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Meiotic behaviour of compound chromosomes in tricomplex heterozygotes in *Drosophila melanogaster*

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SUMMARY

A tricomplex heterozygote has a synthetic chromosome complement consisting of four pairs of arms of chromosomes 2 and 3 in the form of a compound of two homologous arms (a homocompound) and of three compounds of two nonhomologous arms (heterocompounds), each being homologous to an arm of different compounds. In meiosis, pairing of homologous arms results in the formation of a single and a multiple configuration that are structural equivalents of a univalent and a trivalent. Data are presented indicating that, in a given complement, the pattern of the distribution of three heterocompounds at division I is the same in males and in females. The distribution depends on the arrangement of the 2nd and the 3rd chromosome centromeres in the trivalent. In configurations presumed to be homocentric (all three chromosomes having homologous centromeres), the distribution was random or nearly random while, in configurations presumed to be heterocentric, the distribution appears non-random, with one of the segregation alternatives being roughly twice as frequent as either one of the two other alternatives that were more or less equal in frequency. The results could be explained in terms of the 3rd chromosome centromere being 'strong' in directing the two 2nd chromosome centromeres to the opposite pole at division I, an explanation implying a functional differentiation of the two autosomal centromeres or adjacent sequences. Data are also presented showing that in females the distribution of the homocompound is non-random with respect to the distribution of the heterocompounds; the homocompound was recovered preferentially together with the single one of the three heterocompounds. This is inconsistent with the prediction based on the theory assuming an existence of two independent pairing pools.

1. INTRODUCTION

Special chromosomes and chromosome complements have been constructed for the purpose of studying specific cytogenetic problems in *Drosophila melanogaster*. Tricomplex heterozygotes (Puro, 1973) have an autosomal complement consisting of a metacentric compound of two homologous arms and of three metacentrics, each partially homologous to the other two. Such complements provide material for an experimental analysis of chromosome distribution in meiotic configurations which are structural equivalents of a trivalent plus a univalent. It is the purpose

of this paper to investigate the segregation patterns of such tricomplex heterozygotes.

2. TERMINOLOGY

In Drosophila genetics, the word 'compound chromosome' refers to a combination of chromosomes or chromosome arms ordinarily existing separately which share a common centromere and behave as a unit in division (Novitski, 1954). For

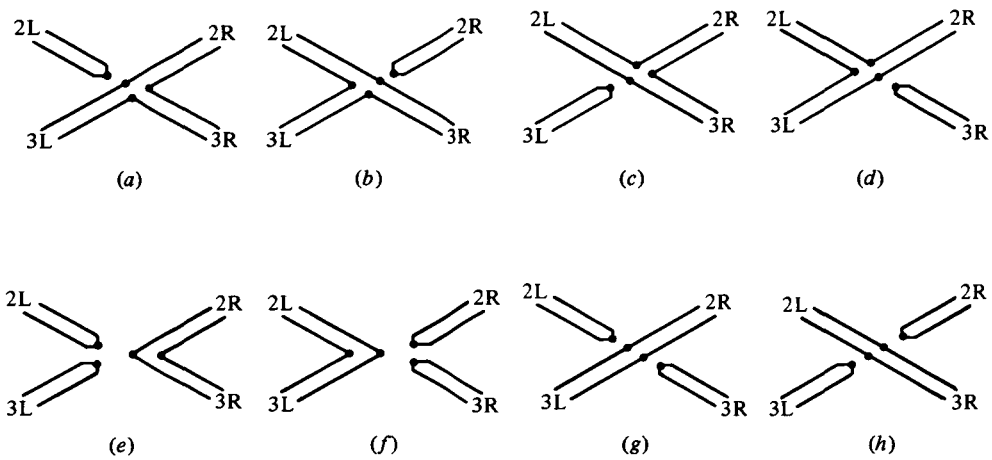

Fig. 1. Diagrams of the large autosomes of *Drosophila melanogaster* in some of the synthetic complements. (*a–d*) Upper row, the four types of tricomplex heterozygotes. Each one of the complements is composed of three metacentric heterocompounds, one pair of arms being present as a homocompound. Accordingly, each complement is fully defined by referring to the respective homocompound as follows: (*a*) C(2L); TRI, (*b*) C(2R); TRI, (*c*) C(3L); TRI, (*d*) C(3R); TRI. By means of a more detailed type of designation, a reference to each individual heterocompound may be given (see the text). (*e–h*) Lower row, four types of complements each comprising a pair of heterocompounds and two homocompounds of different autosomal origin.

historical reasons the term is often applied only to combinations of homologous elements but, as pointed out by Novitski & Childress (1976), the original definition of the word compound does not imply such a restriction. Accordingly, two metacentric autosomes (chromosomes 2 and 3) of *Drosophila melanogaster* may be considered to be compounds of two component arms that still exist as free acrocentrics in many other species of Drosophila (like *D. virilis*). In addition to such 'wild type' compounds (2L·2R and 3L·3R), four general types of compounds with two nonhomologous arms sharing a single centromere are possible: 2L·3R, 3L·2R, 2L·3L, and 2R·3R. Of these, the first two and the last two, respectively, may be generated as whole arm reciprocal translocations.

To distinguish between autosomal compounds with homologous *vs.* those with heterologous arms, the prefix homo- or hetero-is added. Accordingly, 'homocompound' is applied to those combinations of homologous autosomal arms originally called 'attached -2L', 'attached-2R', 'attached-3L', and 'attached-3R' (Rasmussen, 1960), irrespective of whether there were allelic or structural differences

between the two arms. 'Heterocompound', on the other hand, would refer to combinations of nonhomologous chromosomes or chromosome arms. This terminology is particularly useful in referring to the major autosomes of four tricomplex heterozygotes, and of other synthetic autosome complements now available for experimental analysis. Accordingly, tricomplex heterozygotes may be described as being composed of a metacentric homocompound and three metacentric heterocompounds, with each heterocompound having a homologous arm in common with the other two (Fig. 1 *a–d*). The ordinary strains carrying autosomal compounds (e.g. Holm, 1976) involve independently induced homocompounds of the left and right arms of the same autosome. In addition, two homocompounds of arms of different autosomes have been combined in pairs in all four possible ways (Fig. 1 *e–h*). Such strains were used in experiments to induce new autosomal heterocompounds (see below).

3. ORIGIN OF HETEROCOMPOUNDS AND OF THEIR CENTROMERES

There are two principal sources of origin for heterocompounds. First, reciprocal translocations involving whole arms of chromosomes (whole-arm transfers) have been induced in sperm (Muller, 1940) or in oocytes (Puro, 1985). A method of combining heterocompounds of different whole-arm transfers into a tricomplex has been published previously (Puro, 1973). Second, heterocompounds may be recovered directly upon mating irradiated females having standard chromosomes to males of any one of the strains diagrammed in Fig. 1 *e–h*. Of the four classes of offspring recovered in such an experiment (cf. Fig. 2), two are tricomplex heterozygotes (*a*, *b*), one combines two homocompounds and two heterocompounds of different origin (*c*), and one is equivalent to an ordinary translocation heterozygote with its two complementary heterocompounds of different origin (*d*). The four types of offspring can be distinguished phenotypically by means of marker genes located in the paternal homocompounds. More than a hundred new single heterocompounds have been recovered from such experiments (Puro, 1978, and unpublished). Each one of the independently induced compounds was provided with an identifying symbol consistent with the convention used to mark structural rearrangements (cf. Lindsley & Grell, 1968).

In most of the experiments reported and discussed in this paper, the heterocompounds used to construct the tricomplexes were derived from two whole-arm transfers, T(2; 3)N2-29 and T(2; 3)N2-46 (Puro, 1982). T(2; 3)N2-29 consists of an interchange between the left (or right) arm of chromosome 2 and the right (or left) arm of chromosome 3 (2L·3L; 2R·3R), whereas T(2; 3)N2-46 consists of an interchange between the left (or right) arms of the respective chromosomes (2L·3R; 2R·3L). Individual compounds may be designated accordingly, for example C(2L·3L)N2-29. In addition, another two heterocompounds, C(2R·3R)HT10 and C(2L·3R)HT26 were utilized. They were derived from the experiments diagrammed in Fig. 2.

Forming a heterocompound involves breakage and a reunion of the chromosomes at sites in pericentromeric heterochromatin proximal to essential genes. Exact mapping of the point of breakage is not possible with available methods. Therefore,

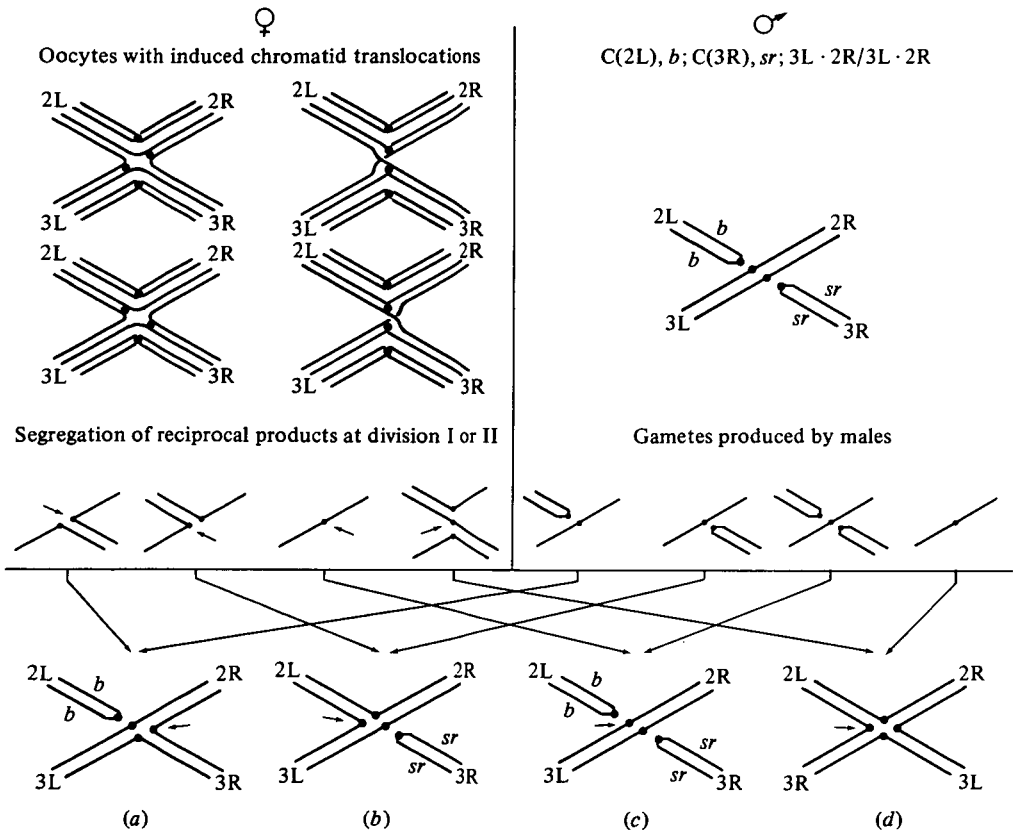

Fig. 2. A method for induction and recovery of heterocompounds involving the arms of chromosomes 2 and 3 of *Drosophila melanogaster*. Irradiated females having standard chromosomes are mated with C(2L); C(3R); 2R·3L/2R·3L males. Female gametes indicated are segmental aneuploids that are formed as a consequence of segregation, at either the first or the second division, of the reciprocal products of whole arm transfers. Small arrows point to centromeres of newly induced heterocompounds.

the position of the breaks with respect to the centromere is usually unknown; as a consequence, the chromosomal origin of the centromere of the heterocompound is usually unknown. Lacking information on the organization of the centromeres in Drosophila, it is possible that centromeres could be split and rejoined into a hybrid centromere. In the light of recent findings in yeast (Fitzgerald-Hayes, Clarke & Carbon, 1982; Bloom, Fitzgerald-Hayes & Carbon, 1983), such hybrid centromeres seem feasible. Nevertheless, it is assumed that at least in most of the autosomal heterocompounds, the centromeres are intact and were derived from either chromosome 2 or chromosome 3.

The break points of T(2; 3)N2-29 and T(2; 3)N2-46 with respect to the centromeres are unknown. Therefore, two possibilities for each one of the translocations should be considered (cf. Fig. 3). As far as the tricomplex complements derived from these translocations are concerned, four possible arrangements of the

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centromeres (A–D) must be considered. One complement is of a type that bears homologous centromeres in all three chromosomes (a homocentric condition) while, in the other three complements, one centromere is of nonhomologous origin (a heterocentric condition).

In a few cases the presumed origin of the centromeres of the induced heterocompounds can be inferred. C(2R·3R)HT10 and C(2L·3R)HT26 were induced in

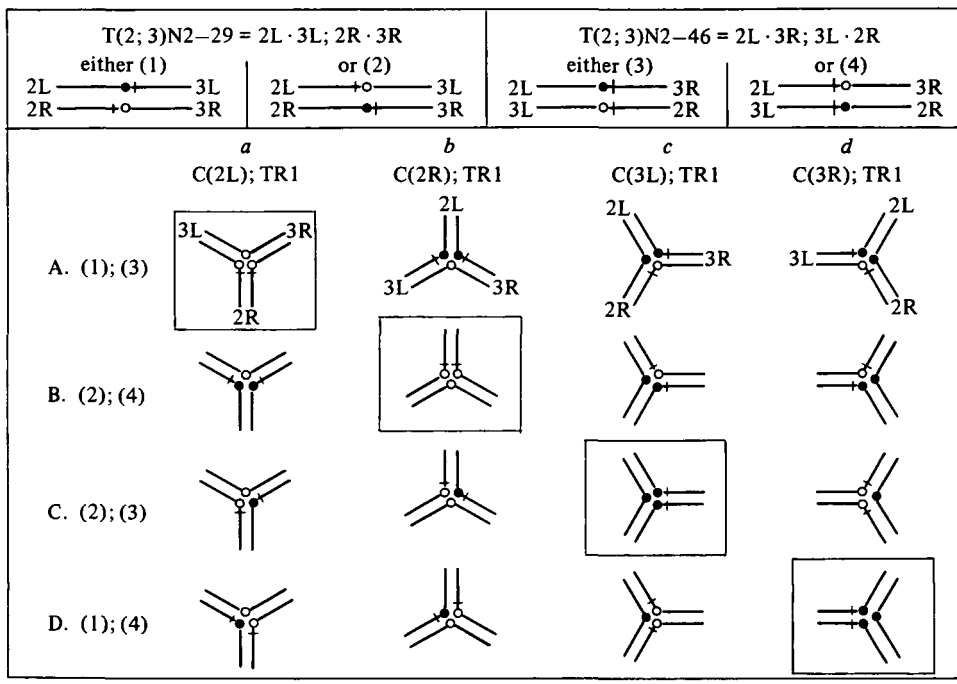

Fig. 3. A diagram illustrating four alternative arrangements of the centromeres (rows A–D) in a series of four tricomplex configurations (*a–d*) having one standard autosome (chromosome 2 or 3) and two heterocompounds derived from two whole-arm translocations of different type. In T(2; 3)N2-29 and T(2; 3)N2-46, the points of breakage with respect to the centromeres are not known. Consequently, two alternatives are possible. Of the four configurations in each series, one is homocentric (framed), the others are heterocentric. ●, ○ refer to chromosome 2 and chromosome 3 centromeres, respectively. The points of breakage are indicated by short lines across the chromosome. The homocompounds are not indicated by drawing.

females having standard chromosomes 2 and 3 that were heterozygous in repulsion for the centromere-linked markers *pr* and *hk* located in 2L, and dsx^{601} and p^{p} located in 3R (Puro, 1978). HT10 was recovered from an egg having, in addition to the newly induced C(2R·3R), a normal chromosome 3 (the leftmost gamete in Fig. 2), and was homozygous for p^{p}. HT26 was recovered from an egg having, in addition to C(2L·3R), both chromosome 2 and chromosome 3 (the rightmost gamete in Fig. 2), and was homozygous for p^{p}. Since homozygosis for a proximal marker is an indication of a recovery of sister chromatids, one of which is intact, the other constituting a cap for the broken heterologue, both C(2R·3R)HT10 and

C(2L·3R)HT26 are concluded to bear the 2nd chromosome centromere (consult fig. 3 and 4 of Puro, 1978, for details). Using a standard chromosome 2 plus HT10 and HT26 a tricomplex was constructed that is presumed to be homocentric for chromosome 2 centromere (i.e. a complement that corresponds to Cc in Fig. 3).

4. METHODS OF ANALYSIS

(i) *Genetic procedures*

Tricomplex heterozygotes can only produce genetically unbalanced gametes. Three different ways of orientation of three heterocompounds result in production

2:3 complement of the mating partner	2L Non-segregation				2R Non-segregation				3R Non-segregation			
STANDARD	–	–	–	–	–	–	–	–	–	–	–	–
C(3L); TR1	+	+	+	+	+	+	+	+	+	+	+	+
C(2L); TR1	+	+	+	+	–	–	–	–	–	–	–	–
C(2R); TR1	–	–	–	–	+	+	+	+	–	–	–	–
C(3R); TR1	–	–	–	–	–	–	–	–	+	+	+	+
C(2L); C(2R); 3/3	–	–	–	–	–	–	–	–	–	–	–	–
C(2L); C(3L); 2R·3R/2R·3R	+	+	+	+	–	–	–	–	–	–	–	–
C(2L); C(3R); 2R·3L/2R·3L	–	–	–	–	–	–	–	–	–	–	–	–
C(2R); C(3L); 2L·3R/2L·3R	–	–	–	–	+	+	+	+	–	–	–	–
C(2R); C(3R); 2L·3L/2L·3L	–	–	–	–	–	–	–	–	–	–	–	–
2/2; C(3L); C(3R)	–	–	–	–	–	–	–	–	+	+	+	+

Fig. 4. A diagram illustrating the twelve types of gametes produced by flies having a karyotype of one of the four tricomplex complements. On the left there are listed a standard and a number of synthetic karyotypes with the + and – designations indicating the types of gametes that can or cannot be complemented by gametes produced by flies having the respective complement.

of six classes of gametes. Of these, three gametes bear one heterocompound and the other three bear two heterocompounds. Each one of the complementary classes of the one-to-two segregations may or may not be accompanied by the homocompound. Thus twelve autosomally different types of gametes are expected (Puro, 1973).

Since viable offspring can only be produced by the union of complementary types of gametes, tricomplex heterozygotes are sterile when bred with flies having a standard chromosome complement. However, semifertile matings are obtained when flies having the same tricomplex karyotype are crossed. Other kinds of semifertile matings are possible (Fig. 4) but, in such matings, the proportion of offspring per given number of eggs laid may be still lower. Various kinds of semifertile matings were used for introducing marker genes into tricomplex stocks or replacing compounds by others of independent origin.

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A general scheme for studying segregation ratios of heterocompounds is given in Fig. 5. By using homozygous recessive marker genes (a through e) in each pair of arms of the heterocompounds, with the maternal and paternal chromosomes marked differentially, all six classes of offspring derived from the three segregation alternatives of the heterocompounds can be distinguished phenotypically. It is

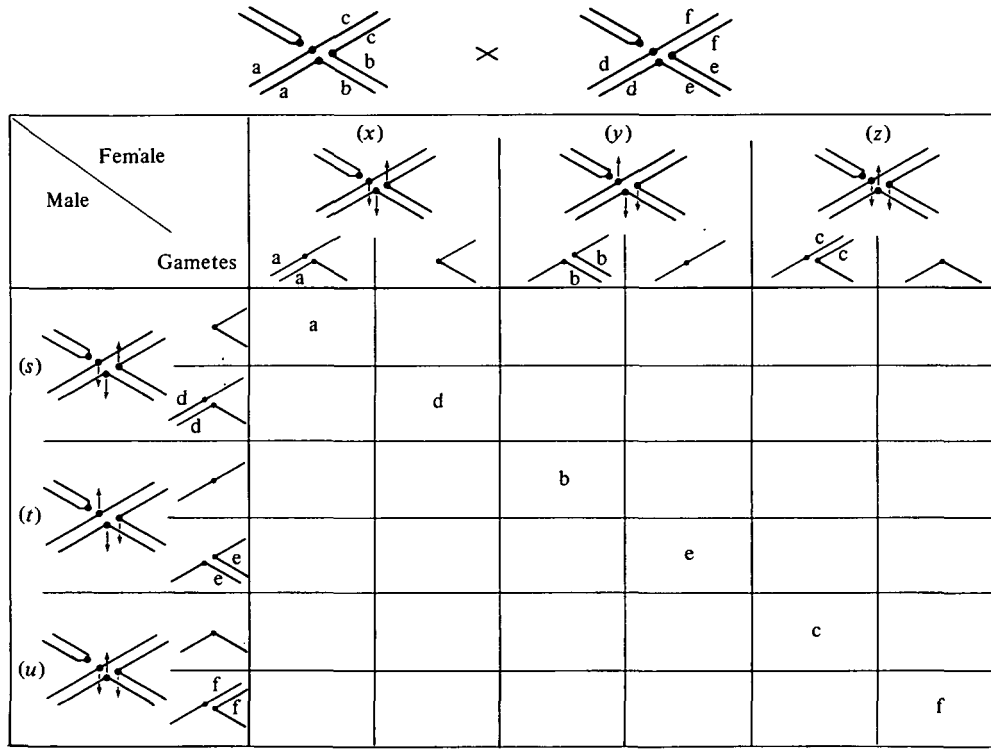

Fig. 5. A diagram showing the type of offspring produced by mating tricomplex heterozygotes having the same type of a complement. The six classes of offspring represent three alternative types of the one-to-two distribution of three heterocompounds. The letters a–f stand for appropriate recessive genes marking each pair of arms.

convenient to refer to each pair of the complementary one-to-two classes as being non-segregational for the arm indicated by the markers. Two markers in one of the parents plus three markers in the other suffice to give full information; then, one class is phenotypically wild type. If only one of the parental complements is fully marked, adequate information is obtained of half of the offspring, the other half falling in a single phenotypic (wild type) class.

Differential marking of parental homocompounds allows their distribution to be followed, too. Then, each of the six tricomplex segregation classes can be divided into two sub-classes according to whether the homocompound was of maternal or of paternal origin.

Mutant alleles showing full penetrance and good viability were used to mark the homocompounds and the pairs of arms of heterocompounds in experiments

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reported in this paper. Details of the genotypes are given along with the results for those cases when such an information bears some significance in interpretation of the results. Information on the mutant genes used are to be found in Lindsley & Grell (1968), Golubovsky & Zaharov (1972), and Puro (1982).

(ii) *Estimating gametic frequencies*

Deducing gametic proportions from ratios observed among the phenotypic classes is difficult because there is no *a priori* reason to suppose that the distribution of the chromosomes in males and in females should be the same. In other words, since the proportions x, y, and z need not be equal to the proportions s, t, and u, respectively, (Fig. 5) one can find a number of solutions to any ratio of $(a+d):(b+e):(c+f)$. However, assuming a similarity of segregational behaviour of heterocompounds in males and in females (an assumption for which evidence is given in the RESULTS), gametic proportions (x, y, z) may be calculated from the equation

$$p:q:r = x^2:y^2:z^2 \tag{1}$$

where p, q, and r represent the respective segregation classes (a+d, b+e, c+f) divided by the total number of offspring, and $x+y+z\ (=s+t+u) = 1$. Then,

$$x(=s) = \frac{\sqrt{p}}{\sqrt{p}+\sqrt{q}+\sqrt{r}} \tag{2}$$

and similarly for $y\ (=t)$ and $z\ (=u)$.

5. RESULTS

(i) *Variation in distribution of the heterocompounds*

A majority of the experimental results was obtained from matings of the strains bearing, as component parts of the tricomplexes, chromosome 2 or chromosome 3 plus two heterocompounds derived from T(2; 3)N2-29 and T(2; 3)N2-46. As an example of the data obtained, results of crossing flies of C(3R)RM; 2/C(2L·3L)N2-29/C(2R·3L)N2-46 homozygous for a series of different marker genes are given in detail in Table 1. Two general rules emerge from such matings. First, the frequencies of complementary types of the same segregation class are about equal, indicating a random recovery of one- *vs.* two-chromosome products of each of the three segregation alternatives. Second, reciprocal matings give essentially similar results (an exception to this rule is given later in this report).

Table 2 summarizes the results of some of the matings using the heterocompounds of translocations T(2; 3)N2-29 and T(2; 3)N2-46 in all combinations. While, in general, the proportion of each of three segregation classes do not show a significant variation between matings using the same complement, there is variation in distributions among different types of complements. Specifically, in the C(2R); TRI type of complement (experiments 3 through 5) the distribution is nearly random, with the frequency of the 2L non-segregational class being only slightly higher than the other two classes, which are roughly equal in frequency. In the C(2L); TRI, C(3L); TRI, and C(3R); TRI type of complements (experiments 1 and

Table 1. *Number of offspring in a cross between differentially marked tricomplex heterozygotes of the constitution C(3R)RM; 2/C(2L·3L)N2–29/C(2R·3L)N2–46*

(The experiment 9*a* and 9*b* in Table 2. The marker genes are as follows: *al* and *dp* for 2L, *px* and *sp* for 2R, and *st* and wild type for 3L. C(3R)RM homozygous for *sr* was used in both females and males.)

Parental marker genes (♀♀ × ♂♂)	Total offspring	Non-segregational for 2L		2R		3L	
		al	*dp*	*sp*	*px*	+	*st*
al sp × *dp px st*	888	112	130	262	258	59	67
dp px st × *al sp*	775	90	103	229	245	59	49

Table 2 *Relative proportion of each of three segregation classes of offspring produced by mating tricomplex heterozygotes composed of a standard chromosome 2 or 3 and two heterocompounds derived from T(2;3)N2–29 and T(2;3)N2–46*

(The numbered experiments differ in the marker combinations used; *a* and *b* refer to reciprocal matings of the same experiment. Gametic frequencies calculated from the pooled data are given in italics.)

Experiment no.	Total offspring	% Non-segregation for 2L	2R	3L	3R	Difference between reciprocals
		A. C(2L)RM; C(2R·3L)N2–46/C(2R·3R)N2–29/3				
1	228	—	63·6	17·1	19·3	
2*a*	344	—	60·2	14·8	25·0	$P < 0.05$
2*b*	615	—	57·4	21·8	20·8	$P < 0.05$
Pooled	1187	—	59·4	18·9	21·7	
			0·46	*0·26*	*0·28*	
		B. C(2R)RM; C(2L·3L)N2–29/C(2L·3R)N2–46/3				
3*a*	345	42·6	—	28·4	29·0	ns*
3*b*	110	33·6	—	38·2	28·2	ns*
4*a*	822	40·9	—	28·6	30·5	ns
4*b*	1500	41·1	—	29·4	29·5	ns
5*a*	595	41·0	—	31·1	27·9	$P < 0.01$
5*b*	1257	49·2	—	26·6	24·2	$P < 0.01$
Pooled	4629	43·2	—	28·8	28·0	
		0·38		*0·31*	*0·31*	
		C. C(3L)RM; 2/C(2L·3R)N2–46/C(2R·3R)N2–29				
6*a*	705	18·7	65·8	—	15·5	ns
6*b*	171	17·0	62·0	—	21·0	ns
7*a*	778	20·2	61·0	—	18·8	$P < 0.01$
7*b*	1355	15·3	66·9	—	17·8	$P < 0.01$
Pooled	3009	17·5	64·8	—	17·7	
		0·25	*0·49*		*0·26*	
		D. C(3R)RM; 2/C(2L·3L)N2–29/C(2R·3L)N2–46				
8*a*	1168	29·1	58·2	12·7	—	ns
8*b*	208	25·5	63·0	11·5	—	ns
9*a*	888	27·2	58·6	14·2	—	ns
9*b*	775	24·9	61·2	13·9	—	ns
Pooled	3039	27·2	59·4	13·4	—	
		0·31	*0·47*	*0·22*		

* ns, not significant.

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2, and 6 through 9) the distribution is non-random with the 2R non-segregational class being represented in excess as compared to the other two classes. Gametic frequencies calculated on the assumption that the distribution is similar in males and in females suggest that, in these strains, the 2R non-segregational type of distribution occurs in almost 50 % of the meiocytes, the other two types being, on an average, only half as frequent.

The reason for the types of non-randomness in distribution is not thoroughly understood. Since both the cytological and genetic lengths of the pairs of arms are about equal (some 50 cM in the standard genetic maps), a random distribution might have been expected. The preference of 2R non-segregation in three types of the tricomplex heterozygotes as well as the slight preference of 2L non-segregation in one type appear to be independent of the marker genes; hence, it is not due to any factor residing in a distal segment of the respective arm.

The differences in the arrangement of the centric sequences between the complements (cf. Fig. 3) suggest the possibility that disjunction is controlled by the centromeres or adjacent heterochromatin. A non-randomness could be due to one or two of the centromeres being stronger (or weaker) in sending the other centromeres to the opposite pole at division I. Consequently, it might be reasonable to suggest that a homocentric condition would best meet the requirements for a random distribution.

Based on this line of reasoning, the results in Table 2 could be interpreted in terms of C(2R); C(2L·3L)N2-29/C(2L·3R)N2–46/3 (experiments 3 through 5) bearing a homocentric tricomplex complement (because this is the type of complement showing a nearly random distribution). In other words, the arrangement of the centromeres in the strains used in these experiments would correspond to those diagrammed on row B of Fig. 3. The preferred type of distribution (i.e. 2R non-segregation) in another three tricomplex configurations (experiments 1 and 2, and 6 through 9) would then correspond to nondisjunction of *homologous* centromeres derived from chromosome 2. The gametic frequencies approaching 50 % non-segregation of 2R suggest a mode of distribution where the centromere derived from chromosome 3 tends to disjoin from either one of the two 2nd chromosome centromeres, with the other 2nd chromosome centromere behaving independently. With certain qualifications concerning the experimental distinction between the properties of the centromere and the properties of adjacent heterochromatin (see p. 304 for further discussion), the chromosome 3 centromere may be described as being 'strong' in directing the distribution of the chromosomes in the tricomplex.

To test this hypothesis, a complement, C(2L)RM; 2/C(2L·3R)HT26/C(2R·3R)HT10, involving an actual or a presumed chromosome 2 centromere in all three tricomplex chromosomes, i.e. a complement that is homocentric for the 2nd chromosome centromere, was constructed. Markers were introduced and differentially marked lines were tested for segregation. The results of two pairs of independent tests (Table 3) agree in showing that the distribution is clearly different from those obtained by using the C(3L)RM; 2/C(2L·3R)N2-46/C(2R·3R)N2-29 lines (Table 2). In one pair of the tests (experiments 10*a* and *b*) the distribution was not significantly different from the 1:1:1 ratio expected

if the chromosomes were distributed at random. However, the other pair of experiments as well as the pooled results show a significant deviation from this ratio probably indicating a slight non-randomness between the segregation alternatives. The frequencies 0·35, 0·34 and 0·31 given on the bottom line of Table 3 probably are reasonably close approximations of the true frequencies of the 2L, 2R, and 3R non-segregational classes of gametes, respectively.

Table 3. *Relative proportion of each segregational class of offspring produced by mating females and males of differentially marked lines of C(3L)RM; 2/C(2L·3R)HT26/C(2R·3R)HT10*

(Experiments 11*a* and *b* were independent repeats of reciprocal matings of experiments 10*a* and *b*, respectively. Gametic frequencies are given in italics.)

Experiment no.	Total offspring	% Non-segregationals for 2L	2R	3R	X^2 test (1:1:1)
10*a*	862	33·6 *0·33*	36·3 *0·35*	30·1 *0·32*	ns
10*b*	257	40·1 *0·37*	31·9 *0·33*	28·0 *0·30*	ns
11*a*	669	33·9 *0·34*	38·4 *0·36*	27·7 *0·30*	$P < 0{\cdot}01$
11*b*	532	43·2 *0·38*	25·9 *0·30*	30·8 *0·32*	$P < 0{\cdot}001$
Pooled	2320	36·6 *0·35*	34·1 *0·34*	29·3 *0·31*	$P < 0{\cdot}001$

(ii) *Similarity of the distribution in males and females*

Further matings were designed to test the assumption that, in each line, the distribution was the same in males and females. Lines of C(3L)RM; 2/C(2L·3R)N2-46/C(2R·3R)N2-29 and C(3L)RM; 2/C(2L·3R)HT26/C(2R·3R)HT10 were chosen because the difference in the phenotypic ratios was an indication of a difference in the gametic distribution between these strains.

If the phenotypic ratios approaching $\frac{1}{6}:\frac{2}{3}:\frac{1}{6}$ (Table 2) and 1:1:1 (Table 3) were due to gametic ratios approaching 1:2:1 and 1:1:1, respectively, both in females and males, interstrain matings are expected to yield the *same* result (a phenotypic ratio approaching 1:2:1) irrespective of which one of the strains is used as the female parent and which one as the male parent. On the other hand, if there were a difference between females and males in the distribution of the different segregational classes of gametes (consequently, a departure from the calculated 1:2:1 and 1:1:1 ratios in the two strains, respectively), then, reciprocal matings of interstrain crossings should not only differ in their phenotypic outcome but the ratios should depart from 1:2:1 (or from an expectation that is close to 1:2:1).

Results of three pairs of independent tests are given in Table 4. With one exception (experiment 12*b*) the results are in agreement with the expected 1:2:1 phenotypic ratio. Also in experiment 12*b* the proportion of the 2R non-segregational class does conform to the expected 50% but there was a significant departure from

the expected proportions of the 2L and 3R non-segregational classes. The deviation remains unexplained because in experiment 13*b*, which was a repeat of experiment 12*b*, no similar deviation was found. The results may thus be interpreted as supporting the assumption of a similar mode of distribution, within each strain, of the tricomplex chromosomes in females and in males.

Table 4. *Relative proportion of each segregational class of offspring produced by mating females and males of differentially marked lines of C(3L)RM; 2/C(2L·3R)N2–46/C(2R·3R)N2–29 (A) and (C(3L)RM; 2/C(2L·3R)HT26/C(2R·3R)HT10 (B)*

Experiment no.	Total offspring	% Non-segregational for			X^2 tests*	
		2L	2R	3R	(1:2:1)	(diff.)
12*a* (A♀ × B♂)	233	28·8	45·5	25·7	ns	$P < 0{\cdot}001$
12*b* (B♀ × A♂)	1026	20·0	50·8	29·2	$P < 0{\cdot}001$	
13*a* (A♀ × B♂)	260	24·6	45·4	30·0	ns	ns
13*b* (B♀ × A♂)	360	26·7	46·9	26·4	ns	
14*a* (A♀ × B♂)	245	24·5	49·4	26·1	ns	ns
14*b* (B♀ × A♂)	302	25·5	49·7	24·8	ns	

* X^2 was tested for an expected ratio of 1:2:1 and for the difference between the reciprocal matings, respectively.

(iii) *Tests for the cause of inequality in the distribution*

It was inferred above that the distribution of chromosomes in tricomplex heterozygotes depends on the arrangement, in the tricomplex configuration, of the centromeres derived from the 2nd chromosome and those derived from the 3rd chromosome. The hypothesis that an inequality in distribution in some of the complements is due to the centromere derived from the 3rd chromosome being 'stronger' than the one derived from the 2nd chromosome in sending the other two chromosomes to the opposite pole was further tested by replacing, in C(3L)RM; 2/C(2L·3R)N2-46/C(2R·3R)N2-29, particular heterocompounds by C(2L·3R)HT26 or C(2R·3R)HT10. If the break points in T(2; 3)N2-29 and T(2; 3)N2-46 were as indicated by alternatives (2) and (4), Fig. 3, respectively, and consequently, if the tricomplex configuration of 2/C(2L·3R)N2-46/C(2R·3R)N2-29 were as shown in Bc (Fig. 3), substituting C(2L·3R)HT26 for C(2L·3R)N2-46 should convert the heterocentric configuration into a homocentric one. As a consequence, the distribution of the three chromosomes in such a complement should approach the 1:1:1 ratio. On the other hand, substituting C(2R·3R)HT10 for C(2R·3R)N2-29 should not change segregation because both are presumed to bear a chromosome 2 centromere.

Results of a series of tests (Table 5) well meet the expectations based on this line of reasoning and provide additional evidence for the hypothesis developed above.

Table. 5. *Results of experiments designed to test the distribution of the heterocompounds in C(3L); 2/C(2L·3R)HT26/C(2R·3R)N2–29 and in C(3L); 2/C(2L·3R)N2–46/C(2R·3R)HT10*

(Flies of the type indicated were mated to 'tester' flies of C(3L); 2/C(2L·3R)HT26/C(2R·3R)HT10 (experiments 15 through 17 and 19) or to those of C(3L); 2/C(2L·3R)N2–46/C(2R·3R)N2–29 (experiment 18). Expectations were based on the assumption that, in the tester strains, the gametic proportions were approximately 1:1:1 and 1:2:1, respectively.)

Experiment no.		TRI complement tested	Total offspring	% Non-segregational for 2L	2R	3R	Expected ratio (approximately)
15*a*	♀♀	2/C(2L·3R)HT26/C(2R·3R)N2–29	323	38·1	41·5	20·4	1:1:1
15*b*	♂♂	2/C(2L·3R)HT26/C(2R·3R)N2–29	428	30·8	42·3	26·9	1:1:1
16*a*	♀♀	2/C(2L·3R)HT26/C(2R·3R)N2–29	803	32·0	39·6	28·4	1:1:1
16*b*	♂♂	2/C(2L·3R)HT26/C(2R·3R)N2–29	503	31·0	36·4	32·6	1:1:1
17*a*	♀♀	2/C(2L·3R)HT26/C(2R·3R)N2–29	836	38·0	35·3	26·7	1:1:1
17*b*	♂♂	2/C(2L·3R)HT26/C(2R·3R)N2–29	163	28·8	31·9	39·3	1:1:1
Pooled	♀♀	2/C(2L·3R)HT26/C(2R·3R)N2–29	1962	35·6	38·1	26·3	1:1:1
Pooled	♂♂	2/C(2L·3R)HT26/C(2R·3R)N2–29	1094	30·6	38·0	31·4	1:1:1
18*a*	♀♀	2/C(2L·3R)HT26/C(2R·3R)N2–29	331	26·6	52·6	20·8	1:2:1
18*b*	♂♂	2/C(2L·3R)HT26/C(2R·3R)N2–29	616	19·8	52·8	27·4	1:2:1
19*a*	♀♀	2/C(2L·3R)N2–46/C(2R·3R)HT10	381	30·2	50·1	19·7	1:2:1
19*b*	♂♂	2/C(2L·3R)N2–46/C(2R·3R)HT10	624	26·4	45·4	28·2	1:2:1

(iv) *Distribution of the homocompound with respect to the heterocompounds*

Several experiments have been carried out to test an earlier assumption that the homocompound is distributed independently of the group of three heterocompounds (Puro, 1973). In a series of experiments, lines of C(3L)RM; 2/C(2L·3R)N2-46/C(2R·3R)N2-29 with maternal and paternal homocompounds marked differentially were mated with each other and the progeny was classified according to the parental homocompounds. In Table 6, results are given of a pair of tests using homocompounds of different origin.

The use of C(3L)RM, *ale* in one of the parents did not change the distribution of the tricomplex chromosomes; the relative proportions of three non-segregational classes were essentially similar to those given in Table 2C, where C(3L)RM, *ri* was used in both parents. However, Table 6 shows that parental homocompounds are recovered in unequal frequencies, with the maternal compounds, C(3L), *ale* in experiment 20*a* and C(3L), *ri* in experiment 20*b*, being present in 61·4 and 56·3 % of the offspring, respectively. The cause of this inequality is not understood but obviously it is not due to different viability.

Another type of non-randomness is evident from these results. In each segregational class, the maternal C(3L) was recovered, on an average, 2·2 times more often along with the single maternal heterocompound as compared to its recovery in the complementary two-chromosome class. Conversely, the paternal C(3L) was recovered, on an average, 1·9 times more often along with the single paternal heterocompound as compared to its recovery in the complementary class. This

Table 6. *Distribution of maternal* vs. *paternal homocompounds in the progeny of reciprocal matings between flies of differentially marked lines of C(3L)RM; 2/C(2L·3R)N2–46/C(2R·3R)N2–29*

(The parental markers were as follows: In experiment 20*a* (♀♀), *ale* for C(3L) and +, *px*, and e^{11} for 2L, 2R, and 3R, respectively; (♂♂), *ri* for C(3L) and *dp*, *sp*, and p^{p} and ro^{64c} for 2L, 2R, and 3R, respectively. In experiment 20*b* females and males were marked reversely.)

			% Non-segregationals for					
			2L		2R		3R	
Experiment no.	Number of offspring		I/II*	II/I	I/II	II/I	I/II	II/I
20*a*	Total	925	10·5	8·5	31·3	28·8	9·2	11·7
	Maternal C(3L)	*568*	*14·2*	*6·2*	*38·2*	*22·4*	*9·9*	*9·1*
	Paternal C(3L)	*357*	*4·5*	*12·3*	*20·5*	*38·9*	*8·1*	*15·7*
20*b*	Total	1159	9·3	5·7	34·2	31·4	11·3	8·1
	Maternal C(3L)	*653*	*11·9*	*4·0*	*40·3*	*24·0*	*15·2*	*4·6*
	Paternal C(3L)	*506*	*5·9*	*7·9*	*26·3*	*40·9*	*6·3*	*12·7*

* I/II refers to offspring derived from eggs with one heterocompound fertilized by sperm with two heterocompounds of the tricomplex and II/I refers to offspring derived from eggs with two heterocompounds fertilized by sperm with one heterocompound.

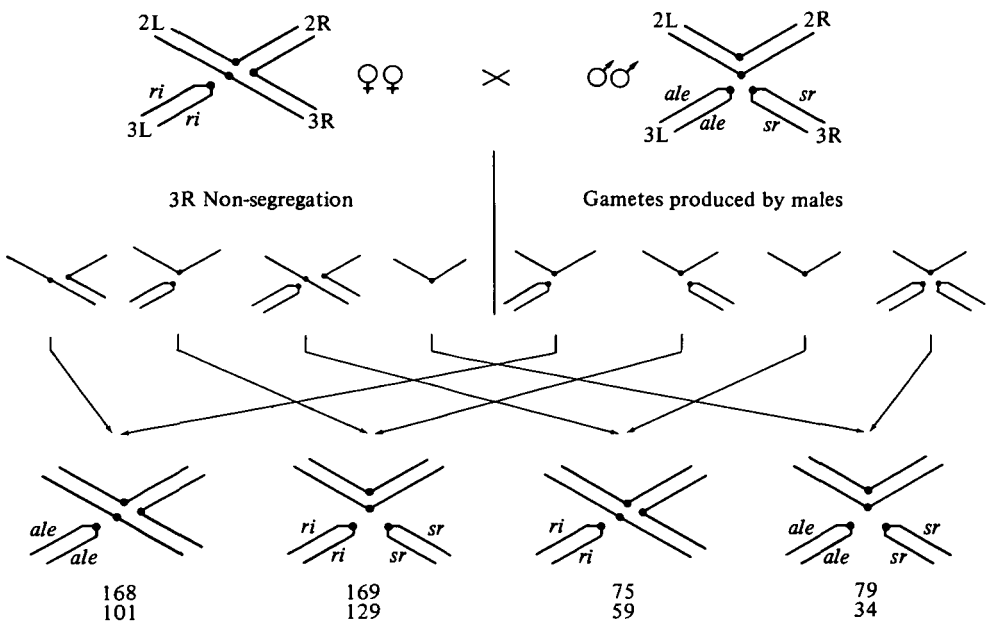

Fig. 6. A diagram showing the type of offspring produced by mating C(3L); TRI type of females with C(3L); C(3R) type of males. Numbers below the diagram refer to results of two experiments using different lines of C(3L)RM,*ri*;2/C(2L·3R) HT26/ C(2R·3R)HT10 as females.

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suggests that in either males or females, or in both, the homocompound is distributed non-randomly with respect to the tricomplex chromosomes.

Independent evidence showing that the distribution of the homocompound is non-random in females was obtained from matings of tricomplex heterozygous females with males of a compound-3 stock. Offspring produced by such matings are derived from the four types of eggs produced by one of the segregation alternatives of the tricomplex complement (Fig. 6). Since, in males, compound-3's are generally distributed at random (Holm, 1976), the proportions of the four classes of offspring are expected to reflect the relative frequencies of the respective classes of the female gametes.

Results, given in Fig. 6, of two tests using different lines of C(3L)RM, *ri*; 2/C(2L·3R)HT26/C(2R·3R)HT10 suggest that, in females bearing this complement, C(3L)RM, *ri* and chromosome 2 are distributed to the same pole in about 70% of this type of one-to-two segregation. Data from reciprocal matings are noninformative because, in females, autosomal compounds show a high incidence of disjunction and, consequently, the four types of gametes are produced in unequal frequencies.

(v) *Effect of inversion heterozygosity on the distribution of heterocompounds*

Exceptions to the rule that reciprocal matings result in similar patterns of distribution were found in matings between certain lines of C(2L); C(2R·3L)N2-46/C(2R·3R)N2-29/3. Results shown in Table 7 serve as an example. In experiment 21*a*, the frequencies of three segregational classes were roughly comparable to those given in Table 2(A) whereas, in experiment 21*b*, the pattern was different with the 3L non-segregational class being represented in excess. The deviation frome the expectation was found to be due to the presence, in line B, of an inversion in the left arm of chromosome 3. (Salivary chromosome analysis indicated that the break points were identical with or closely similar to those of In(3L)P.) The dissimilar patterns in reciprocal crossings suggest that inversion heterozygosity affects the distribution of heterocompounds differently in males (experiment 21*a*) and in females (experiment 21*b*).

A more systematic study of the effect of inversion heterozygosity was done by using lines of C(3L); 2/C(2L·3R)N2-46/C(2R·3R)N2-29. Females (or males) carrying In(2R)*Cy* in chromosome 2, and those having no inversion, were mated with males (or females) of the same tester strain. Results (experiments 22 and 23, Table 8) show that while in females In(2R)*Cy* resulted in a 17% increase in the proportion of the 2R non-segregational class of offspring (an increase from 64·8 to 75·5%), in males In(2R)*Cy* resulted in no change. On the assumption that, in the tester strain, the proportion of the 2R non-segregation type of gametes consisted of 50% of all (Table 2), it may be calculated that in females of the inversion line the respective proportion must have been about 61% (an increase of 22%). This was supported by the results (experiment 24*a*, Table 8) obtained by using another tester strain, C(3L); 2/C(2L·3R)HT26/C(2R·3R)HT10, that is homocentric and produces gametes of all three segregation classes in equal frequencies. On the other hand, the results of the reciprocal meeting (experiment 24*b*) agreed with those of

experiment 22*b* in showing that, in males of the inversion line, the proportion of the 2R non-segregation was not significantly different from 50%.

For another series of tests, a line of C(3L); 2/C(2L·3R)HT26/C(2R·3R)HT10 was provided with chromosome 2 bearing In(2L)*Cy*. In crossings with an inversion-

Table 7. *Different patterns of segregation in reciprocal matings between lines of C(2L); C(2R·3L)N2–46/C(2R·3R)N2–29/3 differing in one of the parental lines (line B) having In(3L)36A-B; 72E in chromosome 3*

(In the lower half of the table, the percentage distribution of offspring in each segregation class is given to show a non-random distribution of the parental homocompounds.)

Experiment no.		Total offspring	% Non-segregation for 2R	3L	3R
21*a*	(A♀♀ × B♂♂)	683	52·4	23·0	24·6
21*b*	(B♀♀ × A♂♂)	381	25·4	62·5	12·1

			2R		3L		3R	
			I/II*	II/I	I/II	II/I	I/II	II/I
21*a*	Maternal C(2L)	395	34·9	17·5	17·2	7·1	13·4	9·9
	Paternal C(2L)	288	23·6	28·8	6·6	14·6	10·4	16·0
21*b*	Maternal C(2L)	225	26·7	1·3	35·1	24·9	11·6	0·4
	Paternal C(2L)	156	3·2	18·6	30·8	35·2	1·3	10·9

* See the footnote in Table 6.

Table 8. *Tests for the effect of heterozygous In(2R)Cy on the distribution of heterocompounds*

(In experiments 22 and 23, flies of C(3L); 2/C(2L·3R)N2–46/C(2R·3R)N2–29 having In(2R)*Cy* in chromosome 2 (line I) and those having a standard chromosome 2 (line S) were mated with flies of the same tester strain (Tester 1) of the constitution C(3L); 2/C(2L·3R)N2–46/C(2R·3R)N2–29. In experiment 24, flies of the inversion line were mated with those of C(3L); 2/C(2L·3R)HT26/C(2R·3R)HT10 (Tester 2).)

Experiment no.		Total offspring	% Non-segregation for 2L	2R	3R	X^2 test (diff.)
22*a*	I ♀♀ × Tester 1 ♂♂	274	15·3	75·5	9·2	$P = 0{\cdot}05$
23*a*	S ♀♀ × Tester 1 ♂♂	105	18·1	64·8	17·1	
22*b*	Tester 1 ♀♀ × I ♂♂	322	15·8	65·2	19·0	ns
23*b*	Tester 1 ♀♀ × S ♂♂	509	14·1	68·4	17·5	
24*a*	I ♀♀ × Tester 2 ♂♂	523	19·7	62·3	18·0	$P < 0{\cdot}0001$
24*b*	Tester 2 ♀♀ × I ♂♂	451	22·2	49·4	28·4	

free line this inversion resulted in an increase of 2L non-segregational class of offspring from the average of 36·6% (Table 3) to 55·1 and 72·2% in males and females, respectively. Thus it may be concluded that inversion heterozygosity in one pair of arms affects the distribution of the tricomplex chromosomes by increasing the frequency of non-segregation of that arm, and that the effect is quantitatively different in different sexes; in males either there is no effect or there is an effect that is distinctly less pronounced than in females.

6. DISCUSSION

The tricomplexes constitute special cases of translocation heterozygosity with the principal difference being in the number of the centromeres involved in chromosome multiples at meiosis and, consequently, in the number of segregational alternatives. While, in ordinary translocation heterozygotes, the distribution of the chromosomes depends on the type of interaction of four chromosomes with two pairs of non-homologous centromeres giving rise to four orientation alternatives with numerically equal segregations (John & Lewis, 1965) and four alternative ways to produce one-to-three segregation, in tricomplex heterozygotes, the trivalent configurations have only three centromeres with three disjunctional alternatives. Thus the tricomplexes with the four theoretically possible types of homocentric and twelve heterocentric complements (cf. Fig. 3) provide a rather simple system for analysing various types of homologous and nonhomologous interactions.

The data presented in this paper do not cover all possible arrangements of the centromeres in tricomplex heterozygotes. Therefore one should be cautious not to make extensive generalizations. Occasionally, results obtained from repeated experiments show inconsistencies that are difficult to be ascribed simply to a chance variation or to differences in viability. Evidently factors that are beyond reach of experimental control in an individual test can affect the distribution of chromosomes in tricomplex heterozygotes. Therefore, a gross parallel between the results of a set of experiments is more revealing than any result of a statistical evaluation of even large experiments.

One of the most important inferences from the results presented in this paper is the notion that the distribution of the tricomplex chromosomes is random or nearly random in some of the complements but non-random in others with the type of preference depending on the arrangement of the centromeres derived from the 2nd and 3rd chromosomes. This is evidence for a functional differentiation between the two autosomal centromeres. On the assumption that the centromeres of the heterocompounds were intact (the breaks being either to the left or to the right of the centromeres) the results can be interpreted as the centromere derived from the 3rd chromosome being 'strong' in directing two 2nd chromosome centromeres of given tricomplex complements to the opposite pole at division I.

This conclusion bears directly upon the theories of the control of the centromere orientation. First, it is important to note that, in at least some of the complements, the type of directed disjunction accomplished by the 'strong' centromere tends to send two homologous (chromosome 2) centromeres to the same pole with a frequency that corresponds to a random distribution of these two. Thus, homology *per se* seems to be non-essential in determining co-orientation of the centromeres in multiple associations (cf. John & Lewis, 1965, pp. 76–83).

Second, results from inversion-free complements suggest that the behaviour of the three chromosomes in each strain is similar in females and in males. This would appear to favour a model that similar mechanisms determine disjunction in both sexes (consequently, that crossing over and chiasmata, which occur only in females, were immaterial to centromere orientation). On the other hand, differential

patterns of disjunction in females and males heterozygous for an inversion indicate that, in females, the control mechanism is more sensitive to an interference caused by structural heterozygosity than in males. Evidently this is related to the basic difference in the meiotic mechanisms of the two sexes.

The mechanism underlying the 'strong' behaviour of the centromere showing a preferential (directed) disjunction in heterocentric complements remains obscure. On purely morphological grounds, the trivalents formed by the tricomplex complements showing differential modes of distributions as, for example, 2/C(2L·3R)N2-46/C(2R·3R)N2-29 *vs.* 2/C(2L·3R)HT26/C(2R·3R)N2-29, are expected to present no such differences which would account for their differential behaviour. Structural euchromatic differences, should there be any, are expected to change the frequency of crossing over in females. However, data (not included in this report) on the frequency of homozygosis in non-segregational 2R's (that were heterozygous for specific markers) indicates that there is no essential difference in crossing over that could be related to the segregational differences between the complements. The only difference between C(2L·3R)N2-46 and C(2L·3R)HT26 resides in the region defined by the breaks around the centromeres that in these two chromsomes are presumed to be of different chromosomal origin.

It is difficult to make an experimental distinction between the contribution of the centromere proper and that of the adjacent heterochromatin. Therefore the possibility cannot be rejected that the 'weak' and 'strong' behaviour could be ascribed to differences in the quantity of heterochromatic 'disjunction determinants' suggested by Falk *et al.* (1985*a*, *b*). At any rate, ultrastructural details of chromosome 2 and chromosome 3 centromeres and adjacent heterochromatin (Lin, Ault & Church, 1981; Church & Lin, 1982) reveal no difference which would suggest their functional differentiation.

The preferred type of disjunction could be explained if the centromeres were activated in sequence. The centromere derived from the 3rd chromosome might be the first to be activated, its orientation with respect to one pole effecting the orientation of one or both of the partner centromeres to the opposite pole. It is of interest to note that, in the presumed heterocentric complements, the proportion of the preferred type of segregation approaches 50 % of all segregations with the two unpreferred types being roughly equal. A 2:1:1 ratio would be expected, if the 'strong' centromere would always determine one of the partner centromeres to be disjoined from it with the other centromere being distributed at random. A preference higher than 50 % nonsegregation of two centromeres would be expected, if the 'strong' centromere would effect the distribution of both centromeres to the opposite pole. In fact, such results were observed when inversion heterozygosity was present in female in one pair of arms. A parallel to this type of interaction of three chromosomes is to be found in the behaviour of three sex chromosomes in females having structurally heterozygous *X* chromosomes plus and extra *Y* (Cooper, 1948). Here, too, two homologous (i.e. *X* chromosome) centromeres tend to be disjoined from a heterologous (*Y* chromosome) centromere with a frequency that significantly exceeds 50 %.

A temporal sequence of activation of the centromeres has been cited to be the reason for varying types of orientations in multivalents (Östergren, 1951) but there is no evidence for the sequence being specific or strictly ordered.

The mechanism outlined above for explaining preferential centromere orientations in tricomplexes is in line with the current theory that the process of orientation in multivalents (as well as in bivalents) takes place in three steps (cf. Rickards, 1983): First, as a result of pairing during prophase the centromeres achieve a bidirectional conformation that is viewed as the kinetochores lying back-to-back and facing to opposite directions. In the next step, this *pre-orientation* is followed by *initial orientation* with respect to the poles when the kinetochores first associate with the spindle. A stable configuration may be established directly. However, in the third step, *reorientation* of maloriented centromeres, documented from living cells of various organisms and indirectly by independent criteria (references in Rickards, 1983), still reduces the frequency of misorientations. A stable orientation is achieved whenever a tension is developed by at least one pair of adjacent centromeres being oriented to opposite poles.

As far as the tricomplexes are concerned, reorientation is not expected to change the spindle fibre tension (unless all three centromeres were initially oriented to the same pole). Therefore, initial orientation with the assumed specificity in the orientation sequence probably is the critical phase. In female of Drosophila, a lack of continuous reorientation during the course of arrest at metaphase I is also suggested by the achiasmatic pairs of chromosomes (like the 4ths) showing regular co-orientation and precocious disjunction (Puro & Nokkala, 1977). If the same principle is to be applied also to secondary nondisjunction involving non-exchange *X* chromosomes in *XXY* females heterozygous for inversions, the significance of the initial orientation and the relative insignificance of re-orientation will be obvious; the mode of segregation in any given complement must be largely pre-determined by factors that influence the centromeres' initial orientation kinetics.

The non-random behaviour of the homocompound presents a problem of its own. Its preferential recovery together with the single one of the three heterocompounds is not predicted by any of the numerous theories concerning meiosis in Drosophila. Clearly, it is in a sharp contrast to the prediction based on the theory by R. F. Grell (1976) of distributive pairing. According to this theory, non-exchange chromosomes as well as (homo)compounds forming only internal chiasmata are involved in a 'distributive pool' the members of which associate in pairs ('distributive pairing') only later in meiosis and independently of the rest of the chromosomes that underwent 'exchange pairing' in prophase. Since the homocompound and the heterocompounds are members of separate pools they are not expected to interact with each other. Yet, the results presented in this paper suggest to the contrary; the type of preference can only be explained by assuming that the homocompound and one of the heterocompounds (the one not involved in co-orientation with the other heterocompound) can interact (i.e. pair) to result in their disjunction. Data (not included in this paper) on crossing over in non-segregational arms render it unrealistic to assume that the frequency of chiasmata in the tricomplex would be reduced to any appreciable extent, so that one of the heterocompounds would often be avaible in the distributive pool. Thus, there is no conceptual necessity for assuming an existence of two independent pairing pools.

The present evidence is insufficient to discriminate between the two possibilities, viz. that the non-random behaviour of the homocompound is only taking place

in females and that it, in addition, occurs in males. Results of a preliminary cytological analysis of meiosis in both females and males of a tricomplex line (unpublished) support the first alternative. Thus, the behaviour of the homocompound in tricomplex heterozygotes is another piece of evidence for nonhomologous interactions occurring in females but lacking in males. Any theory that may be advanced for meiosis in Drosophila females must consider the fact that exchange chromosomes as well as non-exchange chromosomes are involved in nonhomologous interactions. Attention should be paid to the chromocentral organization of the centric regions as the likely mechanism bringing nonhomologous centromeres in mutual interaction (Novitski & Puro, 1978). According to this view, one function of the chromocenter (probably not the primary function) is to establish and maintain homologous and nonhomologous associations that determine initial prometaphase orientation of the centromeres. Accordingly, the chromocenter may be viewed as a cytological manifestation of those interactions.

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