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Spontaneous Interchanges in Females of *Drosophila melanogaster*

Part 1: Formation of Half-translocations in XX and XXY Females

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Summary. Herein is described an attempts to establish chromosome pairing-interchange relationships in *Drosophila melanogaster* female. For this purpose, the formation of half-translocations was studied in XXY and XX females bearing compounds of the second pair of autosomes. With respect to XXY females, it was expected that the free Y chromosome would pair with these compounds and that half-translocations involving 2L would arise. In as much as compound chromosomes in XX females had no partner for pairing, the formation of half-translocations involving 2L was not expected.

Half-translocations were registered in the F_1 from crosses of XX and XXY females to b j pr cn/T(Y;2)C males. The cross was designed to permit the detection of very rarely occurring non-homologue interchanges.

Offspring number was 335 in XX females and 550 in XXY females. The majority of offspring consisted of individuals arisen from the spontaneous restitution of compounds and the formation of 2n egg cells. Based on phenotype, the offspring of XX females contained 4 individuals with half-translocations involving 2L; there were 48 such flies among the offspring of XXY females. As confirmed by progeny analysis, 38 half-translocations occurred in XXY females and none in XX females. Of the 31 spontaneous interchanges in XXY females 28 were recorded between the Y and the left compound, one between the Y and the right compound, and one between the X and the left compound. Non-homologue interchanges were of oogonial origin judging by the fact that individuals with half-translocations arose in clusters. Unlike Y – left compound interchanges, the interchanges between autosomal compounds seem to be of meiotic origin.

Key words: *Drosophila melanogaster* – Chromosome – Spontaneous interchange – half-translocation – Non-homologous pairing – Mitosis.

1 Introduction

By definition translocation is the exchange product of non-homologous chromosomes. Knowledge of the mechanisms of the spontaneous formation of translocations is scanty. With respect to *Drosophila*, about 30 of the spontaneous translocations described were occasional observations (Alexander 1962; Roberts 1976) and attempts to produce interchanges without mutagenic treatment have not been successful (Stein 1934, 1939). The fact that interchanges underlie structural mutations, translocations in particular, has led early to the conclusion that non-homologous associations are needed for translocations to arise (Serebrovsky 1929, 1930; Muller 1932; Morgan 1939). Kostoff (1938) has put forward the hypothesis that translocations are the result of a somatic crossing-over between non-homologous chromosomes.

Recent developments in the area of non-homologous chromosome pairing during meiosis in *Drosophila* have made it possible to study the role of pairing in translocation formation. Establishment of relationships between non-homologous pairing and non-homologue interchanges would be tangible proof of the so-far speculative pairing of non-homologues and would also be the first step towards investigations of the mechanism of spontaneous translocation formation. The hypothesis of non-homologous pairing implies the participation of univalents in this process. These are either chromosomes lacking a homologous partner in the genome or chromosomes that fail to pair for some reasons (Cooper et al. 1955; Grell 1976; Chadov 1978). Data have been obtained indicating that non-homologue pairing also occurs during mitosis (Grell 1976; Grell and Day 1970; Moore 1971).

Our basic assumption was that non-homologue pairing is the first necessary condition ensuring interchange. Under this assumption, non-homologue interchange frequency was suggested to be highest in those genomes where the respective non-homologues pair, and the lowest

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where they do not pair. The aim of this work was to correlate non-homologue pairing and interchange occurrence.

In our first attempts to relate pairing and interchanges (Chadov 1975a, b, 1976, 1977), crosses were designed that permitted one to base the registration of low frequency spontaneous interchanges in F_1s on half-translocation formation. Preference was given to the registration of half-translocations rather than those of translocations because Panshin (1941 a, b), in his comparative study of half-translocations and translocations induced by X-rays, had established that the former arise more frequently: he explained the higher number of half-translocations observed by the failure of chromosome fragments to associate. The detailed studies of Parker (1968) and Parker et al. (1976) have demonstrated the important role that segregation of the elements of translocation plays in this phenomenon.

This is a study on spontaneous interchanges in females bearing the compound autosome of the second pair. Some of these females had normal X chromosomes (XX females), others carried an additional Y chromosome (XXY females), and yet others bore a heterozygous XY compound (X/XY females). It was expected that spontaneous interchanges between the Y chromosome and autosomal compounds would occur in XXY females but not in females of the other two genotypes where the compounds lacked a partner for non-homologous pairing.

The data on spontaneous interchanges in X/XY females will be dealt with in a separate communication.

2 Material and Methods

Spontaneous interchanges were studied in y/y; C(2L)RM, b pr; C(2R), cn females (XX females) and sc^8 · Y/y/y; C(2L),RM,b pr; C(2R)RM,cn females (XXY females). The former stock was received from the Biology Division of the Oak Ridge National Laboratory (USA); the latter was derived from it and maintained separately. Both stocks contained compounds of autosomes 2 of the same origin. They differed only in the presence of the Y chromosome marked with the genes scute^8 and yellow.

According to Grell (1970), in XXY females with autosomal compounds, meiotic pairing between the free Y chromosome and C(2L) and C(2R) compounds takes place. Based on these data, it was expected that the pairing of the Y chromosome to compounds would be associated with interchanges and result in Y;C(2L) and Y;C(2R) translocations, each composed of two chromosomes, i.e., half-translocations. If the interchange between the compound the Y-chromosome occurred in the centromeric region of the compound, the resulting half-translocation would include material of the 2L whole arm (Y-C(2L) interchange), or that of the 2R whole arm (Y – C(2R) interchange). In both cases the half-translocation would include some region of the Y chromosome. In broad terms, without specifying the Y chromosome region involving the half-translocation, F(Y·2L) refers to a half-translocation containing the left arm of autosome 2 and F(Y·2R) refers to the one containing the right one. The position of the centremere is represented by a point (.).F is the abbreviation for fragment.

The appearance of an F_1 individual with a half-translocation was the criterion of interchange occurrence. The euploidy of individuals with half-translocations was provided by complementation of the aneuploid set of the egg with the corresponding aneuploid set of the sperm. This approach has been used to record a radiation induced X; 2 half-translocation (Herskowitz and Schalet 1957) and a 2;3 half-translocation (Parker 1968) in *Drosophila* females.

Females of both genotypes were crossed to b j pr cn/T(Y;2)C males. Translocation T(Y;2)C comprises a $(2L)^T$ chromosome containing a 2L arm with the centromere of autosome 2 and a small region of 2R heterochromatin, as well as a $(Y\cdot 2R)^T$ chromosome with all the fertility factors of the Y chromosome, its centromere and the 2R arm with a small deletion of pericentromeric heterochromatin (Dobzhansky 1931).

Table 1 presents a diagram of chromosome complementation with 16 possible sperm variants in a b j pr cn/T(Y;2)C male. Six of these are the result of a 2:2 segregation of the chromosome set, while 3:1 and 4:0 segregation types give rise to 8 and 2 variants, respectively. Sperm variants are assigned into 4 groups. In the sperm group euploid for autosomes, the frequency of AC + BD sperm is 95-99%, that of ACD+B is 1%-5% (Dobzhansky 1931). Special studies were carried out on aneuploid gametes in males. These studies demonstrated that the sperm most freuqently formed is AD and BC; sperm ABD+C is formed with a frequency an order of magnitude lower and sperm BCD+A and AB+CD is formed with a frequency 2 orders of magnitude lower than that of AD and BC. Chromosome distribution in these males may be schematically represented as follows:

$$X \longleftrightarrow (Y\cdot 2R)^T$$

$$2 \longleftrightarrow (2L)^T$$

According to this scheme, four types of sperm are predominantly formed; two types euploid for autosomes, X;2 and $(2L)^T$;$(Y\cdot 2R)^T$ and two aneuploid types, X;$(2L)^T$ and 2/$(Y\cdot 2R)^T$.

The expected gametes in a female resulting from Y-C(2L) and Y-C(2R) interchanges as well as from segregation of compounds are listed in the vertical rows. The egg types unexpectedly found in the experiment are given in the lines 'Restitution of compounds' and 'Formation of 2n eggs'. The processes underlying the formation of these eggs are considered in the section 'Results'.

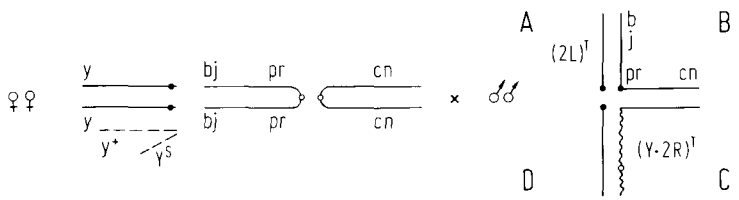
As shown in the Table, the euploid viable F_1 should consist of a small number of individuals with half-translocations and rare occurrences of succesful complementation of gametes resulting from chromosome disjunction in males and females. Because sperm AB,CD,ABD and C is less frequently formed than sperm AD and BC types, F(Y·2L),b pr was expected to be the predominant registered translocation.

The experimental design used has several advantages. It permits the observation of interchange products in the first generation; it makes unnecessary the screening of the numerous F_1's, and it has a high resolving capacity of $10^{-5} - 10^{-6}$.

The compounds of XX females lacked a pairing partner (unlike the XXY females which have the Y chromosome), and, accordingly, chromosomes of the 2L type were not expected in these females. Their occurrence in XX females, under the effect of same other presumptive process, would make doubtful the exclusive role suggested for non-homologue pairing of compounds with the Y in the formation of type 2L chromosomes.

The females employed were XXY and XX 3-day old virgins. Six females and 6 males were mated in vials with *Drosophila* medium. Every three days, the flies were transferred to vials with fresh medium. The experimental matings were replicated twice. 3,640

Table 1. Expected progenies of XX and XXY females mated to b j pr cn/T(Y;2) males



Genetic	Female gametes	Male gametes																	
		Euploid for autosomes				Aneuploid for autosomes				Complementary to 2L – half-translocation				Complementary to 2R – half-translocation			
		AC	BD	ACD	B	ABC	D	ABCD	0	AD	BC	BCD	A	AB	CD	ABD	C
Interchange Y–C(2L)	F(Y·2L), b pr F(Y·2L), pr; C(2R), cn									♀ cn	♂ b pr ♀ b pr		♂ cn				
Interchange Y–C(2R)	F(Y·2R), cn C(2L), b pr; F(Y·2R), cn													♂ cn	♀ b pr	♀ cn	♂ b pr
Disjunction of compounds	C(2L), b pr C(2R), cn																
Non-disjunction of compounds	0 C(2L), b pr; C(2R), cn					♂ y ♂ +	♀ b pr cn	♀ +	♂ b pr cn ♂ y; b pr cn								
2n egg formation	C(2L), pr; C(2R), cn	Intersex (y; +)	(b pr cn)	(+)	(b pr cn)				♀ y; b pr cn								
Compound restitution	2L·2R, b pr cn 2L·2R, b pr cn/2L·2R, b pr cn	♂ y ♂ +	♀ b pr cn	♀ +	♂ b pr cn ♂ y; b pr cn		♀ b pr cn		♂ y; b pr cn								

XXY and 5,130 XX females were employed in the first experiment, and 4,114 XXY and 5,040 XX in the second. 100 unnumbered vials were placed into a numbered cage. Egg-laying in each experiment took 21 days for XXY females and 15 days for XX females.

The matings were performed on an agar-yeast medium supplemented with an antibiotic (Chlortetracycline chlorhydrate 100,000 mg per litre of the medium). In suppressing the growth of bacterial flora, this antibiotic promoted the development of larvae under weak crowding conditions (as a rule, there was one fly per vial with 5 ml medium). The presence of the antibiotic did not affect the pattern of half-translocation formation. The results obtained in preliminary experiments, in which the antibiotic was not added to the culture medium, agreed well with those in which it was a component of the medium. The sex-linked recessive lethals were also tested and preliminary evidence was obtained indicating that the antibiotic, in the concentration range used, has no mutagenic effect.

3 Results

The progenies produced by XX and XXY females are presented in Table 2. The majority of the progenies of both XX and XXY females have b pr cn and b^+ pr^+ cn^+ individuals. As expected, cn and b pr flies were mainly produced by XXY females; there were only 2 exceptional cn females and 2 y;cn males produced by XX females.

3.1 Analysis of cn Females

According to expectations (Table 1), cn females should most likely have the following genotype: y/+;F(Y·2L),b pr/$(2L)^T$; C(2R)RM,cn. Two-step progeny tests were done to ascertain whether there was a correspondence between the actually observed and the expected genotypes. Each female obtained was crossed to b j pr cn/T(Y;2)C males. Matroclinous cn daughters appeared among the F_1's from such crosses. These daughters were subdivided into three groups and mated to males of the following genotypes: 1) b j pr cn/T(Y;2)C,b j pr 2) sc^8 · Y/y;C(2L)RM,b pr; C(2R)RM,cn 3) b j pr cn. Subsequently, the stock derived from each cn female was maintained by crossing cn daughters to '+' sons.

Table 3 summarizes the results of the first test cross. Each experimentally derived female was numbered. Females which appeared in the same vial were assigned the same number but a different index. Of 26 daughters from XXY females, two died soon after hatching, one female was sterile and one gave rise to a particular progeny, which will be discussed separately. A group of 18 females produced standard progeny, namely: cn females, + and y, and cn males.

F_1 analysis demonstrated that the cn daughters have the maternal genotype and, when crossed to b j pr cn/T(Y;2)C males, these daughters consistly produce cn females and +, y and cn males. Wild type and yellow males have +;b j pr cn/T(Y;2)C and y;b j pr cn/T(Y;2)C genotypes, respectively. No progeny was obtained from matings between cn males and either b j pr cn females or C(2L); C(2R) females. Possibly, these males have an F(Y·2L),b pr/$2L)^T$; C(2R),cn genotype and are sterile because the Y is missing. An unexpected finding was the absence of b pr males in F_1. This may be explained by the poor complementation between the newly arisen F(Y·2L) and 2;$(Y·2R)^T$. Thus, it appeared that the cn females obtained have + and y chromosomes, as well as a $(2L)^T$ chromosome which, presumably, complements with $F(Y·2L)^T$,b pr. That cn females possess a newly formed F(Y·2L),b pr chromosome was proven by crossing them to b j pr cn/T(Y;2)C,b j pr males, that have a $(2L)^T$ element marked with the genes b j pr (Table 4). This type of cross differs from the preceding in that the progeny contains, besides cn daughters, b pr cn daughters which possess F(Y·2L),b pr. It should be noted that all the cn females involved in matings to b j pr cn/T(Y;2)C,b j pr

Table 2. Summary of counts of the offsprings of XX and XXY females, mated to b j pr cn/T(Y;2)C males

Genotype of females	Phenotype of offspring											Total offspring number
	♀ b pr cn	♂ b pr cn	♀ +	♂ +	♂ y	♀ cn	♂ cn	♂ y; cn	♂ b pr	♂ y; b pr	Others	
XX												
Experiment 1	108	5	–	–	32	–	–	2	–	–	♀ y; b pr cn ♀ pr; cn	149
Experiment 2	139	12	–	–	30	2	–	–	–	–	♀ b j pr cn 2 ♀ y	186
Total	247	17	–	–	62	2	–	2	–	–	5 individuals	335
XXX												
Experiment 1	79	18	5	18	16	12	–	2	1	–	♀ b cn	152
Experiment 2	220	41	2	65	36	14	2	1	13	2	♀ b j pr cn ♀ y; b pr	398
Total	299	59	7	83	52	26	2	3	14	2	3 individuals	550

Table 3. Results of test cross of cn females to b j pr cn/T(Y;2)C males

Genotype of mother producing cn female	Strain	Offspring of cn female				Total number of offspring	Commentary
		♀ cn	♂ +	♂ y	♂ cn		
XX	33	–	–	–	–	–	Sterile
Experiment 1	100	–	–	–	–	–	Sterile
XXY	16_1	8	–	–	–	8	
Experiment 1	16_2	8	2	4	1	15	
	45	29	7	6	2	44	
	66	9	–	–	1	10	
	129_1	72	7	3	3	85	
	129_2	40	8	1	1	50	
	129_3	32	10	11	12	65	
	145	–	–	–	–	–	Exceptional offspring
XXY	36_3	35	9	4	1	49	
Experiment 2	38	11	1	1	–	14	b pr males in offspring
	43	2	–	–	–	2	
	56	24	7	2	2	35	
	71_1	11	3	2	–	16	
	71_2	17	13	10	1	41	
	71_3	12	3	3	–	18	
	121_1	–	–	–	–	–	Sterile
	121_2	–	–	–	–	–	Sterile
	121_5	1	6	–	1	8	
	246_1	–	–	–	–	–	Sterile
	339_1	11	1	2	–	14	
	339_2	9	–	2	1	12	
	339_3	21	2	6	1	30	
	Σ 24	352	79	57	27	516	

Table 4. Results of a test cross of cn females to b j pr cn/T/Y;2)C, b j pr males

Strain	Number of females mated	Offspring of cn females						Total number of offspring
		♀ cn	♀ b pr cn	♂ +	♂ y	♂ cn	♂ b pr cn	
16_1	2	–	14	2	–	–	–	16
16_2	4	25	21	19	3	–	1	69
45	5	16	56	34	23	3	1	133
129_1	4	15	44	27	16	7	–	109
129_2	4	6	16	23	–	2	–	47
129_3	3	7	16	3	3	2	–	31
36_3	9	14	59	28	11	7	2	121
56	16	5	16	10	2	–	–	33
71_1	9	9	1	–	1	–	–	11
71_2	9	22	26	16	–	2	1	67
71_3	16	20	23	18	–	–	2	63
339_1	25	55	128	26	13	8	–	230
339_2	22	23	95	17	–	4	–	139
339_3	24	18	71	19	4	4	–	116
Σ 14	152	235	586	242	76	39	7	1185

Table 5. Results of a test cross of cn females to sc^8 · Y/y; C(2L)RM, b pr; C(2R)RM, cn males

Strain	Number of females tested	Offspring of cn females						Total number of offspring
		♀ cn	♀ y; cn	♀ b pr cn	♀ y; b pr cn	♂ cn	♂ b pr cn	
16_1	4	10	–	8	–	14	16	48
16_2	4	2	6	2	6	4	9	29
45	5	7	–	10	–	4	8	29
66	1	–	–	–	–	–	–	–
129_1	4	26	3	25	7	40	40	141
129_2	4	15	4	13	2	25	22	81
129_3	4	26	12	22	7	29	28	125
36_3	13	24	2	24	4	14	35	103
56	12	26	3	26	5	16	35	111
71_1	3	3	–	5	–	5	6	19
71_2	13	5	4	11	2	11	15	48
71_3	6	7	1	9	–	4	3	24
339_1	20	31	11	27	7	39	45	160
339_2	8	30	3	31	2	33	31	130
339_3	36	49	7	45	4	41	53	199
Σ 15	137	261	57	258	46	279	346	1247

males, had b pr cn daughters in the first generation and, hence, were $(2L)^T/F(Y\cdot 2L)$, b pr heterozygotes. Females $(2L)^T/(2L)^T$; C(2R),cn seem to arise only rarely among the progeny of cn females because of their low viability.

Matings between cn females and sc^8 · Y/y;C(2L)RM,b pr;C(2R)RM, cn males (Table 5) demonstrated the presence of the C(2R),cn compound and, concomitantly, the absence of regular disjunction of F(Y·2L),b pr and $(2L)^T$ chromosomes in cn females. This should occur only of the Y – derived material were present in the newly arisen chromosome and if this chromosome paired regularly with the X. Eleven of the 18 half-translocations did not have the y^+ marker in the Y chromosome; these produced y daughters and seemed to contain the short arm of this chromosome (Table 5). In one case (stock No. 38), a half-translocation included y^+ Y. The progeny of cn females (stock No. 38) in crosses to b j pr cn/T(Y;2)C (Table 3) males gave rise to a small number of b pr males. The progeny from matings between these males and y;b j pr cn females confirmed the presence of the y^+ marker in the F(Y·2L),b pr chromosome from stock No. 38. As to 6 of the 18 daughters of XXY females, it is unclear which arm of the Y chromosome was involved in the half-translocation.

Crosses between matroclinous cn females to b j pr cn males were sterile, as expected. Both cn daughters of XX females, when crossed to b j pr cn/T(Y;2)C males, produced no progeny. The genotype of one of these females (No. 33, Table 3) was clarified by mating her to compound tester males. It was found that, in addition to the C(2R)RM, cn compound, she possesses the newly arisen C(2L),+ compound, which resulted from $(2L)^T$ in a male. These spontaneous arisal compounds in *Drosophila* females has been described earlier (Chadov 1970; Chadov and Davydova 1971; Chadov et al. 1970).

Females of stock No. 145 (Table 3), mated to b j pr cn/T(Y;2)C males, gave rise to exceptional progeny: 34 cn and 26 b j pr cn females, 5 pr cn and 4 b j cn females, 14 yellow and 19 wild type males. Being heterozygous for yellow, these females could not have arisen from contamination and most have carried b j pr cn and cn chromosomes. From an F_1 analysis, it emerged that each wild type and yellow male had a paternally derived T(Y;2)C chromosome and a maternally derived b j pr cn chromosome. None had a cn chromosome. Subsequent analysis showed that homozygotes for cn autosomes were unviable. Thus, the cn chromosome was considered to be a translocation composed of $(2L)^T$ and F(Y·2R),cn. The latter is a half-translocation resulting from a C(2R),cn – Y interchange (Table 1).

From this genetic analysis of cn females, it follows that the daughters of XXY females contain F(Y·2L),b pr half-translocations. In one case a half-translocation involving 2R was the result of a Y – C(2R) interchange. The occurrence of half-translocations, involving either 2L or 2R, was never proven in XX females.

3.2 *Males b pr and y; b pr*

All 16 males (14 wild type males and 2 y; b pr males) were produced by XXY females (Table 2). The predicted genotype of the former was y;b j pr cn/F(Y·2L),y^+ b pr; $(Y\cdot 2R)^T$ and that of the latter was y; b j pr cn/F(Y·2L),b pr; $(Y\cdot 2R)^T$. Table 6 shows the results of test-crosses of b pr males to y; b j pr cn females. Five males were sterile; the rest produced offspring conforming with the expected genotype. There was a small number of unusual individuals among their progeny: b pr females and sterile y;b j pr cn males. Their occurrence may be attributed to the formation of X^O;2 and X; $(2L)^T$; $(Y\cdot 2R)^T$ gametes in +/T(Y;2)C males (Dobzhansky 1931). Consequently, the males contained newly arisen half-translocations. They included, in 10 stocks, material from the long arm of the Y chromosome, with the y^+ marker, and the short arm in one stock (No. 246_2, Table 6).

3.3 *Female y;b pr*

XXY females gave rise to a single y;b pr daughter in Experiment 2. Judging by phenotype this female arose from

Table 6. Results of a test cross of b pr and y; b pr males to y; b j pr cn females

Strain	Male phenotype in the strain	Offspring of b pr male					Total number of offspring
		♀ y;b j pr cn	♂ b pr	♂ y;b pr	♀ b pr	♂ y;b j pr cn	
34	b pr	–	–	–	–	–	–
36_1	„	2	1	–	–	–	3
36_2	„	153	88	–	2	3	246
121_3	„	122	91	–	–	1	214
121_4	„	112	83	–	1	–	196
233_1	„	–	–	–	–	–	–
233_2	„	103	57	–	–	2	162
233_3	„	61	45	–	–	–	106
242	„	–	–	–	–	–	–
256	„	–	–	–	–	–	–
299_1	„	45	51	–	–	2	98
299_2	„	30	22	–	1	–	53
299_3	„	122	94	–	–	–	216
299_4	„	82	67	–	1	2	152
246_2	y;b pr	39	–	31	–	–	70
284	„	–	–	–	–	–	–
Σ 16		871	599	31	5	10	1516

a y/y;2L,b pr egg and a 2;$(Y \cdot 2R)^T$ sperm. By mating her to XY, y; b j pr cn males, it was shown that she bears two X chromosomes with the gene y as well as b j pr cn and b pr autosomes. The actual constitution of the b pr autosome was established, when y;b pr sons were analysed. Seventy-seven y;b pr males, mated to 150 y;b j pr cn females, produced only 7 y;b pr daughters and 72 sterile y;b j pr cn sons. It was concluded that chromosome distribution in the y;b pr males gives rise, predominantly, to aneuloid gametes and that euploids are exceptions. Euploid gametes are so formed that all the sperm with an X contain, in an obligatory way, a b pr chromosome, and all the sperm without X, contain a b j pr cn chromosome. This was taken to mean that X and b pr chromosomes are linked. It was concluded that the y;b pr female contains a F(X;2L),y b pr half-translocation involving the entire X and 2L,b pr arm. The genotype of this female was specified as $\frac{y;b\ j\ pr\ cn}{F(X \cdot 2L),y\ b\ pr;(Y \cdot 2R)^T}$.

3.4 *Cinnabar Males*

Three cn males and two y;cn males appeared among the progeny of XXY females and two y;cn males among the progeny of XX females (Table 2). All the males were infertile. Efforts to obtain progeny from matings of these males to y;b j pr cn females, as well as to compound females, were not successful. Based on phenotypic criteria, half-translocations are possible in cn males (Table 1) and it was expected that the absence of the entire Y chromosome would confer sterility to the majority of these males. A constitution of this kind seems unlikely in as much as the type of sperm needed for their complementation is very rare. The genotype of these males remains an open question; it cannot be ruled out that they contain a newlyformed C(2L),+ compound, as one of the cn females do.

3.5 *Females b pr cn*

The great majority of the progeny of XX and XXY females were represented by b pr cn females. The results of the test crosses to b j pr cn males made it possible to distinguish three groups of b pr cn females. Group 1 was very fertile and produced 6 offspring classes: b j pr cn and b pr cn daughters, b j pr cn and b pr cn sons as well as y;b j pr cn and y;b pr cn sons. In females of this group, the wild X and b j pr cn autosome were paternally derived; the yellow X chromosome, as well as the newly arisen b pr cn chromosome, were maternally derived. The latter was formed during the reconstitution of autosomal compounds and the union of 2L and 2R in the sequence characteristic of the structurally normal autosome 2.

Females of group 2 were composed of triploid females. Although normal with respect to egg production, these females produced a large number of late embryonic lethals (brown eggs) and showed decreased fertility. The number of offspring from each female rarely exceeded 20. The offspring consisted of b pr cn and b j pr cn individuals, some of which were yellow females and intersexes. Triploid females resulted from the fertilization of 2n eggs with X^+.b j pr cn sperm.

Females of group 3 produced no progeny in crosses to b j pr cn males. Some laid no eggs, others laid eggs turning brown with time (late embryonic lethals) and the rest laid many white eggs. The origin of females of Group 3 is unclear.

3.6 *Wild Type Males*

XXY mothers produced males of the wild type (Table 2). These varied in their phenotype. Some were phenotypically intersexes which were infertile in matings to y;b j pr cn females, as well as to C(2L); C(2R) females. These males possibly resulted from fertilization of 2n eggs with $(2L)^T$; $(Y \cdot 2R)^T$ sperm. Some of the wild type males were phenotypically normal. In the test crosses to the y;b j pr cn females, these males produced b pr cn daughters and y sons. The results of this cross and F_1 analysis indicated that these wild type males contained a newly arisen b pr cn chromosome and T(Y;2) translocation.

3.7 *Yellow Males*

XX and XXY mothers and y sons are shown in Table 2. Some were sterile in matings to y;b j pr cn females, the rest gave y;b pr cn daughters and y sons. Quite possibly, these males contain a b pr cn chromosome plus a T(Y;2)C translocation.

3.8 *Black Purple Cinnabar Males*

These were produced by XX and XXY mothers (Table 2). Some showed phenotypic characters of the intersexes. The majority was phenotypically normal but all were sterile in matings to compound females as well as to y;b j pr cn females. The genetic constitution of these males in unclear. It seems unlikely that they originated in the same way as (Table 1) b pr cn males; if they did then y;b pr cn males would appear among the offspring, and this was not the case for XX and XXY mothers. It appears more probable that fertilization of X^O;C(2L); C(2R) eggs with X^+; 2^O sperm (see Table 1, type 'D' sperm) was the mechanism underlying the formation of these b pr cn males.

Seven wild type females were also observed among the

offspring from XXY mothers (Table 2). Three of these 7 females were the result of the union of X;2^{O} egg with X^{+};b j pr cn/T(Y;2)C sperm (Table 1, ABCD sperm); two females had a newly arisen b pr cn chromosome and a X^{+}; $(2L)^{T}$; $(Y \cdot 2R)^{T}$ paternally derived set (Table 1, ACD sperm). Two females died before the test cross was started.

The origin of the phenotypically different flies, listed in the column 'Others' of Table 2, is unclear. They produced no progeny in matings to y;b j pr cn males or compound males. The females that gave progenies were an y;b pr female (already mentioned) and two y females resulting from the union of y/y; 2^{O} eggs with X^{O};b j pr cn/T(Y;2)C sperm.

3.9 F_1 Distribution Pattern

The establishment of the distribution pattern of offspring, arising under the effect of a genetic event, makes it possible to decide whether the event is mitotic or meiotic. The experimental design did not include any analysis of F_1 distribution in the vial cultures. However, there were clear-cut differences in the F_1 distribution pattern between individuals with half-translocations and those without. Tables 7 and 8 show the distribution of flies with half-translocations in successive broods and cages with vial cultures in each replicate mating of XXY females ('Material and Methods'). In all, there are 48 individuals: 26 cn females, 2 cn males, 3 y;cn males, 14 b pr males, 2 y;b pr males and an y;b pr female. Their phenotypes testify to the presence of half-translocations. Test cross data demonstrate the presence of half-translocations in 31 of 48 individuals. Four died prior to analysis (these are marked with [a] and 13 produced no offspring in the test crosses (these are designated 'st'). The latter 17 may be tentatively referred to as individuals with half-translocations. Every individual in the Table was numbered in the course of F_1 examination. Flies that appeared in the same vial have the same number assigned but different indices.

From the Tables it is evident that half-translocations arose in clusters. Five of 15 flies arose in 2 clusters in Experiment 1 (Table 7), and 24 of 33 arose in clusters in Experiment 2 (Table 8). More than half of the flies in Experiment 2 were obtained in matings performed in cage No. 3 (Table 8). It cannot be excluded that they all were produced by a single female. However, it is very doubtful that a Y;C(2L) translocation – bearing female was included in the experiment; if so, even a single female would produce much more progeny than was actually present in cage No. 3. This holds true for other vial cultures in which there were not more than 3-5 flies per cluster. Obviously, chance formation of clusters is unlikely in view of the very low interchange rate.

The data obtained indicate that spontaneous interchanges do occur in mitotically dividing oogonia. A single interchange leads to the appearance of an individual or of a whole cluster of individuals with identical half-translocations. Under the experimental conditions used, the appearance of individuals with half-translocations in different vials of the same brood may be considered as independent events. In successive broods events are independent when they are registered in different cages. There are 20 independent events of half-translocation formation (9 in Experiment 1, and 11 in Experiment 2) provided

Table 7. Summary of counts by brood and vials of offspring with half-translocations (XXY mothers, experiment 1)

Brood number	Cage number							Number of flies for brood
	1	2	3	4	5	6	7	
1	–	No. 6[a] ♀ cn No. 3 ♂ y;cn(st)	No. 16_1 ♀ cn No. 16_2 ♀ cn	–	No. 45 ♀ cn	–	No. 66 ♀ cn	6
2	No. 34 ♂ b pr(st)	No. 42[a] ♀ cn	–	–	–	–	–	2
3	No. 48 ♂ y;cn(st)	–	–	–	No. 95[a] ♀ cn	–	–	2
4	–	–	–	No. 96[a] ♀ cn	No. 129_1 ♀ cn No. 129_2 ♀ cn No. 129_3 ♀ cn	–	No. 145 ♀ cn	5
5	–	–	–	–	–	–	–	0
6	–	–	–	–	–	–	–	0
7	–	–	–	–	–	–	–	0
	2	3	2	1	5	0	2	15

[a] Flies died prior to analysis
(st) = flies produced no offspring in the test crosses

Table 8. Summary of counts by brood and vials of offspring with half-translocations (XXY mothers, experiment 2)

Brood number	Cage number								Number of flies per brood
	1	2	3	4	5	6	7	8	
1	No. 9 ♀ y; b pr	–	No. 36_1 ♂ b pr No. 36_2 ♂ b pr No. 36_3 ♀ cn	No. 38 ♀ cn No. 43 ♀ cn	No. 56 ♀ cn	No. 71_1 ♀ cn No. 71_2 ♀ cn No. 71_3 ♀ cn	–	–	10
2	–	–	No. 121_1 ♀ cn(st) No. 121_2 ♀ cn(st) No. 121_3 ♂ b pr No. 121_4 ♂ b pr No. 121_5 ♀ cn	–	–	–	No. 147 ♂ y;cn(st) No. 151 ♂ cn (st)	–	7
3	–	–	No. 233_1 ♂ b pr(st) No. 233_2 ♂ b pr No. 233_3 ♂ b pr	–	–	No. 242 ♂ b pr(st) No. 246_1 ♀ cn(st) No. 246_2 ♂ y;b pr No. 246_3 ♂ cn(st)	No. 256 ♂ b pr(st)	–	8
4	–	No. 284 ♂ y;b pr(st)	No. 299_1 ♂ b pr No. 299_2 ♂ b pr No. 299_3 ♂ b pr No. 299_4 ♂ b pr	–	–	–	–	–	5
5	–	–	No. 339_1 ♀ cn No. 339_2 ♀ cn No. 339_3 ♀ cn	–	–	–	–	–	3
6	–	–	–	–	–	–	–	–	0
7	–	–	–	–	–	–	–	–	0
	1	1	18	2	1	7	3	0	33

(st) = Flies produced no offspring in the test crosses

that all the flies listed in Tables 7 and 8 are taken into account; this number is 10, when only those flies are taken into account in which the presence of half-translocations was proven in the test cross. The majority of individuals with half-translocations were produced in the first broods. 45 such individuals (15+30) were detected in broods 1-4, and only 3 in broods 5-7. The decrease in the number of flies with half-translocations seems to be related to the smaller number of eggs laid by the end of the experiment due to the increasing death of parents and decreasing egg productivity of females with age. For example, the number of offspring produced by XXY females in Experiment 2 decreased in 7 successive broods as follows: 121-106-61-58-19-16-17.

The distribution of compound restitution events differed considerably from that of half-translocation events. The interchanges between the compound autosomes seem to occur during meiosis. Of 293 cases containing the 2L · 2R, b pr cn chromosome (confirmed by the test-cross), there were two flies per vial in 8 cases and 3 per vial in 3 cases.

None of the 191 triploid flies arose in clusters.

4 Discussion

A summary of the progeny, obtained from XX and XXY females, is presented in Table 9. All progeny were classified according to genetic origin. The progeny were composed of individuals produced as a result of the reconstitution of compounds, the formation of 2n eggs and half-translocations involving 2L and 2R. Individuals whose genotype is unclear are listed separately. In matings to tester flies, these individuals gave no progeny; their phenotype also provides no clue to their genetic origin. In the column 'Half-translocation formation', the individuals sterile in the test crosses are represented by (st).

Thus, the first aim of the experiment was achieved. By means of the complementation method about 50 spontaneous interchanges were obtained. There were 45 spontaneous interchanges in XXY females and 4 interchanges in XX females, judging by phenotypic criteria; there were 31 spontaneous interchanges in XXY females, and no interchanges in XX females, according to data of progeny analysis. The crosses performed do not permit the accurate estimation of the interchange frequency for XX and XXY mothers; however, taking into account the total number of parents and offspring, it is clear tht the interchange frequency in XXY females is an order of magnitude higher than that in XX females and that non-homologous pairing indeed plays an important role in translocation formation.

The most frequent interchange in XXY females was Y – C(2L). This interchange type occurred in 29 of the 30

Table 9. Genotypic constitution of offspring of XX and XXY females

Genotype of females	Number of experiment	Restitution of compounds			2n egg formation		Half-translocation formation			Individuals of unknown nature				Other unknown phenotypes	Total offspring number
		♀ b pr cn	♂ +	♂ Y	♀ b pr cn	♂ +	♀ cn	♂ cn (st)	♂ Y,cn (st)	♂ b pr	♂ Y,b pr	♂ Y (st)	♀ Y,b pr (st)	♀ b pr cn (st)	♂ b pr cn (st)		
XX	1	33	–	19	27	–	–	–	2	–	–	–	8	44	5	11	149
	2	51	–	24	37	–	1	–	–	–	–	–	6	48	12	7	186
	Total	84	–	43	64	–	1	–	2	–	–	–	14	92	17	18	335
XXY	1	27	6	13	20	12	12	–	1	1	–	–	2	18	18	22	152
	2	77	30	22	66	35	14	2	2	13	2	1	14	73	41	6	398
	Total	104	36	35	86	47	26	2	3	14	2	1	16	91	59	28	550

(st) = Flies produced no offspring in the test crosses

proven test cross cases of half-translocation formation. The new chromosome contained 2L material (presence of the genes b and pr) and Y-material (presence of y^+). The presence of Y-material was undoubtedly due to the presence of y^+ in only 11 of 29 cases (cn females No. 38 and 10 b pr males). The other 18 half-translocations seemed to contain Y^S. Indirect evidence for the presence of Y-material in these half-translocation was the high rate of the non-disjunction of $(2L)^T$ and F(Y·2L) chromosomes in cn females, resulting in the appearance of cn and b pr cn sons and wild type daughters in matings of cn females to b j pr cn/T(Y;2)C males (Table 3) and b j pr cn/T(Y;2)C, b j pr males (Table 4). Other evidence was the appearance of offspring from matings of cn females to compound males (Table 5). In the latter mating, y;cn females appeared in 11 strains, and it was suggested that their half-translocations involved Y^S without the y^+ marker. From all these observations, it follows that half-translocations contained different, possibly reciprocal regions, of the Y chromosome. These half-translocations may also differ in 2L material. Matings of cn females to b j pr cn/T(Y;2)C b j pr males (Table 3), as well as of these females to b j pr cn/T(Y;2)C, b j pr males (Table 4), demonstrated that F(Y·2L), b pr half-translocations, contained in the majority of cn females, are lethal when associated with $2;(Y\cdot 2R)^T$, and, hence, these females have no b pr males in their progeny. The only exception was strain No. 38 (Table 3). However, it is precisely in this chromosome combination, F(Y·2L), that b pr half-translocations occurred in b pr males produced by XXY females. These half-translocations did not decrease male viability, nor fertility. They presumably differed from half-translocations carried by cn females in 2L material.

During the maintenance of stocks with half-translocations it was observed that females from different stocks differed in viability and fertility. This prompted the idea that they bear half-translocations differing in 2L material. In compound 2, breaks may take place in distinct sites of the centromere region during interchanges with the Y.

Half-translocations with Y^L occurred predominantly in males, while those with Y^S were restricted to females. The material of different Y chromosome arms was hardly the cause of the different death of zygotes with X;F(Y^S·2L) and X;F(Y^L·2L);C(2R) maternal set. It seems that this phenomenon is either caused by meiotic disjunction F(Y^L·2L)-C(2R) in XXY females, or is the result of the specific position of Y and C(2L) during interchange.

Interchange Y – C(2R) occurred once. This was not contrary to expectations. However, such an interchange should be recovered rarely since the corresponding complementary gametes arise only infrequently.

Half-translocation X·2L was not expected. Its occurrence is evidence of the possible pairing between the X-chromosomes and C(2L). This X and C(2L) association appears even possible during meiotic non-homologous pairing in XXY females. For example, during the pairing of an X to a Y, the other X may pair with the C(2L) chromosome. Support comes from our previous observations that the formation of two pairs of non-homologously paired chromosomes is characteristic of meiotic non-homologous pairing (Chadov et al. 1970; Chadov and Davidova 1971).

In this paper, the distribution of flies with half-translocations in vials and broods was analysed. The appearance of F(Y·2L), b pr individuals allows the conclusion that the C(2L)-Y interchange occurs in the pool of mitotically dividing sex cells. Cells in which interchanges take place pass through several mitotic divisions, and an individual may give rise to a cluster of offspring with half-translocations. We believe that mitotic interchanges should lead to both half-translocations and translocations. Chromosome translocations arise first. When the elements of a translocation part during meiosis, individuals with half-translocations arise; if not, individuals with translocations arise. In our experiments, gametes with a translocation consisting of Y^L·2L and Y^S·2L would have been rare because both interchange products regularly part during meiosis. However, the data obtained do not rule out the possibility that some individuals have resulted from meiotic pairing and interchange.

From this study on mitotic interchanges there is definitely more sense in relying on the search for half-translocations than for translocations, which should be observed more rarely because of the regular disjunction of the translocated elements. This seems to be also true for meiotic interchanges between non-homologues. Meiotic interchanges are associated with the formation of pseudobivalents, the disjunction of which results in the disjunction of translocated elements as early as at M_1 (Parker 1968; Parker and Williamson 1976). Consistent with thus line of reasoning are the data of Panshin (1941a, b) which indicates that radiation-induced translocations are rarer than half-translocation as a result of the frequent non-union of chromosome fragments. And, finally, the complementation method of detecting half-translocations in F_1 has, indisputably, a higher resolving capasity than the 'classical' one used for translocations.

Analysis of translocation formation provides a new approach to the non-homologue pairing problem developed earlier on the basis of chromosome distribution data. The appearance of clusters of individuals with half-translocations is direct proof of the occurrence of mitotic pairing in XXY females. Such interchanges did not occur in XX females. This again confirms the idea that non-homologue pairing is decisive in the formation of spontaneous translocations. The absence of 2L half-translocations in the offspring of XX females may be attributed to be absence of the Y; however, if the C(2L) exchanges with other chro-

mosomes, other types of 2L half-translocations would be detected. These types would presumably include in addition to 2L, material of autosome 4, regions of the X-chromosome, as well as telomeric pieces of large autosomes. Translocations of these types were not detected in XX females. However, to eliminate ambiguities concerning half-translocations in XX females, a rigorous control experiment was needed. Translocation formation was analysed in X/XY;C(2L);C(2R) females. These females had a Y-chromosome, but, being a component of the XY compound, this Y did not pair with autosomal compounds. Interchange data on X/XY females, as well as non-homologous pairing – interchange relationships, will be considered in a separate paper.

Two rare events were disclosed in the experiments performed: the reconstitution of compounds and the formation of 2n egg cells. These events have been examined in detail elsewhere (Chadov 1976); only some aspects of compound restitution are discussed here.

Bateman (1968) was the first to describe X-ray induced restitution of compounds. Spontaneous restitution of compounds has been rarely observed in *Drosophila melanogaster* males (Chadov et al. 1970). Compound restitution is, undoubtedly, the result of an exchange in the pericentromeric region of compounds. It appears to be a specific process. On the one hand, interchanges between compounds seem to be of a crossing-over type. In fact, in most stocks, compounds contain homologous blocks in the pericentromeric heterochromatin (Rasmussen 1960; Holm 1976), and meiotic interchanges of crossing-over type between compounds are possible. In this study, the distribution pattern of compound restitution events is in favour of a meiotic origin of C(2L)-C(2R) interchanges. On the other hand, some data indicate that autosomal compounds associate in the manner of non-homologous pairing. In fact, compounds are randomly distributed during male meiosis (Holm et al. 1967; Holm 1976) because non-homologous pairing does not occur in males (Grell 1976). The compounds of XX females regularly disjunct during meiosis but they are distributed independently of each other as a result of the introduction of the Y-chromosome into the female genome (Grell 1970). Thus, in their distribution pattern, autosomal compounds are identical to non-homologues, in spite of the presence of homologous heterochromatin blocks in their centromeric regions. It follows that compound restitution is a two-step process in which non-homologous pairing provides the association of compounds and homologous pairing provides exchange between compounds.

Compound restitution may take place during meiosis and mitosis. In all probability, the meiotic variant occurs in females; their compound restitution frequency is about 1-2 orders of magnitude higher than that of Y-C(2L) interchanges in females. The mitotic variant of compound interchanges occurs in males (Chadov, Chadova 1977). The frequency of these interchanges is of the same order of magnitude as that of Y-C(2L) interchanges in females. It is not clear why the same interchange is of meiotic origin in one case and mitotic in the other.

The first attempt to clarify the relationships between translocation formation-non-homologue pairing is presented here. The data obtained are only qualitative. However, the method developed for the detection of half-translocations may be hopefully applied to some aspects of the problem of non-homologous interchange.

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