A NEW TYPE OF TRANSLOCATION IN *DROSOPHILA MELANOGASTER*[1]

MARCUS M. RHOADES
Cornell University, Ithaca, New York

Received November 28, 1930

TABLE OF CONTENTS

INTRODUCTION

The first known translocation in Drosophila was the "Pale" translocation found by BRIDGES (1919, 1923) in which a piece from the end of the right arm of the second chromosome, including the genes from plexus to speck, had become attached to the side of the third chromosome near the locus of ebony. This, and a few other translocations found by BRIDGES, occurred spontaneously, that is, in a fly which had not been subjected to irradiation. Following the discovery by MULLER (1928a, 1928b) and WEINSTEIN (1928) that the frequency of translocations in Drosophila could be markedly increased through the agency of X-rays, a number of papers (DOBZHANSKY 1929a, 1929b, 1930a, MULLER and PAINTER 1929, PAINTER and MULLER 1929, MULLER and ALTENBURG 1930) have appeared presenting the frequency and the cytological and genetical characteristics of translocations.

In the published cases of translocations induced by X-ray treatment the broken-off piece of chromosome involved in the translocation was an end or terminal portion. However, DOBZHANSKY (1930b) found two translocations in which a piece had been taken from the middle region of the second chromosome and had become permanently attached to the Y chromosome. He designated these as translocations G and H respectively. Doctor DOBZHANSKY was so kind as to turn over his translocation G to the present author for analysis and this paper reports the results obtained. I wish

[1] This paper reports research conducted at the CALIFORNIA INSTITUTE OF TECHNOLOGY.

here to express my sincere appreciation to Professors DOBZHANSKY and STURTEVANT for advice and suggestions so freely given during the course of this investigation.

ORIGIN OF TRANSLOCATION

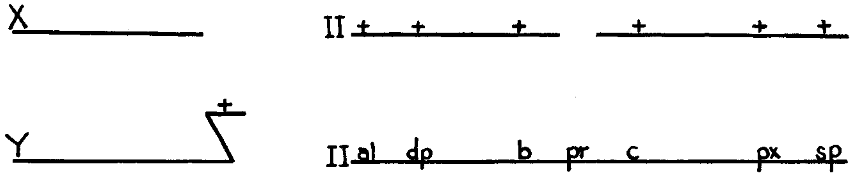
The translocation, with which this paper is concerned, was produced by irradiation with X-rays. Wild-type Oregon males were rayed for 60 minutes with a current of 5 m.a. and a potential of 50 k.v. at a distance of 16 centimeters from the target (for details see papers by DOBZHANSKY) and mated to $\frac{+\ +\ C_y + p_r + +\ +}{a_l\ d_p + \ b\ \ p_r\ \ c\ \ p_x\ s_p}\ \frac{e_y}{e_y}$ females. (C_y-Curly, p_r-purple, a_l-aristaless, d_p-dumpy, b-black, c-curved, p_x-plexus, s_p-speck are all second chromosome factors, and e_y-eyeless is a gene located in the small fourth chromosome. The "$C_y p_r$" chromosome carries inversions that suppress nearly all crossing over.) Among the F_1 offspring, $\frac{+\ +\ \ +\ +\ \ +\ \ +\ +}{a_l\ d_p\ \ b\ \ p_r\ \ c\ \ p_x\ s_p}\ \frac{+}{e_y}$ males were selected and individually crossed to $\frac{+\ +\ C_y + p_r + +\ +}{a_l\ d_p + \ b\ \ p_r\ \ c\ \ p_x\ s_p}\ \frac{e_y}{e_y}$ females. One of the F_2 cultures gave the following progeny:

	Females	*Males*
Wild type	0	10
e_y	0	8
$a_l-d_p-b-p_r-c-p_x-s_p$	8	0
$a_l-d_p-b-p_r-c-p_x-s_p\ e_y$	4	0
C_y	0	15
C_y-p_r	16	0
$C_y\ e_y$	0	21
$C_y-p_r\ e_y$	11	0
$a_l-d_p-b-c-p_x-s_p$	0	5

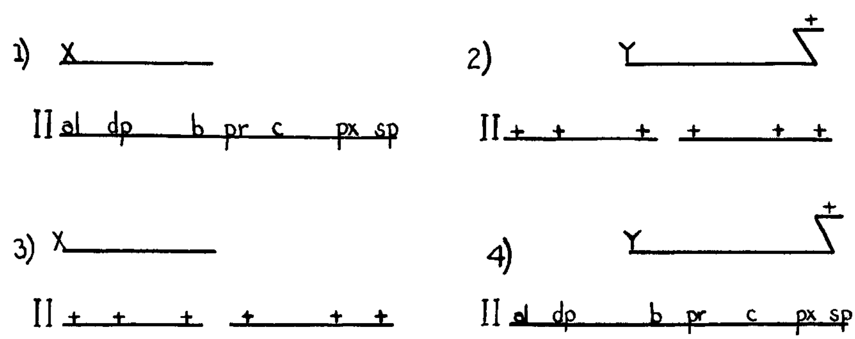
Only 8 of the 16 expected classes appeared, and the data show a coupling or linkage between the irradiated second chromosome, carrying no recessive genes, and the treated Y chromosome. These aberrant results were interpreted as the consequence of a translocation involving the second and Y chromosomes. Further analyses proved the correctness of this interpretation and showed that a small piece from near the middle of the second chromosome, including the locus of p_r, had become fastened to the Y chromosome. The third chromosome was tested and found to be free from the translocation. Some of the wild-type F_2 males were again mated to $\frac{+\ +\ C_y + \ p_r\ \ +\ \ +\ +}{a_l\ d_p + \ b\ \ p_r\ \ c\ \ p_x\ s_p}$ females and among the ensuing F_3 offspring (disregarding C_y flies) were found:

wild-type males	290
$a_l-d_p-b-c-p_x-s_p$ males	30
$a_l-d_p-b-p_r-c-p_x-s_p$ males	4
$a_l-d_p-b-p_r-c-p_x-s_p$ females	255

Assuming that the hypothesis of a II-Y translocation is correct, the 30 a_l-d_p-b-c-p_x-s_p and the 4 a_l-d_p-b-p_r-c-p_x-s_p males are unexpected classes whose origin can be explained by the types of gametes formed in the maturations divisions. Let the constitution of the males carrying the translocation be diagrammatically designated as follows:



From the maturation divisions in the male 4 types of gametes are possible (their frequencies being equal only if assortment is random). They are



Since C_y flies are disregarded, the eggs may all be considered as having the same genetic constitution, that is,

X________
II $\underline{a_l \quad d_p \quad b \quad p_r \quad c \quad p_x \quad s_p}$

Sperm from classes 1 and 2 give rise to regular or expected types of offspring. Sperm from class 4 will produce males, carrying a duplication for a portion of the second chromosome, which show the recessive characters a_l d_p b c p_x s_p but not p_r since their Y chromosome carries the normal allelomorph or p_r in the attached piece, and 1 normal allelomorph is dominant over 2 recessive genes. The 30 a_l d_p b c p_x s_p males were of this constitution. A check was afforded by crossing duplication males from similar cultures to

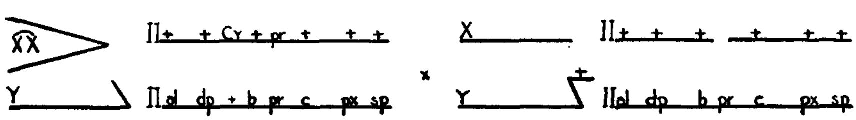
$a_l\ d_p\ b\ p_r\ c\ p_x\ s_p$ females. Only $a_l\ d_p\ b\ p_r\ c\ p_x\ s_p$ daughters and $a_l\ d_p\ b\ c\ p_x\ s_p$ sons should be produced (excepting occasional cases of non-disjunction where sperm carrying both a paternal X and a paternal Y chromosome are formed). Such was found to be the case.

The 4 $a_l\ d_p\ b\ p_r\ c\ p_x\ s_p$ males could result if sperm carrying neither an X or Y fertilized an X bearing egg. Such males would be of XO constitution as they would lack a Y chromosome. They should be sterile, since the presence of a Y in the male Drosophila is necessary for fertility. Although these 4 males were not tested similar males from other cultures were tested for fertility and no offspring were ever obtained.

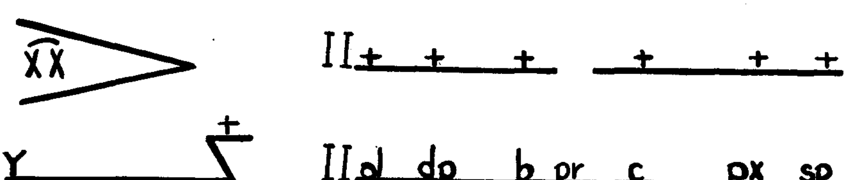
Sperm of class 3 would produce daughters showing only the recessive character purple eye. They would, however, carry a deficient second chromosome and the absence of this class of females among several thousand flies is taken to indicate that the deficiency is lethal although the duplication gives rise to viable and fertile flies of both sexes.

EFFECT OF TRANSLOCATION ON CROSSING OVER IN THE SECOND CHROMOSOME

Since the translocation involved the second and Y chromosomes it was possible to study the effect of the translocation on crossing over in the second chromosome only in attached-X females (females which are XXY in constitution but whose 2 X chromosomes are attached to a single spindle fiber and, therefore, always pass to the same pole). To secure the desired stock the following breeding procedure was followed. Attached-X females carrying the dominant gene C_y and the recessive gene p_r in one of the second chromosomes and the recessive factors $a_l\ d_p\ b\ p_r\ c\ p_x\ s_p$ in the other were mated to wild-type males carrying the translocation. Diagrammatically the procedure was as follows:



(Although the attached-X-'s were homozygous for the factor forked (f) only second-chromosome factors will be listed.) The F_1 wild-type daughters were of



constitution and were mated with normal males homozygous for the 7 recessive second-chromosome genes. The data from these crosses are presented in tables 1 and 2 but the summarized crossover values are given below:

Region	*Percents of crossing over in females with translocation*	*Percents of crossing over in control series*	*Difference*
1 a_l-d_p	1.9	10.0	$-$ 8.1
2 d_p-b	4.8	29.0	$-$24.2
3 $b-p_r$*	0.0	8.9	$-$ 8.9
4 p_r-c	24.6	20.0	+ 4.6
5 $c-p_x$	24.1	21.1	+ 3.0
6 p_x-s_p	6.7	5.1	+ 1.6

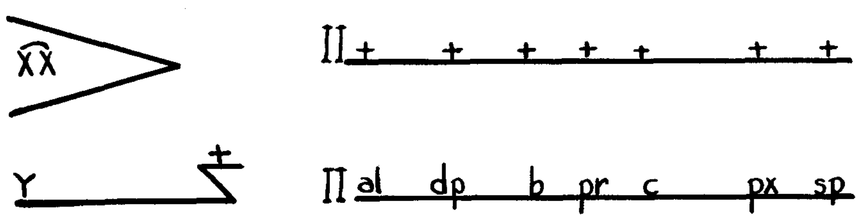
* Crossing over in region 3 calculated from females only.

Certain classes of females in table 1 and certain classes of males in table 2 are listed as arising from non-disjunctional gametes. Failure of the attached-X's and the Y (carrying the deleted piece of the second chromosome) to pass to opposite poles in the heterotypic meiotic division in females carrying the translocation would result in (1) eggs with both the attached-X pair and the Y and (2) eggs with neither the attached-X pair or the Y. Fertilization of class 1 eggs by sperm with a normal Y would presumably yield females with 2 Y chromosomes, one with a piece of the second chromosome, and an attached-X pair, although no direct evidence of their constitution exists. Fertilization of class 2 eggs by X-bearing sperm would give XO males, which would be purple eyed, since the normal allelomorph is in that piece of the second chromosome attached to the missing Y. Several of the supposed XO males were tested for fertility and invariably found to be sterile. DOBZHANSKY (1930a and in press) in his analyses of 8 different translocations found similar exceptional males. He had an additional check upon their XO constitution as he crossed translocation females with attached-X chromosomes to normal males whose X chromosomes carried the recessive factor bobbed (*bb*). Since the normal allelomorph of bobbed is located in the Y chromosome, XY males are not-bobbed in appearance while XO males are bobbed as well as sterile. In this experiment the sterility of the purple-eyed males was considered adequate evidence as to their XO constitution.

The data show crossing over to be greatly reduced in the left arm of the second chromosome, the greatest proportional reduction being in the $b-p_r$ region, which included the portion involved in the translocation, where no crossing over took place. Regions 1 and 2 also showed a marked reduction in the amount of crossing over. The amount of crossing over in the right limb of the second chromosome is consistently higher in all 3 regions than the control. This agrees with the results found by DOBZHANSKY (1929, in press and unpublished data), whose data usually show in II-IV, III-IV and II-Y translocations an increase in crossing over in those limbs of the second and third chromosomes which were not concerned in the translocation.

CROSSING OVER IN FEMALES CARRYING THE DUPLICATION

The above data show that in females carrying the translocation there is a great reduction in the amount of crossing over taking place in the left arm of the second chromosome. It is, perhaps, instructive to consider the causal agents of this reduction in crossing over. Among the several possibilities are (1) that an inversion in the linear order of the genes occurred at the time the translocation was produced; (2) that an injury of some kind to the chromosome prevents or inhibits normal pairing and crossing over; (3) a mechanical interference or hindrance to normal synapsis resulting from the formation of rings or chains during the prophases of the maturation divisions; or (4) an effect produced by a combination of factors. Fortunately, it was possible to study the effect of the duplicated portion of the second chromosome on crossing over between 2 normal second chromosomes since females carrying the duplication were both viable and fertile. Some light might, therefore, be gained on the cause of the decrease in crossing over when a translocation is involved. From an appropriate series of crosses, attached-X females were obtained that had the following constitution



They were mated to normal males homozygous for the 7 recessive second-chromosome factors. The data from this type of cross are given in tables 4 and 5. The summarized percentages of recombination are listed below with the percentages found for the same regions in the translocation and control series.

Region	*Duplication percentages*	*Control percentages*	*Difference*	*Translocation percentages*	*Control percentages*	*Differences*
1 a_l-d_p	10.8	10.0	+0.8	1.9	10.0	− 8.1
2 d_p-b	21.8	29.0	−7.2	4.8	29.0	−24.2
3 $b-p_r$	2.0*	8.9	−6.9	0.0*	8.9	− 8.9
4 p_r-c	20.0*	20.0	0.0	24.6	20.0	+ 4.6
5 $c-p_x$	21.7	21.1	+0.6	24.1	21.1	+ 3.0
6 p_x-s_p	6.0	5.1	+0.9	6.7	5.1	+ 1.6

* Calculated from female offspring only.

The unusual feature of the duplication data is that although crossing over in the right limb is almost exactly of the same order as in the control there is a decided and significant decrease in region 3, which is in the left arm, a proportionately smaller decrease in region 2, and an approximately normal amount of crossing over in region 1. It might reasonably be inferred from these data that at least a portion of the decrease in crossing over in females carrying the translocation is caused by the disturbing influence of that portion of the second chromosome attached to the Y, since a plausible explanation of the effect of the duplicated piece on crossing over between 2 normal second chromosomes is that it pairs with them, the presence of the Y mechanically interfering with normal synapsis. It logically follows that the greatest disturbance would be expected in that region of the chromosome including the duplicated piece with a progressive decrease in effect proceeding away from the duplicated portion. Actually this was realized, since crossing over was normal in region 1, but was greatly decreased in region 3 with an intermediate value in region 2. That the duplicated piece had little or no effect on crossing over in the right arm of the second chromosome is shown by the very close agreement in values with the control.

It would seem that if the reduction in crossing over is caused by the pairing of the duplicated piece with the normal second chromosomes that the distribution of the Y with respect to the attached-X pair might be such that the frequency of non-disjunction (where both the attached-X pair and the Y go to the same pole in the reduction division) would be increased. However, the low frequency of non-disjunctional gametes from females with the duplication indicates that the attached-X pair and the Y nearly always pass to opposite poles. It is apparent, therefore, that the distribution of the Y and the sex chromosomes proceeds in an approximately normal manner even though the reduction in crossing over in the left arm of the second chromosome may be caused by the pairing of the duplicated piece with the second chromosomes. The calculated percentage of non-disjunction is not greater than 3 percent in duplication females. It is impossible to calculate the true amount of non-disjunction since some untested flies might be due either to certain crossovers or to non-disjunction. But the inclusion of all doubtful cases does not give a percentage of non-disjunction greater than 3.

GENETICAL DETERMINATION OF SIZE OF DUPLICATED PIECE

Since duplication flies, that is, flies carrying the piece of the second on the Y in addition to 2 normal seconds, were viable it was possible to determine which genes were included in the duplicated piece by the following scheme. For example, to ascertain whether the locus of rolled wing (r_l) was included, wild-type males carrying the translocation but with the recessive genes black (b) and rolled (r_l) in their normal second chromosomes were mated with $b\ r_l$ females. The regular offspring would consist of $b\ r_l$ daughters and wild-type sons. Duplication sons would be either b, if r_l is included in the extra piece, or $b\ r_l$, if r_l is not included. A recessive factor such as black (b), known to be not included in the duplicated piece was used in testing all loci, except for hooked (h_k), to facilitate the detection of duplication males. In the case of hooked the absence of hooked males was taken to mean that this locus was included in the duplication. The following genes, located near the p_r locus, were tested and are listed below with their current map positions, as determined by BRIDGES:

Locus	*Map position*	*Determination*
Black (b)	48.5	Not included in duplicated piece
Scraggly (r_d^s)	51.0	Not included in duplicated piece
Hooked (h_k)	53.9	Included in duplicated piece
Purple (p_r)	54.5	Included in duplicated piece
Light (l_t)	55.0	Included in duplicated piece
Rolled (r_l)	55.1	Not included in duplicated piece
Thick (t_k)	55.3	Not included in duplicated piece
Cinnabar (c_n)	57.5	Not included in duplicated piece

Three genes, hooked, purple and light (an allelomorph of pink-wing) were found to be included in that portion from the middle of the second chromosome which is attached to the Y. Genetically the minimum distance included is 1.1 map units and the maximum distance is 4.1 map units. The position of the spindle-fiber attachment is known to be approximately 0.5 of a map unit to the right of purple. Therefore the rightmost end of the translocated section must lie very close to the insertion point of the spindle fiber. The mutant Bristle, whose locus at 54.7 apparently lies in the translocated section, offered difficulties in testing, on account of its dominance, and positive inclusion has not yet been proven.

Cytological examination of ganglion cells from male larvae carrying the translocation failed to disclose any discrepancy in length between the two second chromosomes, one of which had a deficiency while the other was normal.

SUMMARY

1. From a male which was treated with X-rays a translocation was secured that involved the second and Y chromosomes.

2. Analyses showed that a small piece had been removed from near the middle of the second chromosome, including the loci of the genes hooked (h_k), purple (p_r), and light (l_t) and had become attached to the Y chromosome. The minimum map distance of the translocated piece is 1.1 units while the maximum length is 4.1 map units.

3. Cytological examination failed to show a discrepancy in length between the two second chromosomes, one of which was normal and the other deficient for the translocated piece.

4. Studies of crossing over in females carrying the translocation showed a great reduction in the left arm of the second chromosome and slightly higher values than the control in the right limb.

5. Studies of crossing over in females carrying the extra piece of the second attached to the Y in addition to two normal seconds (that is, duplication females) showed a significant reduction in the left limb of the second chromosome and approximately normal percentages for the right limb. The greatest reduction in crossing over was in region 3, which includes the piece involved in the translocation, with a proportionately lesser decrease in region 2, while region 1 showed about the same amount of crossing over as the control.

6. It is suggested that the Y carried by the translocated piece may interfere with synapsis of the second chromosomes, and possibly may account for a portion of the reduction in crossing over in translocation females, since in duplication females there is a decreased amount of crossing over in the left limb of the second chromosome.

LITERATURE CITED

Bridges, C. B., 1919 Duplication. Anat. Rec. **15**: 357–358.

1923 The translocation of a section of chromosome-II upon chromosome-III in Drosophila. Anat. Rec. **24**: 426–427.

Dobzhansky, Th., 1929a Genetical and cytological proof of translocations involving the third and the fourth chromosomes of *Drosophila melanogaster*. Biol. Zbl. **49**: 408–419.

1929b A homozygous translocation in *Drosophila melanogaster*. Proc. Nat. Acad. Sci. Wash. **15**: 633–638

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

1930b Cytological map of the second chromosome of *Drosophila melanogaster*. Biol. Zbl. **50**: 671–685.

MULLER, H. J., 1928a The problem of genic modification. Proceedings of the 5th International Congress, Supplementband of the Z. indukt. Abstamm.-u. VererbLehre. **1**: 234–260.

1928b The production of mutations by X-rays. Proc. Nat. Acad. Sci. Wash. **14**: 714–726.

MULLER, H. J., and ALTENBURG, E., 1930 The frequency of translocations produced by X-rays in Drosophila. Genetics **15**: 283–311.

MULLER, H. J., and PAINTER, T. S., 1929 The cytological expression of changes in gene alignment produced by X-rays in Drosophila. Amer. Nat. **63**: 193–200.

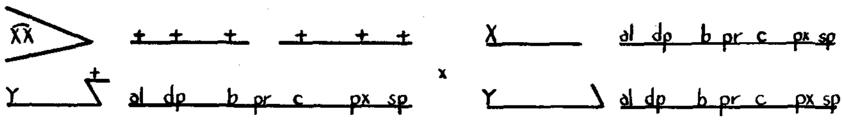
PAINTER, T. S., and MULLER, H. J., 1929 Parallel cytology and genetics of induced translocations and deletions in Drosophila. J. Hered. **20**: 287–298.

WEINSTEIN, A., 1928 The production of mutations and rearrangements of genes by X-rays. Science **67**: 367–377.

TABLE 1

Translocation data.

Crossing over in attached-X females carrying the translocation.

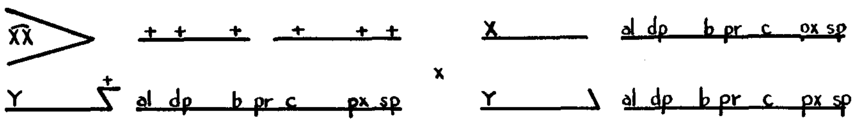


FEMALES ONLY		
$0 = a_l\ d_p\ b\ p_r\ c\ p_x\ s_p$	449	
0 = Wild	8	(non-disjunction)
$1 = d_p\ b\ p_r\ c\ p_x\ s_p$	8	
$2 = b\ p_r\ c\ p_x\ s_p$	28	
$4 = a_l\ d_p\ b\ p_r$	201	
$4 = c\ p_x\ s_p$	2	(non-disjunction)
$5 = a_l\ d_p\ b\ p_r\ c$	206	
$5 = p_x\ s_p$	2	(non-disjunction)
$6 = a_l\ d_p\ b\ p_r\ c\ p_x$	43	
$6 = a_l\ d_p\ b\ c\ p_x$	3	(non-disjunction)
$1-4 = d_p\ b\ p_r$	3	
$1-5 = d_p\ b\ p_r\ c$	4	
$1-6 = d_p\ b\ p_r\ c\ p_x$	2	
$2-4 = b\ p_r$	3	
$2-4 = b$	1	(non-disjunction)
$2-5 = b\ p_r\ c$	8	
$2-6 = b\ p_r\ c\ p_x$	5	
$4-5 = a_l\ d_p\ b\ p_r\ p_x\ s_p$	16	
$4-6 = a_l\ d_p\ b\ p_r\ s_p$	11	
$5-6 = a_l\ d_p\ b\ p_r\ c\ s_p$	2	
$1-4-5 = d_p\ b\ p_r\ p_x\ s_p$	1	
$1-5-6 = d_p\ b\ p_r\ c\ s_p$	1	
$2-5-6 = b\ p_r\ c\ s_p$	2	
$4-5-6 = a_l\ d_p\ b\ p_r\ p_x$	1	
Total	1010	

TABLE 2

Translocation data.

Crossing over in attached-X females carrying the translocation.



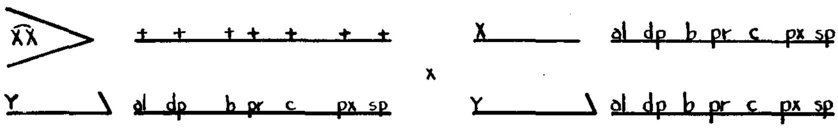
MALES ONLY

0 = wild	386	1–5 = d_p b c	2
0 = a_l d_p b c p_x s_p	289	1–5 = a_l p_x s_p	1
0 = a_l d_p b p_r c p_x s_p (XO)	4	2–4 = b	4
		2–4 = a_l d_p c p_x s_p	9
1 = a_l	15	2–5 = b c	4
1 = d_p b c p_x s_p	3	2–5 = a_l d_p p_x s_p	6
2 = a_l d_p	21	2–6 = a_l d_p s_p	2
2 = b c p_x s_p	22	2–6 = b c p_x	4
4 = a_l d_p b	141	4–5 = a_l d_p b p_x s_p	9
4 = c p_x s_p	179	4–5 = c	19
5 = a_l d_p b c	143	4–6 = c p_x	10
5 = p_x s_p	171	4–6 = a_l d_p b s_p	7
5 = a_l d_p b p_r c (XO)	1	5–6 = a_l d_p b c s_p	9
		5–6 = px	1
6 = a_l d_p b c p_x	30	1–5–6 = d_p b c s_p	1
6 = s_p	37	2–4–5 = b p_x s_p	2
1–2 = d_p	1	2–4–5 = a_l d_p c	3
1–4 = a_l c p_x s_p	5	4–5–6 = c s_p	3
1–4 = d_p b	1		
		Total	1545

TABLE 3

Control data.

Crossing over in attached-X females carrying 2 normal second chromosomes and a normal Y.

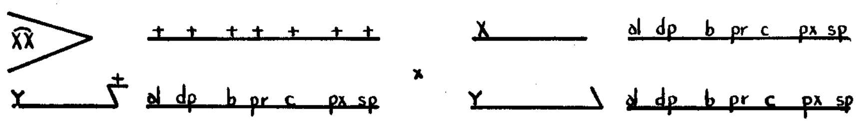


MALES AND FEMALES			
$0=$	436	$2\text{–}6=a_l\, d_p\, s_p$	18
$0=a_l\, d_p\, b\, p_r\, c\, p_x\, s_p$	312	$2\text{–}6=b\, p_r\, c\, p_x$	17
$1=a_l$	58	$3\text{–}4=a_l\, d_p\, b\, c\, p_x\, s_p$	9
$1=d_p\, b\, p_r\, c\, p_x\, s_p$	63	$3\text{–}4=p_r$	13
$2=a_l\, d_p$	189	$3\text{–}5=a_l\, d_p\, b\, p_x\, s_p$	16
$2=b\, p_r\, c\, p_x\, s_p$	193	$3\text{–}5=p_r\, c$	21
$3=a_l\, d_p\, b$	52	$3\text{–}6=a_l\, d_p\, b\, s_p$	8
$3=p_r\, c\, p_x\, s_p$	55	$3\text{–}6=p_r\, c\, p_x$	5
$4=a_l\, d_p\, b\, p_r$	111	$4\text{–}5=a_l\, d_p\, b\, p_r\, p_x\, s_p$	17
$4=c\, p_x\, s_p$	119	$4\text{–}5=c$	23
$5=a_l\, d_p\, b\, p_r\, c$	110	$4\text{–}6=a_l\, d_p\, b\, p_r\, s_p$	3
$5=p_x\, s_p$	138	$4\text{–}6=c\, p_x$	10
$6=a_l\, d_p\, b\, p_r\, c\, p_x$	18	$5\text{–}6=a_l\, d_p\, b\, p_r\, c\, s_p$	0
$6=s_p$	29	$5\text{–}6=p_x$	2
$1\text{–}2=a_l\, b\, p_r\, c\, p_x\, s_p$	8	$1\text{–}2\text{–}4=a_l\, b\, p_r$	1
$1\text{–}2=d_p$	5	$1\text{–}2\text{–}4=d_p\, c\, p_x\, s_p$	1
$1\text{–}3=a_l\, p_r\, c\, p_x\, s_p$	4	$1\text{–}2\text{–}5=a_l\, b\, p_r\, c$	1
$1\text{–}3=d_p\, b$	5	$1\text{–}2\text{–}6=a_l\, b\, p_r\, c\, p_x$	1
		$1\text{–}3\text{–}4=a_l\, p_r$	2
$1\text{–}4=a_l\, c\, p_x\, s_p$	17	$1\text{–}3\text{–}4=d_p\, b\, c\, p_x\, s_p$	1
$1\text{–}4=d_p\, b\, p_r$	18	$1\text{–}3\text{–}5=d_p\, b\, p_x\, s_p$	1
		$1\text{–}3\text{–}6=d_p\, b\, s_p$	1
$1\text{–}5=a_l\, p_x\, s_p$	28	$1\text{–}4\text{–}5=d_p\, b\, p_r\, p_x\, s_p$	1
$1\text{–}5=d_p\, b\, p_r\, c$	18	$1\text{–}4\text{–}6=a_l\, c\, p_x$	2
		$1\text{–}4\text{–}6=d_p\, b\, p_r\, s_p$	1
$1\text{–}6=a_l\, s_p$	3	$2\text{–}3\text{–}4=b\, c\, p_x\, s_p$	1
		$2\text{–}3\text{–}4=a_l\, d_p\, p_r$	3
$2\text{–}3=a_l\, d_p\, p_r\, c\, p_x\, s_p$	4	$2\text{–}3\text{–}5=a_l\, d_p\, p_r\, c$	4
$2\text{–}3=b$	9	$2\text{–}3\text{–}6=a_l\, d_p\, p_r\, c\, p_x$	2
		$2\text{–}4\text{–}5=a_l\, d_p\, c$	7
$2\text{–}4=a_l\, d_p\, c\, p_x\, s_p$	45	$2\text{–}4\text{–}5=b\, p_r\, p_x\, s_p$	3
$2\text{–}4=b\, p_r$	68	$2\text{–}4\text{–}6=a_l\, d_p\, c\, p_x$	3
		$3\text{–}4\text{–}5=a_l\, d_p\, b\, c$	1
$2\text{–}5=a_l\, d_p\, p_x\, s_p$	61	$4\text{–}5\text{–}6=c\, s_p$	1
$2\text{–}5=b\, p_r\, c$	60	$1\text{–}3\text{–}4\text{–}5=a_l\, p_r\, p_x\, s_p$	1
		$1\text{–}2\text{–}4\text{–}5=d_p\, c$	1
		$1\text{–}3\text{–}4\text{–}5=d_p\, b\, c\, p_x$	1
		Total	2439

TABLE 4

Duplication data.

Crossing over in attached-X females carrying 2 normal second chromosomes and the translocation Y chromosome.



MALES ONLY

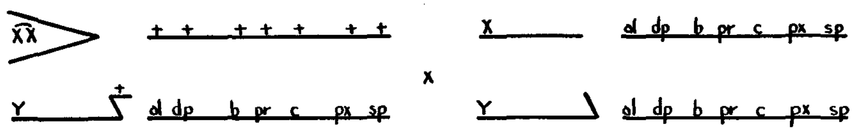
0=wild	259	?2–4= $a_l\ d_p\ c\ p_x\ s_p$	16
0= $a_l\ d_p\ b\ c\ p_x\ s_p$	120	?2–4= b	17
0= $a_l\ d_p\ b\ p_r\ c\ p_x\ s_p$	1		
(XO)		2–5= $a_l\ d_p\ p_x\ s_p$	24
		2–5= $b\ c$	27
1= a_l	36		
1= $d_p\ b\ c\ p_x\ s_p$	7	2–6= $a_l\ d_p\ s_p$	5
		2–6= $b\ c\ p_x$	8
2= $a_l\ d_p$	52		
2= $b\ c\ p_x\ s_p$	67	?4–5= $a_l\ d_p\ b\ p_x\ s_p$	7
2= $b\ p_r\ c\ p_x\ s_p$	1	?4–5= c	6
(XO)			
		4–5= $a_l\ d_p\ b\ p_r\ p_x\ s_p$	2
3= $p_r\ c\ p_x\ s_p$	1	(XO)	
(XO)		?4–6= $a_l\ d_p\ b\ s_p$	2
?4= $a_l\ d_p\ b$	70	?4–6= $c\ p_x$	4
?4= $c\ p_x\ s_p$	55		
4= $a_l\ d_p\ b\ p_r$	1	5–6= $a_l\ d_p\ b\ c\ s_p$	1
(XO)			
		?1–2–4= $a_l\ b$	1
5= $a_l\ d_p\ b\ c$	55		
5= $p_x\ s_p$	78	?1–4–5= $a_l\ c$	1
6= $a_l\ d_p\ b\ c\ p_x$	10	?1–4–6= $a_l\ c\ p_x$	2
6= s_p	23		
1–2= $a_l\ b\ c\ p_x\ s_p$	1	?2–4–5= $a_l\ d_p\ c$	1
1–2= d_p	1	?2–4–6= $b\ p_x\ s_p$	3
?1–4= $a_l\ c\ p_x\ s_p$	8	2–5–6= $a_l\ d_p\ c\ p_x$	1
?1–4= $d_p\ b$	6	?2–4–5–6= $b\ p_x$	1
1–5= $a_l\ p_x\ s_p$	22		
1–5= $d_p\ b\ c$	9		——
1–6= $a_l\ s_p$	4	Total	1017
1–6= $d_p\ b\ c\ p_x$	1		

It is impossible to tell crossovers in region 3 from those in region 4 in the male offspring except in cases of non-disjunction.

TABLE 5

Duplication data.

Crossing over in attached-X females carrying 2 normal second chromosomes and the translocation Y chromosome.



FEMALES ONLY			
0=	249	2–6 $= a_l\ d_p\ s_p$	6
0 $= a_l\ d_p\ b\ p_r\ c\ p_x\ s_p$	116	2–6 $= b\ p_r\ c\ p_x$	3
*0 $= a_l\ d_p\ b\ c\ p_x\ s_p$	4	†3–4 $= a_l\ d_p\ b\ c\ p_x\ s_p$	2
		†3–5 $= a_l\ d_p\ b\ p_x\ s_p$	4
1 $= a_l$	46		
1 $= d_p\ b\ p_r\ c\ p_x\ s_p$	25	†3–6 $= a_l\ d_p\ b\ s_p$	1
2 $= a_l\ d_p$	63	4–5 $= a_l\ d_p\ b\ p_r\ p_x\ s_p$	6
2 $= b\ p_r\ c\ p_x\ s_p$	68	4–5 $= c$	9
		*4–5 $= a_l\ d_p\ b\ p_x\ s_p$	1
†3 $= a_l\ d_p\ b$	6		
3 $= p_r\ c\ p_x\ s_p$	2	4–6 $= a_l\ d_p\ b\ p_r\ s_p$	3
		4–6 $= c\ p_x$	3
4 $= a_l\ d_p\ b\ p_r$	56		
4 $= c\ p_x\ s_p$	65	5–6 $= a_l\ d_p\ b\ p_r\ c\ s_p$	2
5 $= a_l\ d_p\ b\ p_r\ c$	49	1–2–4 $= a_l\ b\ p_r$	1
5 $= p_x\ s_p$	78		
		1–2–5 $= a_l\ b\ p_r\ c$	1
6 $= a_l\ d_p\ b\ p_r\ c\ p_x$	6	1–2–5 $= d_p\ p_x\ s_p$	2
6 $= s_p$	20		
		1–3–4 $= a_l\ p_r$	1
1–2 $= a_l\ b\ p_r\ c\ p_x\ s_p$	0	†1–3–4 $= d_p\ b\ c\ p_x\ s_p$	1
1–2 $= d_p$	1		
		1–4–5 $= d_p\ b\ p_r\ p_x\ s_p$	1
1–4 $= a_l\ c\ p_x\ s_p$	8	1–4–6 $= d_p\ b\ p_r\ s_p$	1
1–4 $= d_p\ b\ p_r$	8		
		1–5–6 $= d_p\ b\ p_r\ c\ s_p$	1
1–5 $= a_l\ p_x\ s_p$	5		
1–5 $= d_p\ b\ p_r\ c$	8	2–4–5 $= a_l\ d_p\ c$	3
1–6 $= a_l\ s_p$	4	2–4–6 $= b\ p.\ s_p$	1
1–6 $= d_p\ b\ p_r\ c\ p_x$	5	2–4–6 $= a_l\ d_p\ c\ p_x$	1
†2–3 $= b$	1	†2–3–6 $= b\ s_p$	1
2–4 $= a_l\ d_p\ c\ p_x\ s_p$	8	1–2–4–5 $= a_l\ b\ p_r\ p_x\ s_p$	1
2–4 $= b\ p_r$	22	†2–3–4–5 $= a_l\ d_p\ p_r\ p_x\ s_p$	1
2–5 $= a_l\ d_p\ p_x\ s_p$	13	Total	1014
2–5 $= b\ p_r\ c$	21		

* non-disjunction.

† not tested for non-disjunction.