosome attached to the fourth at the reduction division (this produces an increase of the $C_y\ p_r\ e_y$ class). It is certain in any case that no non-disjunction of the fragment of the second chromosome retaining its own spindle fibre takes place in b-translocation.

The data presented in this chapter show, therefore, that in all four II-IV translocations studied the section of the second chromosome retaining its own spindle fibre always goes to the opposite pole from the normal second chromosome at the reduction division. On the other hand, the section of the second chromosome attached to the fourth is distributed at random in respect to the normal second (except, possibly, in b-translocation). These results might give rise to a supposition that the disjunction of chromosomes at the reduction division is determined simply by their spindle fibres, that is, that the points of the attachment of the homologous spindle fibres always pass to the opposite poles at the reduction division.

Facts are known that disprove this supposition. In translocations in-

volving chromosomes III and IV (DOBZHANSKY 1930a), the general nature of which is very similar to that of the II-IV translocations described here, the fragment of the third chromosome attached to the fourth is not distributed at random in respect to the normal third chromosome, but passes to the opposite pole from it at the reduction division more frequently than it passes to the same pole. On the other hand, the section of the third chromosome retaining its own spindle fibre sometimes passes to the same pole with the normal third chromosome. MULLER (1930b) described a translocation involving a transfer of a rather short section of the third chromosome onto the second chromosome. As shown by MULLER, the section of the third chromosome attached to the second usually passes to the opposite pole from the normal third chromosome at the reduction division. The section of the third chromosome retaining its own spindle fibre in MULLER's case does not undergo non-disjunction.

There exist reasons for supposing that one of the factors determining the disjunction of sections of chromosomes involved in translocations is the relative lengths of these sections. The influence of the spindle fibres is a phenomenon of rather secondary importance. STURTEVANT and DOBZHANSKY (1930, also data in press) and KARPECHENKO (unpublished) have shown that in translocations in which the second and the third chromosomes have exchanged sections the length of which equals approximately one-half of the length of either chromosome, all four resulting fragments undergo non-disjunction equally frequently. The influence of the spindle fibres in these cases seems to be nil. If, however, the exchanged sections are not equal in length, the shorter sections undergo non-disjunction more frequently than the longer sections. As soon as the difference in the relative length of the exchanged sections becomes great enough, the longer sections do not undergo non-disjunction at all, and the shorter sections are distributed more or less at random in respect to their homologues.

In II-IV translocations described in this paper the sections of the second chromosome transposed onto the fourth chromosome are mostly shorter than the sections of the third chromosome involved in the III-IV translocations referred to above. This fact may, at least partly, account for the difference in behavior between the II-IV and the III-IV translocations

CYTOLOGY OF THE TRANSLOCATIONS

Two methods were applied for the study of the chromosomes in the translocations, namely the investigation of the oögonial divisions in ovaries of freshly hatched adult females, and of the cell divisions in the nerve-ganglia of larvae. For the investigation of the oögonial divisions,

ovaries of females heterozygous for the translocations were fixed successively in strong Flemming's fluid (1 hour) and in 1 percent solution of chromic acid (20–24 hours). The 5μ thick sections were stained in iron haematoxylin. For the investigation of the nerve-cell divisions males and females heterozygous for the translocations and for the gene C_v were mated together. One-half of the individuals in the progeny of this mating are heterozygous for the translocation, one-quarter may be homozygous for the translocation, and one-quarter die in early stages of development because of the lethal effect of the gene lying in the C_v chromosome. The nerve ganglia of larvae appearing in these cultures were dissected and fixed in strong Navashin's fluid. The 7μ sections were stained in gentian-violet (gentian-violet-KKI-clove oil method).

The chromosomes do not appear the same in the oögonial divisions (plate 1, figures 1–12) and in the nerve-cell divisions (plate 1, figures 13–18, plate 2 figures 19–32). The oögonial chromosomes are rather short and thick, exhibit a strong tendency toward somatic pairing, and the constrictions are usually not very strongly pronounced. The chromosomes in the nerve-cells are considerably longer and more slender than the oögonial chromosomes and lie far apart from each other, somatic pairing being as a rule rather weak. The chromosomes frequently are bent, and the different parts of the same chromosome frequently lie in different planes. The constrictions are usually strongly pronounced. Sometimes certain of the constrictions are so strong that the chromosome seems to be broken into fragments connected by a very slender thread (the second chromosome in figure 13, the X chromosome in figure 20, the third chromosome in figure 26). Because of these differences in the appearance of the chromosomes in the oögonial and the nerve-cells, oögonial divisions and nerve-cell divisions were studied in each of the translocations. The results obtained by both methods are in agreement with each other.

The chromosomes of individuals heterozygous for the translocations are shown in figures 1–19 and 21–30. All chromosomal plates contain a more or less short rod-shaped chromosome which is absent in the chromosomal plate of normal *Drosophila melanogaster*. This "new" chromosome represents, evidently, the section of the second chromosome attached to the fourth chromosome. The compound nature of this rod-shaped chromosome is in some cases marked by the presence of a constriction dividing the body of this chromosome into two parts (figures 5, 13, 15–17, 21–25, 27, 29–31). One of these parts, usually lying closer to the center of the plate than the other part, is equal in size to the free fourth chromosome present in the

Explanations of Plates 1 and 2

The drawings represent the chromosomes of flies carrying the translocations. Figures 1–12 are oögonial metaphase plates, Figures 13–32 are divisions of the neurocytes of the larval ganglia. Figures 1–15, 17–19, 21, 23–27, 29–31 contain two X chromosomes (females). Figures 16, 20, 22, 28, 32 contain one X chromosome and one Y chromosome (males). All the drawings are done at the level of the work-table, with the aid of camera lucida. The magnification is Zeiss objective 120 (1.5), and comp. oc. 30.

Plate 1

Figures 1–5, a-translocation (heterozygous), figure 6, b-translocation (heterozygous), figures 7–9, c-translocation (heterozygous), figures 10–12, d-translocation (heterozygous), figures 13–15, a-translocation (heterozygous), figures 16–18, b-translocation (heterozygous).

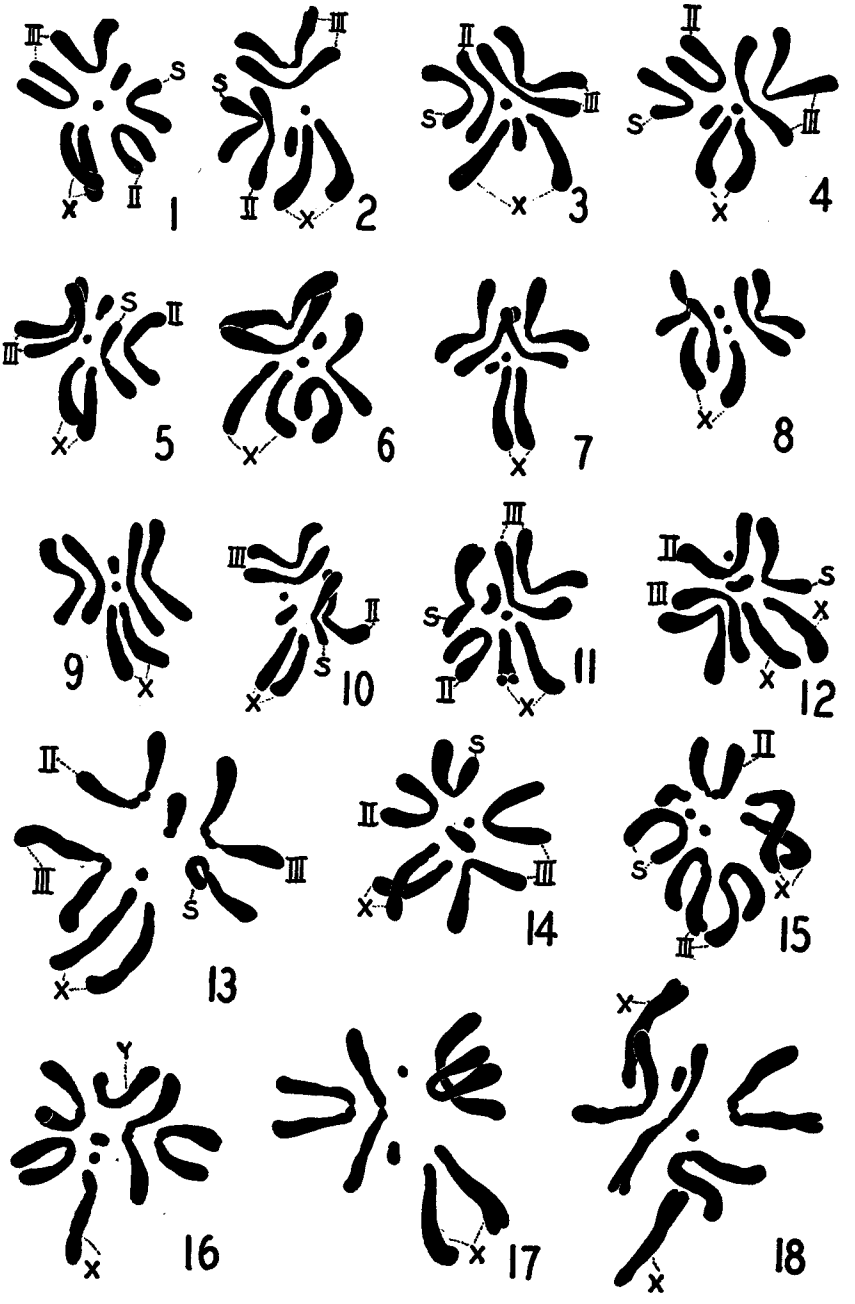
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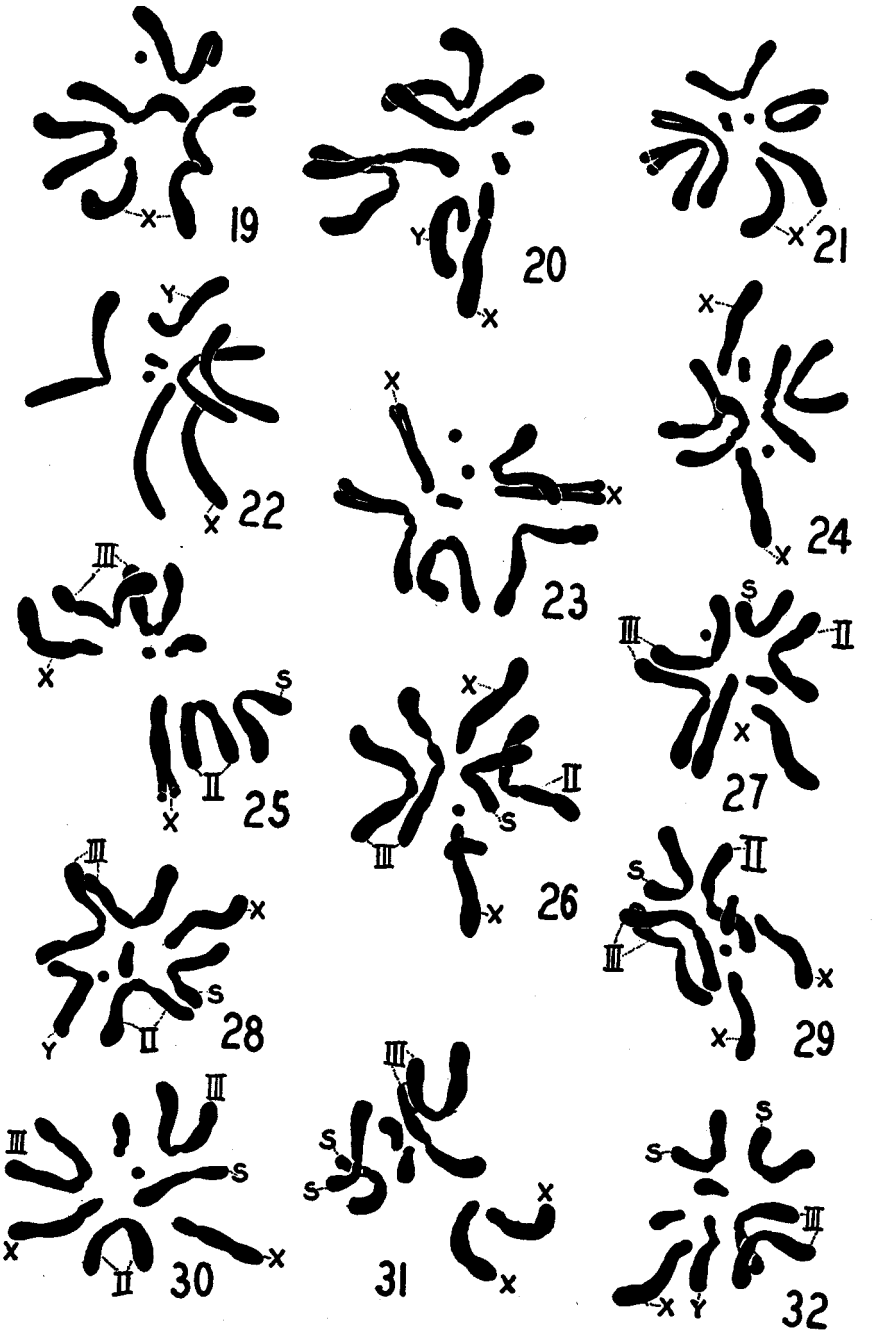
PLATE 2

FIGURE 19, b-translocation (heterozygous), figure 20, b-translocation (homozygous), figures 21–24, c-translocation (heterozygous), figures 25–30, d-translocation (heterozygous), figures 31–32, d-translocation (homozygous).

In all figures X = the X chromosome; Y = the Y chromosome; s = the second chromosome having one limb shorter than the other; II = the normal second chromosome; III = the third chromosomes. The second and the third chromosomes are marked only in those figures in which the shortening of one of the second chromosomes is clearly visible. The small round chromosomes (unmarked) are the fourth chromosomes, and the very short rod-shaped chromosomes (also unmarked) are the fourth chromosomes with a fragment of the second chromosome attached to them.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same plate. This is, probably, the fourth chromosome to which the fragment of the second chromosome is attached.

Most of the chromosomal plates studied contain only one free fourth chromosome (the small round autosome), instead of the two present in the chromosomal plates in normal flies. This is to be expected, since the other fourth chromosome is included in the "new" rod-shaped chromosome. The appearance of the few individuals possessing the "new" rod-shaped chromosome together with two free fourth chromosomes (figures 15 and 23) is due to the non-disjunction of the fourth chromosomes. This explanation was tested genetically in the III-IV translocations, which are very similar in nature to the II-IV translocations described here, and was found to be valid (DOBZHANSKY 1930a).

In a- and in d-translocation (figures 1–5, 10–15, 25–30) the pair of the shorter V-shaped autosomes consists of two partners of unequal length. One of these partners (marked in figures by the sign II) has both limbs equal in length, like the autosomes of normal flies. The other partner (marked s) has one limb shorter than the other limb. It is obvious from inspection of the figures that the difference in length between the two limbs of the unequal-armed chromosome is in most cases a little smaller than the length of the "new" rod-shaped chromosome. The unequal-armed chromosome is, evidently, the second chromosome minus a section which has been transposed onto the fourth chromosome.

In b- and in c-translocations (figures 6–9, 16–19, 21–24) no unequal-armed chromosome can be identified with certainty. This is due to the fact that the section of the second chromosome transposed onto the fourth chromosome is very short in these translocations, and its loss does not produce an appreciable shortening of the rather long second chromosome. The addition of the same section to the very small fourth chromosome is, however, visible. The longer pair of the V-shaped autosomes (III), which are the genetic third chromosomes, is normal in all plates studied in all translocations. The same holds for the two X chromosomes in females (x, figures 1–15, 17–19, 21, 23–27, 29–31), and for the X-Y pair in males (figures 16, 20, 22, 28, 32).

Individuals homozygous for translocations (figures 20, 31, 32) have two "new" rod-shaped chromosomes, and no free fourth chromosome. In homozygous d-translocation both shorter V-shaped autosomes are unequal armed (s, figures 31, 32).

The cytological evidence is, thus, in agreement with the interpretation of the genetic behavior of the translocations given in foregoing sections of this paper.

The lengths of the broken off sections of the second chromosome are both genetically and cytologically different in different translocations. In a-translocation the second chromosome is broken to the left of the locus of the gene *c* (see figure 2). The section of the second chromosome attached to the fourth contains, therefore, the genes from *c* to s_p. The length of this section equals more than 35 map-units. Since the whole right limb of the second chromosome (that is, the distance between the gene p_r and the right end of the chromosome) is about 55 map-units long, the section which is broken off in a-translocation represents in any case more than one-half of

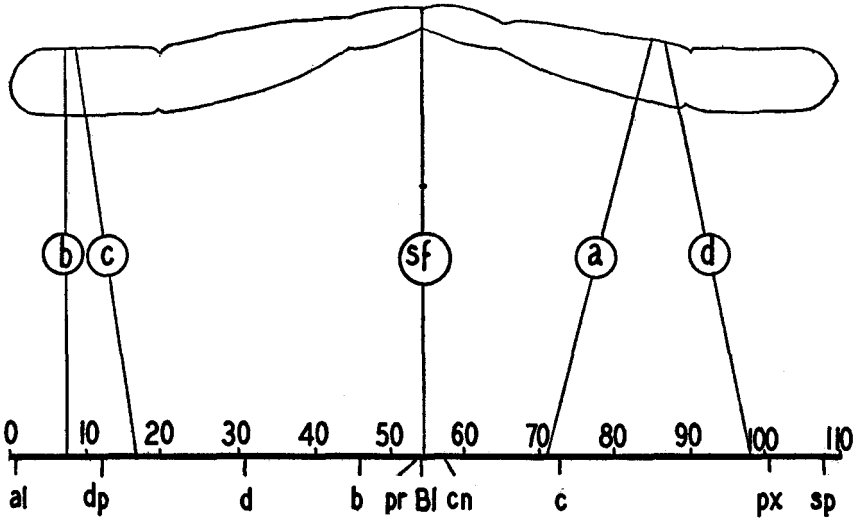

DIAGRAM 2.—The genetic and the cytological maps of the second chromosome. Letters below the line representing the genetic map of the second chromosome indicate the location of certain of the genes of the second linkage group. Letters in the circles indicate the loci of the breaks observed in translocations on the genetic and the cytological maps respectively. Sf—the spindle fibre.

the length of the limb. Cytologically, however, its length is obviously less than one-half of the length of one limb of the shorter V-shaped autosome (figures 1–5, 13–15). In d-translocation the second chromosome is broken to the left of the gene p_x. The broken-off section carries, therefore, the genes from p_x to s_p, and is much shorter than the section broken off in a-translocation. Cytologically a- and d-translocations are nearly indistinguishable, although a careful comparison shows that the rod-shaped chromosome is a little shorter in d-translocation than in a-translocation.

In both a- and d-translocation the second chromosome is broken between the subterminal constriction (which lies at about one-third of the limb-length from the end of the chromosome) and the spindle fibre, much

closer to the former than to the latter. The position of the locus of the break in respect to the subterminal constriction is very clearly visible in figure 30. The rod-shaped chromosome in this figure has two constrictions. One of these constrictions separates the fourth chromosome from the section of the second chromosome attached to it. The second constriction is probably homologous to the subterminal constriction in the normal second chromosome.

In b- and in c-translocations the second chromosome is broken to the left and to the right of the gene d_p respectively. The genetic determination of the length of the broken-off sections is very inaccurate in these translocations, due to the strong reduction of crossing over in the second chromosome. Nevertheless, one may take it for granted that in b-translocation the broken-off section is less than 13 units long, and in c-translocation its length is more than 13 but less than 30 map-units. That is to say, in c-translocation the length of the broken-off section equals at least one-fifth of the limb-length, and in b-translocation is equal to one-fifth or less than one-fifth of the limb length. Cytologically b-translocation (figures 6, 16–20) and c-translocation (figures 7–9, 21–24) are scarcely distinguishable from each other. The "new" rod-shaped chromosome in these translocations is only from twice to three times longer than the diameter of the free fourth chromosome. The length of the broken-off section of the second chromosome is, therefore, shorter than one-fifth of the length of the limb of the normal second chromosome.

A comparison of the relative genetic and cytological lengths of the sections of the second chromosomes involved in the II-IV translocations studied is presented in diagram 2. The discrepancy between the genetic and the cytological determinations of the relative lengths of these sections is so striking that the evidence derived from the study of these translocations, if taken alone, might make one doubt whether the arrangement of genes on the genetic map of the second chromosome is the same as their arrangement within the second chromosome seen under the microscope. A more complete cytological map of the second chromosome, constructed on the basis of the study of II-IV, II-Y and II-III translocations (see DOBZHANSKY 1930b), shows, however, that the sequence of genes on the genetic and the cytological maps is undoubtedly the same. The discrepancies between the genetic and the cytological maps are, as shown in the paper just referred to, due to the lower frequency of crossing over per unit of the absolute distance in the region around the spindle-fibre attachment and at the ends of the second chromosome, as compared with its frequency in the regions lying in the middle of either limb. These alternating regional dif-

ferences in the frequency of crossing over are, probably, responsible for the great genetic length of the d_p-b and c-p_x intervals which, as our data show, are very short cytologically.

A further evidence in favor of this interpretation of the discrepancies between the genetic and the cytological maps of the second chromosome was recently obtained by Doctor H. REDFIELD (unpublished). According to Doctor REDFIELD'S data the map of the second chromosome constructed on the basis of a study of crossing over in triploid females is generally intermediate between the regular genetic map and the cytological map. It has been shown by REDFIELD (1930) that the map of the third chromosome of *Drosophila melanogaster* constructed on the basis of triploid crossing over is also intermediate between the genetic map and the cytological map.

SUMMARY

1. Four translocations involving the second and the fourth chromosomes were found in the progeny of males treated by X-rays. Flies heterozygous for the translocations are normal in appearance and in viability. The translocations manifest themselves by producing an apparent linkage of genes belonging to the second and to the fourth linkage groups.

2. In each of the translocations a section of the second chromosome became broken off and reattached to the fourth chromosome. In one of the translocations the breakage took place to the left of the locus of the gene c, in the second to the left of d_p, in the third to the right of d_p, and in the fourth to the left of p_x.

3. The frequency of crossing over in translocations is strongly decreased in the limb of the second chromosome in which the breakage took place, and remains normal in the opposite limb. The point dividing the two limbs of the second chromosome, which is the point of the attachment of the spindle fibre, is located near the gene p_r.

4. One of the translocations survives in homozygous form and the homozygote is normal in appearance and fertile. Two of the translocations studied seldom survive in homozygous condition, and one never survives.

5. In individuals heterozygous for translocations the section of the second chromosome attached to the fourth chromosome is distributed independently of the normal second chromosome at the reduction division. The section of the second chromosome retaining its own spindle fibre always passes to the opposite pole from the normal second chromosome.

6. One of the translocations studied produces a viable duplication. Individuals carrying the duplication have two normal second chromosomes plus a section of the second chromosome containing the locus of the gene

a_l, but not of d_p or any other genes located to the right of d_p. Such individuals are abnormal in appearance and sterile.

7. A cytological investigation of flies heterozygous for the translocations revealed the presence in their chromosomal plates of a "new" rod-shaped chromosome. This chromosome is composed of one of the fourth chromosomes with a section of the second chromosome attached. Usually only one free fourth chromosome is present in the chromosomal plates studied, and one of the shorter V-shaped autosomes has one limb shorter than the other limb.

8. In homozygous translocations two "new" rod-shaped chromosomes, two unequal-armed V-shaped autosomes, and no free fourth chromosome are found.

9. The relative lengths of the sections of the second chromosome involved in translocations were determined both genetically and cytologically. Rather striking discrepancies between these determinations are apparent.

10. These discrepancies are, presumably, due to variations in the frequency of crossing over per unit of the absolute distance in the different regions of the second chromosome.

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APPENDIX TABLES 5–8

TABLE 5

Translocation a.

$$\frac{-}{e_y} \quad \frac{1\ 2\ 3\ 4 + {}^{e_y}\ 5\ 6\ 7}{a_l\ d_p\ b\ p_r \qquad c\ p_x\ s_p} \ \text{♀} \times e_y\ a_l\ d_p\ b\ p_r\ c\ p_x\ s_p\ \text{♂}.$$

CLASSES OF THE OFFSPRING	NUMBER OBSERVED
0 Wild-type	665
0 $a_l\ d_p\ b\ p_r\ c\ p_x\ s_p\ e_y$	267
Total non-crossovers	932
1 a_l	119
1 $d_p\ b\ p_r\ c\ p_x\ s_p\ e_y$	51
2 $a_l\ d_p$	297
2 $b\ p_r\ c\ p_x\ s_p\ e_y$	222
3 $a_l\ d_p\ b$	55
3 $p_r\ c\ p_x\ s_p\ e_y$	71
4 $a_l\ d_p\ b\ p_r$	6
4 $c\ p_x\ s_p\ e_y$	7
5 $a_l\ d_p\ b\ p_r\ e_y$	1
6 $a_l\ d_p\ b\ p_r\ c\ e_y$	33
6 $p_x\ s_p$	30
7 $a_l\ d_p\ b\ p_r\ c\ p_x\ e_y$	18
7 s_p	26
Total single crossovers	936
1, 2 d_p	6
1, 2 $a_l\ b\ p_r\ c\ p_x\ s_p\ e_y$	8
1, 3 $d_p\ b$	5
1, 3 $a_l\ p_r\ c\ p_x\ s_p$	3
1, 6 $a_l\ p_x\ s_p$	5
1, 6 $d_p\ b\ p_r\ c\ e_y$	3
1, 7 $a_l\ s_p$	8
1, 7 $d_p\ b\ p_r\ c\ p_x\ e_y$	1

CLASSES OF THE OFFSPRING	NUMBER OBSERVED
2, 3 b	17
2, 3 $a_l\ d_p\ p_r\ c\ p_x\ s_p\ e_y$	8
2, 4 $b\ p_r$	10
2, 4 $a_l\ d_p\ c\ p_x\ s_p\ e_y$	3
2, 6 $b\ p_r\ c\ e_y$	4
2, 6 $a_l\ d_p\ p_x\ s_p$	17
2, 7 $b\ p_r\ c\ p_x\ e_y$	9
2, 7 $a_l\ d_p\ s_p$	7
3, 4 p_r	5
3, 4 $a_l\ d_p\ b\ c\ p_x\ s_p\ e_y$	1
3, 7 $p_r\ c\ p_x\ e_y$	2
3, 7 $a_l\ d_p\ b\ s_p$	2
6, 7 p_x	1
Total double crossovers	125
1, 2, 3 $d_p\ p_r\ c\ p_x\ s_p\ e_y$	1
1, 2, 3 $a_l\ b$	1
1, 2, 4 $a_l\ b\ p_r$	1
2, 3, 6 $b\ p_x\ s_p$	1
2, 4, 6 $b\ p_r\ p_x\ s_p$	1
2, 4, 7 $b\ p_r\ s_p$	1
2, 5, 6 $a_l\ d_p\ c$	1
Total triple crossovers	7
Grand total	2000

TABLE 6

Translocation b.

$$\frac{-}{e_y} \quad \frac{1+^{e_y}\ 2\ \ 3\ 4\ 5\ 6\ 7}{a_1 \qquad d_p\ b\ p_r\ c\ p_x\ s_p} \ \varphi \times e_y\, a_1\, d_p\, b\, p_r\, c\, p_x\, s_p \sigma^{\prime}.$$

CLASSES OF THE OFFSPRING	NUMBER OBSERVED	CLASSES OF THE OFFSPRING	NUMBER OBSERVED
0 Wild-type	448	1, 5 $d_p\, b\, p_r\, e_y$	1
0 $a_1\, d_p\, b\, p_r\, c\, p_x\, s_p\, e_y$	272	3, 6 $b\, p_r\, c$	1
Total non-crossovers	720	3, 4 b	1
		3, 4 $a_1\, d_p\, p_r\, c\, p_x\, s_p\, e_y$	1
		4, 5 p_r	1
1 a_1	1	5, 6 c	21
1 $d_p\, b\, p_r\, c\, p_x\, s_p\, e_y$	1	5, 6 $a_1\, d_p\, b\, p_r\, p_x\, s_p\, e_y$	10
2 $a_1\ e_y$	1	5, 7 $c\, p_x$	4
3 $a_1\, d_p\, e_y$	1	5, 7 $a_1\, d_p\, b\, p_r\, s_p\, e_y$	1
3 $b\, p_r\, c\, p_x\, s_p$	9	6, 7 p_x	3
4 $a_1\, d_p\, b\, e_y$	1	6, 7 $a_1\, d_p\, b\, p_r\, c\, s_p\, e_y$	2
4 $p_r\, c\, p_x\, s_p$	2		
5 $a_1\, d_p\, b\, p_r\, e_y$	113		
5 $c\, p_x\, s_p$	143	Total double crossovers	46
6 $a_1\, d_p\, b\, p_r\, c\, e_y$	127		
6 $p_x\, s_p$	240	4, 5, 6 $a_1\, d_p\, b\, c\, e_y$	1
7 $a_1\, d_p\, b\, p_r\, c\, p_x\, e_y$	30		
7 s_p	86	Total triple crossovers	1
Total single crossovers	755	Grand total	1522

TABLE 7

Translocation c.

$$\frac{-}{e_y} \quad \frac{1\ \ 2+^{ev}3\ \ 4\ \ 5\ 6\ \ 7}{a_1\ d_p \qquad\qquad b\ p_r\ c\ p_x\ s_p} \ \text{♀} \times e_y\ a_1\ d_p\ b\ p_r\ c\ p_x\ s_p\ \text{♂}.$$

CLASSES OF THE OFFSPRING	NUMBER OBSERVED	CLASSES OF THE OFFSPRING	NUMBER OBSERVED
0 Wild-type	571	3, 5 $b\ p_r$	33
0 $a_1\ d_p\ b\ p_r\ c\ p_x\ s_p\ e_y$	228	3, 5 $a_1\ d_p\ c\ p_x\ s_p\ e_y$	6
Total non-crossovers	799	3, 6 $b\ p_r\ c$	11
		3, 6 $a_1\ d_p\ p_x\ s_p\ e_y$	12
1 a_1	3	3, 7 $a_1\ d_p\ s_p\ e_y$	1
1 $d_p\ b\ p_r\ c\ p_x\ s_p\ e_y$	1	4, 5 p_r	28
2 $a_1\ d_p$	2	4, 5 $a_1\ d_p\ b\ c\ p_x\ s_p\ e_y$	7
2 $b\ p_r\ c\ p_x\ s_p$	1	4, 6 $p_r\ c$	5
3 $a_1\ d_p\ e_y$	59	4, 6 $a_1\ d_p\ b\ p_x\ s_p\ e_y$	6
3 $b\ p_r\ c\ p_x\ s_p\ e_y$	34	5, 6 c	14
4 $a_1\ d_p\ b\ e_y$	23	5, 6 $a_1\ d_p\ b\ p_r\ p_x\ s_p$	47
4 $p_r\ c\ p_x\ s_p$	35	5, 7 $c\ p_x$	4
5 $a_1\ d_p\ b\ p_r\ e_y$	278	5, 7 $a_1\ d_p\ b\ p_r\ s_p\ e_y$	8
5 $c\ p_x\ s_p$	96	6, 7 p_x	11
6 $a_1\ d_p\ b\ p_r\ c\ e_y$	112	6, 7 $a_1\ d_p\ b\ p_r\ c\ s_p\ e_y$	3
6 $p_x s_p$	385	Total double crossovers	204
7 $a_1\ d_p\ b\ p_r\ c\ p_x\ e_y$	38		
7 s_p	89	3, 4, 5 $a_1\ d_p\ p_r\ e_y$	1
		3, 4, 6 $b\ p_x\ s_p$	3
Total single crossovers	1156	3, 5, 6 $a_1\ d_p\ c\ e_y$	13
		3, 5, 6 $b\ p_r\ p_x\ s_p$	32
1, 5 $d_p\ b\ p_r\ e_y$	1	4, 5, 6 $p_r\ p_x\ s_p$	11
1, 6 $a_1\ p_x\ s_p$	1	4, 5, 6 $a_1\ d_p\ b\ c\ e_y$	10
3, 4 b	5		
3, 4 $a_1\ d_p\ p_r\ c\ p_x\ s_p\ e_y$	1	Total triple crossovers	70
		Grand total	2229

TABLE 8

Translocation d.

$$\frac{-}{e_y} \quad \frac{1\ 2\ 3\ 4\ 5 + {}^{e_y}\ 6\ 7}{a_l\ d_p\ b\ p_r\ c \qquad p_x\ s_p} \ \text{♀} \times e_y\, a_l\, d_p\, b\, p_r\, c\, p_x\, s_p \text{♂}.$$

CLASSES OF THE OFFSPRING	NUMBER OBSERVED
0 Wild-type	439
0 $a_l\, d_p\, b\, p_r\, c\, p_x\, s_p\, e_y$	181
Total non-crossovers	620
1 a_l	95
1 $d_p\, b\, p_r\, c\, p_x\, s_p$	50
2 $a_l\, d_p$	207
2 $b\, p_r\, c\, p_x\, s_p\, e_y$	156
3 $a_l\, d_p\, b$	49
3 $p_r\, c\, p_x\, s_p\, e_y$	44
4 $a_l\, d_p\, b\, p_r$	33
4 $c\, p_x\, s_p\, e_y$	24
5 $a_l\, d_p\, b\, p_r\, c$	16
5 $p_x\, s_p\, e_y$	15
6 $a_l\, d_p\, b\, p_r\, c\, e_y$	1
6 $p_x\, s_p$	1
7 $a_l\, d_p\, b\, p_r\, c\, p_x\, e_y$	13
7 s_p	15
Total single crossovers	719
1, 2 $a_l\, b\, p_r\, c\, p_x\, s_p\, e_y$	7
1, 2 d_p	15
1, 3 $a_l\, p_r\, c\, p_x\, s_p\, e_y$	11
1, 3 $d_p\, b$	7
1, 4 $a_l\, c\, p_x\, s_p\, e_y$	4
1, 4 $d_p\, b\, p_r$	8
1, 5 $d_p\, b\, p_r\, c$	2
1, 6 $a_l\, p_x\, s_p$	1
1, 6 $d_p\, b\, p_r\, c\, e_y$	1
1, 7 $a_l\, s_p$	1
2, 3 b	8
2, 3 $a_l\, d_p\, p_r\, c\, p_x\, s_p\, e_y$	2
2, 4 $b\, p_r$	24
2, 4 $a_l\, d_p\, c\, p_x\, s_p\, e_y$	8
2, 5 $b\, p_r\, c$	4
2, 5 $a_l\, d_p\, p_x\, s_p\, e_y$	6
2, 6 $b\, p_r\, c\, e_y$	2
2, 6 $a_l\, d_p\, p_x\, s_p$	1
2, 7 $a_l\, d_p\, s_p$	10
2, 7 $b\, p_r\, c\, p_x\, e_y$	1
3, 4 p_r	6
3, 4 $a_l\, d_p\, b\, c\, p_x\, s_p\, e_y$	1
3, 5 $p_r\, c$	2
3, 7 $a_l\, d_p\, b\, s_p$	1
3, 6 $p_r\, c\, e_y$	1
4, 5 c	7
4, 5 $a_l\, d_p\, b\, p_r\, p_x\, s_p\, e_y$	21
4, 6 $c\, e_y$	2
4, 6 $a_l\, d_p\, b\, p_r\, p_x\, s_p$	1
Total double crossovers	165
1, 2, 3 $a_l\, b$	1
1, 2, 4 $a_l\, b\, p_r$	1
1, 2, 4 $d_p\, c\, p_x\, s_p\, e_y$	2
1, 3, 4 $a_l\, p_r$	1
1, 3, 5 $a_l\, p_r\, c$	1
1, 3, 7 $d_p\, b\, s_p$	1
1, 4, 5 $a_l\, c$	1
1, 4, 5 $d_p\, b\, p_r\, p_x\, s_p\, e_y$	4
2, 3, 4 $a_l\, d_p\, p_r$	1
2, 4, 5 $a_l\, d_p\, c$	23
2, 4, 5 $b\, p_r\, p_x\, s_p\, e_y$	35
3, 4, 5 $a_l\, d_p\, b\, c$	4
3, 4, 5 $p_r\, p_x\, s_p\, e_y$	3
Total triple crossovers	78
1, 2, 4, 5 $d_p\, c$	1
1, 2, 4, 5 $a_l\, b\, p_r\, p_x\, s_p\, e_y$	1
1, 3, 4, 5, $d_p\, b\, c$	2
Total quadruple crossovers	4
Grand total	1586