

A GENETIC STUDY OF SEGREGATION IN A TRANSLOCATION HETEROZYGOTE IN *DROSOPHILA*¹

S. ZIMMERING²

Department of Zoology, University of Missouri, Columbia, Missouri

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DURING meiosis, homologous chromosomes normally pair with each other and separate whereas the members of pairs of non-homologous chromosomes assort independently of one another. This behavior is disturbed, however, in individuals carrying a translocation. It is well known that at the first meiotic division separation of the four components of a translocation configuration may take place in a number of different ways and that each type of first division separation gives rise to two kinds of gametes, each the complement of the other. It is ordinarily expected that the two complementary products from any one type of separation will be produced equally frequently.

Certain cases in *Drosophila melanogaster* which did not meet the expectation of equal recovery were reported by GLASS (1934, 1935) who found that from crosses of females, heterozygous for a translocation of the type diagrammed in figure 1, by heterozygous translocation males, female gametes with $2S + 3'$ were recovered twice as frequently as those with $2'L' + 3$ (see the legend to figure 1 for explanation of symbols). The results from other kinds of tests established beyond any doubt that this discrepancy could not be accounted for on the basis of a difference in the viability between these types.

NOVITSKI (1951) showed that from a *Drosophila* female carrying two homologous X-chromosomes differing in length, the shorter of the two is recovered about twice as often as the longer. This phenomenon of non-random disjunction depends upon the occurrence of an exchange between the two homologs, with the formation of a dyad composed of two structurally dissimilar chromatids. He suggested that the inequality of the frequencies of the two types of gametes from the translocation heterozygote described above might also be a manifestation of non-random disjunction. The experiments to be described below were designed to test the validity of this explanation for the unusual behavior of the translocation heterozygote, as well as to test certain other possibilities.

GENETIC CONSEQUENCES OF AN EXCHANGE IN THE INTERSTITIAL REGION

The assumption of non-random disjunction involves a consideration of the relationship between a given type of separation and the types and frequencies of resultant gametes arising from tetrads in which an exchange has taken place in the interstitial

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² Present address: Department of Biology, Trinity College, Hartford 6, Connecticut.

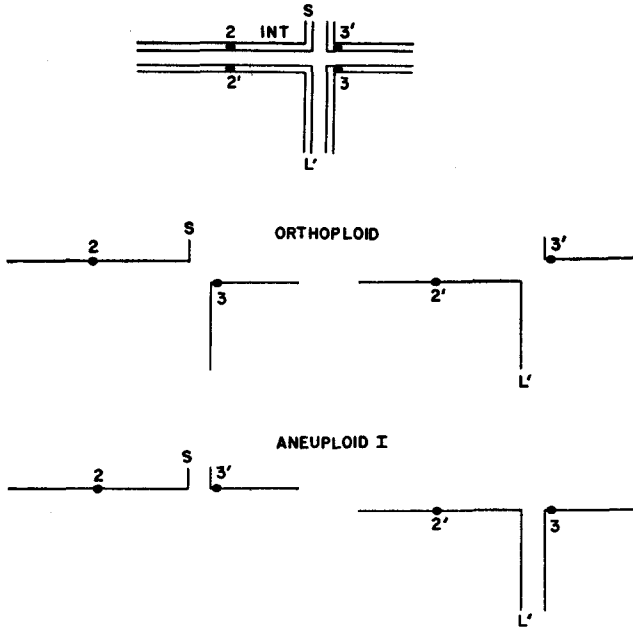


FIGURE 1.—The pairing configuration of a translocation heterozygote and the products derived from alternate disjunction (orthoploid gametes) and from adjacent I disjunction (aneuploid I gametes). The numbers 2 and 3 stand for the centromere regions of the normal second and third chromosomes, respectively, 2' and 3' for the homologous regions of the translocated chromosomes, S denotes 2R, and L' represents 3L of the translocated chromosome. It is implied, of course, that the unmarked arms, 2R and 3R, as well as 3L of the normal chromosome, are always associated with the appropriate centromere.

region (INT, fig. 1) as well as those in which an exchange has not occurred. From no-exchange tetrads (fig. 1), alternate disjunction of chromosomes will give rise to two orthoploid gametes, namely, $2S + 3$ and $2'L' + 3'$ while the aneuploid I gametes, $2S + 3'$ and $2'L' + 3$, arise following adjacent I disjunction. Other types of disjunction in this type of translocation are rare. The recovery of any one type of gamete from the female depends upon the fertilization of the egg by a sperm carrying the complementary type so that the zygote will have a balanced gene complement.

Following an exchange in the interstitial region (fig. 2) so-called asymmetric dyads are produced; that is, the chromatids making up the dyad associated with centromere 2 are of unequal length, S being shorter than L', and, similarly, the dyad linked with centromere 2' consists of a shorter and a longer chromatid. It is under just these conditions that nonrandomness of recovery of chromatids has been shown to hold for the X-chromosome, the shorter chromatid being recovered about twice as frequently as the longer. To understand the significance of this expected inequality as it bears upon the interpretation of the discrepancy between complementary aneuploid I classes, the constitution of the gametes following alternate and adjacent I disjunctions should be considered. The gametic products from alternate disjunction (fig. 3) are (1) the noncrossover orthoploids, O_1 and O_2 and (2) the crossover aneu-

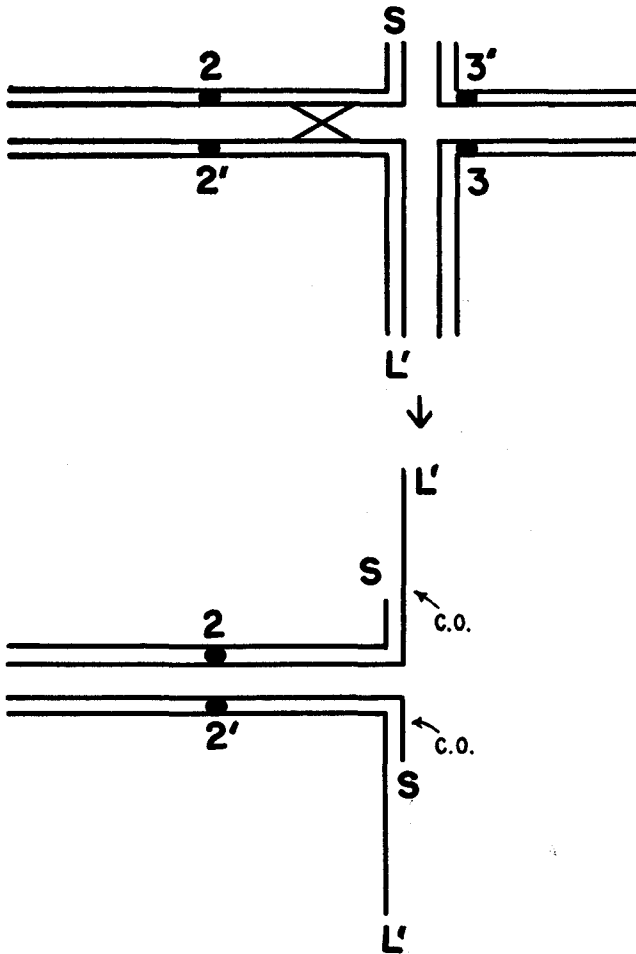


FIGURE 2.—The constitution of the crossover dyads following an exchange in the interstitial region. Note the dissimilarity in the length of the chromatids making up each of these dyads. The symbol *c.o.* stands for a crossover chromatid.

ploids, A_1 and A_2 . Type A_1 , carrying $2L'$, is expected to be produced less frequently than O_1 which contains $2S$, and A_2 , in which is included $2'S$, should be formed in excess of the type bearing $2'L'$, i.e. O_2 . Consequently, of the complementary crossover aneuploids, the type carrying $2L' + 3$ will be recovered in the offspring less frequently than that containing $2'S + 3'$. Although these gametes, when recovered, are recognizable as crossovers when the interstitial region is genetically marked, they would be included in the general class of noncrossovers in situations where crossing over in this region is not followed, that is, they would be recovered in the classes receiving $2'L' + 3$ and $2S + 3'$, respectively, from the female. As was indicated above, these were the discrepant classes found in GLASS' experiments.

From adjacent I disjunction (fig. 4), the noncrossover aneuploids, A_3 and A_4 , and

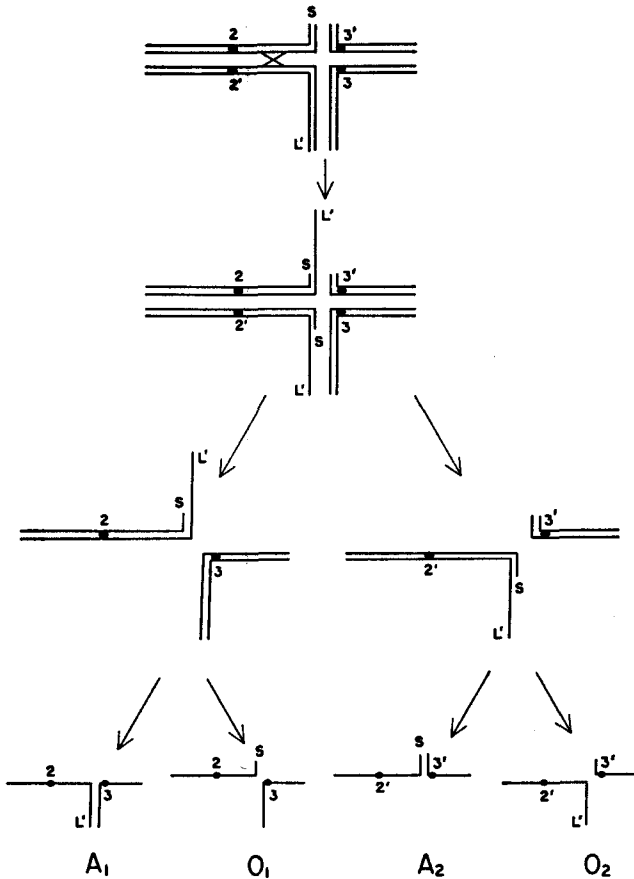


FIGURE 3.—The events leading to the production of complementary aneuploid I gametes (A₁ and A₂) following alternate disjunction at the first division, where A₂, carrying the shorter crossover chromatid is expected to be produced more frequently than A₁ which bears the longer.

the crossover orthoploids, O₃ and O₄, are produced. Assuming the same relationships to hold under these circumstances as those postulated as existing between gametes following alternate disjunction, then the complementary noncrossover aneuploids from exchange tetrads should be recovered with different frequencies. Hence, an inequality in the relative frequencies of complementary noncrossover aneuploids could be inferred to be a consequence of a differential recovery of these types from exchange tetrads. It should be noted that a discrepancy similar to that expected in the complementary crossover aneuploids would be found in the complementary crossover orthoploids since both types come from situations in which an asymmetric dyad is formed. The magnitude of the inequality between complementary noncrossover orthoploids will depend on the rate of alternate disjunction from no-exchange vs. that from exchange tetrads, that is, the greater the former, the smaller the discrepancy and *vice versa*. In brief, then, the following points may be emphasized: (1) the discrepancy between complementary aneuploid I types is interpretable on the basis of non-

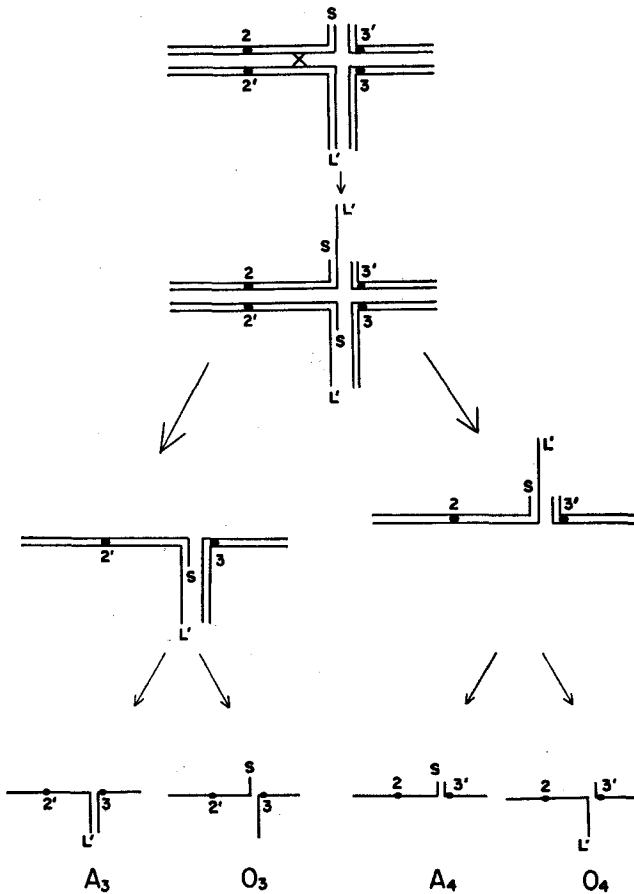


FIGURE 4.—The consequences of adjacent I disjunction following an exchange in the interstitial region.

random disjunction of the structurally dissimilar chromatids making up the asymmetric dyad, such that the shorter is included more frequently than the longer in the egg nucleus; (2) a difference in the frequency of recovery is expected between those complementary aneuploid types coming from exchange tetrads (no difference being expected from those which arise from no-exchange tetrads) and (3) crossover aneuploid I gametes are recovered following alternate disjunction while crossover orthoploid gametes are produced when adjacent I disjunction follows an exchange that is, a reversal of the relationship between the type of disjunction and the kinds of resultant gametes found in the absence of an exchange.

The regular conversion of orthoploid gametes into aneuploid gametes (and vice versa) by the occurrence of an exchange in the interstitial region makes it impossible to relate the recovered gametic frequencies to frequencies of the disjunctional types, alternate vs. adjacent, unless the interstitial region is so marked that the exchange frequency may be estimated. NOVITSKI (1951) pointed out that in a translocation of

the type under consideration here, with an extensive interstitial region, disjunction could be entirely of the alternate type, with the aneuploid gametes originating in exchange tetrads.

The results from experiments set up to throw some light on the various questions raised in the preceding paragraphs showed the following: (1) a non-random distribution of chromosomes occurs such that following an exchange in the interstitial region, the deficient crossover class, made up of individuals bearing the longer crossover chromatid, appears only about one half to one third as frequently as does the complementary class; (2) a discrepancy is found only between complementary crossover types while complementary noncrossovers are recovered with equal frequency; (3) the rate of crossing over in the interstitial region was surprisingly low, (about 12-15%) and possibly related to this was the absence in the data of an inequality of the magnitude of that found in earlier reports and (4) a high frequency of crossover individuals identified as coming from adjacent I disjunction following an exchange in the interstitial region are recovered.

A more detailed account of these experiments is presented below.

DESCRIPTION OF THE TRANSLOCATION

The translocation used in the present study, $T(2;3)bw^{V4}$, abbreviated as $V4$, is associated with a dominant brown variegated eye color, and involves an interchange of unequal segments, the region from the locus of bw (2-104.5) to the tip of 2R having been exchanged for approximately all of 3L. Individuals heterozygous for the translocation are viable and fertile while the translocation homozygotes are semilethal.

RESULTS FROM GLASS' EXPERIMENTS

GLASS (1934, 1935) found that when $V4\ st/st$ females were crossed by $V4\ st\ Pr/Cy\ C(3)x$ males a striking inequality was observed between the numbers of recovered individuals in the complementary aneuploid I classes, namely, 1242 $V4$ and 709 $Cy\ V4\ st\ Pr$ (table 1a). That differential viability was not responsible for this unexpected finding was shown in the results from the reciprocal cross (table 1b) where it is obvious that the difference disappears, the two types being recovered with equal frequency, 608 $V4$ and 609 $Cy\ V4\ st\ Pr$. GLASS proposed the following explanation to account for the difference in the results from the reciprocal crosses. Since the $V4$ translocation had been kept in a balanced condition, newly arisen lethals could accumulate in the translocation stocks. If a recessive lethal were located in L' (3L), crossing over could shift the lethal to the homologous arm so that a gamete of the constitution $2'L' + 3$ might have a lethal in each of the 3L limbs; individuals homozygous for the lethal would, of course, be eliminated. Thus, according to this idea, the reason for the different results in the two experiments lies in the presence of an inversion, $C(3)x$, in the female inhibiting crossing over in L' in one case, and its absence in the female in the other.

It was pointed out by GLASS that this explanation was not entirely satisfactory because the expected loss from homozygosis (theoretical maximum, 25%) would not be sufficient to account for the magnitude of the observed deficiency (about 43%). It might be pointed out further that since the lethal postulated as being present in L'

TABLE 1

*Progeny of V4 st/st females by V4 st Pr/Cy C(3)X males (a) and of the reciprocal cross (b)
(aneuploid II types are omitted)*

| Composition of gametes | | Progeny phenotype | Number | |
|------------------------|-----------|-------------------|--------|-----|
| Male | Female | | (a) | (b) |
| orthoploid | | | | |
| 2'L' + 3' | 2S + 3 | V4 st Pr | 1789 | 963 |
| 2S + 3 | 2S + 3 | Cy | 1900 | 887 |
| 2S + 3 | 2'L' + 3' | Cy V4 | 1700 | 936 |
| 2'L' + 3' | 2'L' + 3' | V4/V4 st Pr | 273 | 240 |
| aneuploid I | | | | |
| 2'L' + 3 | 2S + 3' | V4 | 1242 | 608 |
| 2S + 3' | 2'L' + 3 | Cy V4 st Pr | 709 | 609 |

in the female would presumably be present also in L' in the male, an exchange, shifting the position of the lethal to the homologous arm would eliminate those orthoploid individuals receiving 2S + 3(I) from the female and 2L + 3(I) from the male. Consequently, a marked deficiency would be expected in the V4 st Pr class; inspection of table 1a will show that this is not the case.

DEMONSTRATION OF NONRANDOM DISJUNCTION

Females of the constitution V4 st/ stw³ c st were crossed by normal males homozygous for stw³ c st. If adjacent I disjunction takes place after an exchange in the interstitial region, the gametes carrying the crossover products, 2L' + 3' and 2'S + 3 are recoverable since fertilization by a sperm carrying 2S + 3 gives rise to a zygote having a normal complement of genes. As a consequence of nonrandom disjunction, the gametes carrying 2'S should be recovered more often than those carrying 2L'. On the other hand, if adjacent I disjunction does not occur, the crossover products are not recoverable since they become aneuploid gametes and under the conditions of the experiment would give rise to inviable zygotes. The cross is diagrammed in figure 5 and the results are given in table 2. It is seen that crossover individuals are recovered. Of 2323 crossovers in Region I, stw³-c, 1530 involved the shorter chromatid and 793 the longer, and for Region II, c--breakpoint, 529 involved the shorter and 278 the longer chromatid.

The results from an experiment to determine the extent to which differential viability might have been responsible for this discrepancy between complementary classes are given in table 3 (fig. 5). It may be noted on comparing the two experiments that whereas in the former, the classes carrying the longer crossover chromatid also carried a progressively greater number of mutants, in the latter, the reverse is the case. If a change in the distribution of mutants had the effect of appreciably affecting viability, one might expect to find a striking difference in the degree of non-randomness between complementary crossovers for Region I as compared with those from Region II; it is obvious upon inspection that this is not the case. Attention might

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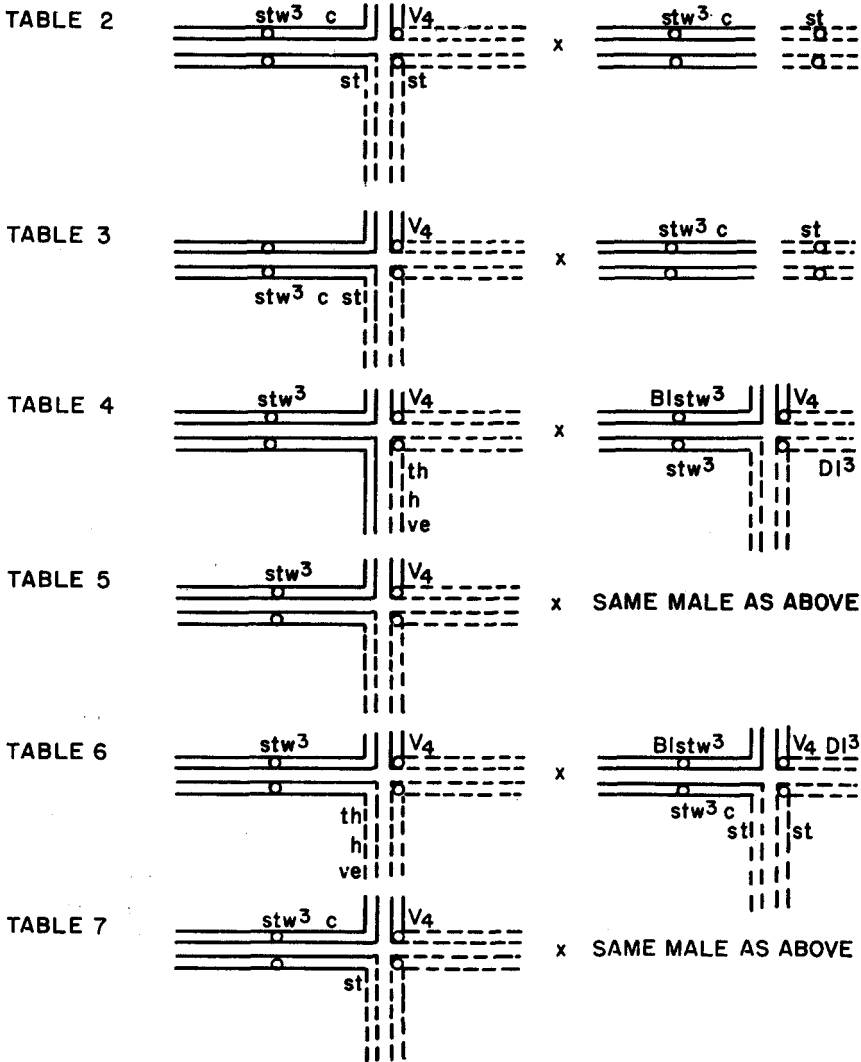


FIGURE 5.—Diagrams of the crosses made showing the position of the markers. In each case the female parent is on the left. In translocation heterozygotes the normal second chromosome is the upper left, the normal third is lower right, and the other two are translocation chromosomes.

be called to the classes *st* and *V4 stw³ c* in table 3. These represent complementary crossover products of an exchange between *st* and the breakpoint, that is, not in the interstitial region but in arm *L'*, their recovered numbers being 105 and 95, respectively. This kind of result is not inconsistent with the non-random interpretation since an exchange not within the limits of the interstitial region occurs between structurally identical chromatids.

TABLE 2

Progeny of $V4\ st/ stw^3\ c\ st$ females by $stw^3\ c\ st$ males. In each case, the composition of the male gamete is $2S + 3$

| Composition of female gamete | Progeny phenotype | Number |
|------------------------------|----------------------------|--------------|
| non-c.o. | | |
| $2S + 3$ $2'L' + 3'$ | $stw^3\ c\ st$ $V4\ st$ | 8691 7616 |
| c.o. Reg. I | | |
| $2'S + 3$ $2L' + 3'$ | $c\ st$ $V4\ stw^3\ st$ | 1530 793 |
| c.o. Reg. II | | |
| $2'S + 3$ $2L' + 3'$ | st $V4\ stw^3\ c\ st$ | 529 278 |
| c.o. Regs. I, II | | |
| $2S + 3$ $2'L' + 3'$ | $stw^3\ st$ $V4\ c\ st$ | 17 29 |

RESULTS FROM CROSSES OF TRANSLOCATION FEMALES BY TRANSLOCATION MALES

The discussion to follow will be concerned with an analysis of results from experiments designed to test the following possibilities: (1) that there is a striking discrepancy in the relative frequencies of the complementary aneuploid I classes and that this may be accounted for on the basis of homozygosis for a lethal in L' or (2) that there is no discrepancy of this order between aneuploid I individuals which do not arise from an exchange in the interstitial region, but that one does exist between the classes representing detectable crossover products arising from an exchange in this region, the discrepancy resulting from the operation of the non-random effect.

The presence or absence of a lethal located at the tip of L' at approximately the same position postulated by GLASS, may be inferred by comparing the results from experiments in which this arm is retained with those in which it is replaced with a normal arm. In the former situation, an appreciable deficiency should appear in the aneuploid I class of the composition $2'L' + 3/2S + 3'$ (female gamete/male gamete) as compared with the complementary class, $2S + 3'/2L' + 3$. Contrarily, this discrepancy should disappear as a result of the removal of this chromosome and its replacement with a normal equivalent. For information on the contribution which might be made to the discrepancy from the loss of individuals as a result of homozygosis for this lethal, this arm may be marked genetically and the frequency of homozygosis determined for some distally located mutant; in two experiments, a chromosome carrying *ve h lh* was used for this purpose. The results from the experiments in which L' was retained are given in tables 4 and 5 (fig. 5). In these cases,

TABLE 3

Progeny of V4 stw³ c st/+ females by stw³ c st males. In each case, the composition of the male gamete is 2S + 3

| Composition of female gamete | Progeny phenotype | Number |
|------------------------------|-------------------------------|--------------|
| non-c.o. | | |
| 2S + 3 2'L' + 3' | + V4 stw ³ c st | 2201 1922 |
| c.o. Reg. I | | |
| 2'S + 3 2L' + 3' | stw ³ V4 c st | 424 170 |
| c.o. Reg. II | | |
| 2'S + 3 2L' + 3' | stw ³ c V4 st | 147 68 |
| c.o. Regs. I, II | | |
| 2S + 3 2'L' + 3' | c V4 stw ³ st | 16 10 |
| c.o. st-bp | | |
| 2S + 3 2'L' + 3' | st V4 stw ³ c | 105 95 |
| c.o. Reg. I, st-bp | | |
| 2'S + 3 2L' + 3' | stw ³ st V4 c | 21 5 |

Cy/V4 males were mated to *stw³; ve h lh* females in one instance, and to *stw³* females in the other, and the non-*Cy* female offspring crossed by appropriate males. When *L'* was replaced with an arm carrying *ve h lh*, and by one carrying *st*, the results that were obtained are those given in tables 6 and 7 (fig. 5).

Since neither *L'* nor the interstitial region was marked genetically in the tests made by GLASS, crossovers in these regions could not be recognized as such. These individuals appeared as noncrossovers and therefore were classified as belonging to some general class which included noncrossovers as well as undetected crossovers. To illustrate the kind of result which would have been expected under these conditions, the noncrossover and corresponding crossover classes from the present experiments have been added together. These totals are given in tables 4-7 in the column headed "Regrouped Classes". Thus, for example, as shown in table 5, each of the complementary aneuploid I classes, is a mixture of individuals identified as noncrossovers and those identified as crossovers. In one are included 1110 noncrossovers, *V4 stw³ Dl³*, and 331 *V4 Dl³* individuals carrying the shorter crossover chromatid, while the other includes 824 noncrossovers, *Bl V4*, and 125 *Bl V4 stw³*

TABLE 4
Progeny of V4/stw³ ve h th females by V4 stw³/Bl stw³ Df³ males

| Composition of gametes | | Progeny phenotype | Number | Regrouped classes | Correction |
|---------------------------------------|-----------|---|--------|-------------------|------------|
| Male | Female | | | | |
| non-c.o. orthoploid | | | | | |
| 2S + 3 | 2S + 3 | <i>Bl Df³ stw³</i> | 299 | 339 | 274 |
| 2'L' + 3' | 2S + 3 | <i>V4 stw³</i> | 331 | 355 | 306 |
| 2S + 3 | 2'L' + 3' | <i>Bl V4 Df³</i> | 282 | 302 | 271 |
| 2'L' + 3' | 2'L' + 3' | <i>V4/V4</i> | 54 | | |
| non-c.o. aneuploid I | | | | | |
| 2'L' + 3 | 2S + 3' | <i>V4 stw³ Df³</i> | 174 | 199 | 142 |
| 2S + 3' | 2'L' + 3 | <i>Bl V4</i> | 99 | 147 | 116 |
| c.o. orthoploid | | | | | |
| 2S + 3 | 2'S + 3 | <i>Bl Df³</i> | 40 | | |
| 2'L' + 3' | 2'S + 3 | <i>V4</i> | 24 | | |
| 2S + 3 | 2L' + 3' | <i>Bl V4 Df³ stw³</i> | 20 | | |
| c.o. aneuploid I | | | | | |
| 2'L' + 3 | 2'S + 3' | <i>V4 Df³</i> | 25 | | |
| 2S + 3' | 2L' + 3 | <i>Bl V4 stw³</i> | 11 | | |
| c.o. in L' | | | | | |
| 2S + 3' | 2'L' + 3 | <i>Bl V4 ve..</i> | 32 | | |
| c.o. in interstitial region and in L' | | | | | |
| 2S + 3' | 2L' + 3 | <i>Bl V4 stw³ ve..</i> | 5 | | |

individuals carrying the longer crossover chromatid. The ratio of these classes to one another from experiments in which *L'* was not replaced are 199/147 and 1441/949, differences of 26.1% and 34.1%, respectively. From those experiments in which *L'* was replaced with a normal equivalent, they are 782/527 and 663/497, differences of 32.5% and 25.0%, respectively. The information on the frequency of homozygosis for *ve* is given in table 4, 37/147 or 25.2%, and in table 6, 104/527 or 19.6%.

These two results, the failure to modify the discrepancy by replacing the section of the chromosome, presumed to carry the lethal, by a homologous section of a chromosome from another stock, and the relatively low rate of homozygosis for the distal marker *ve*, provide experimental evidence that homozygosity for lethals is not the cause of the discrepancy.

INTERPRETATION OF THE RESULTS ON THE BASIS OF THE NON-RANDOM HYPOTHESIS

Although it is not possible to determine directly the relative frequencies with which noncrossover individuals come from exchange and no-exchange tetrads, these

TABLE 5
Progeny of V4/stw³ females by V4 stw³/ Bl stw³ D^{l3} males

| Composition of gametes | | Progeny phenotype | Number | Regrouped classes | Correction |
|------------------------|-----------|---|--------|-------------------|------------|
| Male | Female | | | | |
| non-c.o. orthoploid | | | | | |
| 2S + 3 | 2S + 3 | <i>Bl D^{l3} stw³</i> | 2046 | 2512 | 1715 |
| 2'L' + 3' | 2S + 3 | <i>V4 stw³</i> | 2202 | 2608 | 1871 |
| 2S + 3 | 2'L' + 3' | <i>Bl V4 D^{l3}</i> | 1966 | 2164 | 1841 |
| 2'L' + 3' | 2'L' + 3' | <i>V4/V4</i> | 189 | | |
| non-c.o. aneuploid I | | | | | |
| 2'L' + 3 | 2S + 3' | <i>V4 stw³ D^{l3}</i> | 1110 | 1441 | 674 |
| 2S + 3' | 2'L' + 3 | <i>Bl V4</i> | 824 | 949 | 626 |
| c.o. orthoploid | | | | | |
| 2S + 3 | 2'S + 3 | <i>Bl D^{l3}</i> | 466 | | |
| 2'L' + 3' | 2'S + 3 | <i>V4</i> | 406 | | |
| 2S + 3 | 2'L' + 3' | <i>Bl V4 D^{l3} stw³</i> | 198 | | |
| c.o. aneuploid I | | | | | |
| 2'L' + 3 | 2'S + 3' | <i>V4 D^{l3}</i> | 331 | | |
| 2S + 3' | 2'L' + 3 | <i>Bl V4 stw³</i> | 125 | | |

may be inferred from those of the recovered crossover types. For example, after adjacent disjunction following an exchange in the interstitial region, the gametes $2L' + 3'$ and $2S + 3'$ are formed from the dyads $2S:2L' + 3'$ (the chromatids of the dyad are separated by a colon) and gametes of the constitution $2'S + 3$ and $2'L' + 3$ are produced from the complementary dyads, $2'S:2'L' + 3$. Now, from the frequencies with which the crossover types $2L' + 3'$ and $2'S + 3$ are recovered may be inferred those of the noncrossover types, $2S + 3'$ and $2'L' + 3$, respectively, which have come from exchange tetrads. Subtracting this number from the total number of noncrossover individuals, gives a figure representing the number of noncrossovers which came from no-exchange tetrads. A consideration, from this aspect, of the data for the complementary aneuploid classes from table 5 will serve to illustrate the nature of this correction. From the kind of situation just described, that is, from adjacent disjunction at the first division, 198 $2L' + 3'$, *Bl V4 D^{l3} stw³*, individuals representing the recovery of the longer crossover chromatid, and an average of 436 $2'S + 3$, 466 *Bl D^{l3}* and 406 *V4*, individuals carrying the shorter crossover chromatid appeared. Hence, 436 offspring carrying the shorter noncrossover chromatid, $2S + 3'$, *V4 stw³ D^{l3}*, and 198 carrying the longer, $2'L' + 3$, *Bl V4*, are calculated to have come from exchange tetrads. Thus, 674 *V4 stw³ D^{l3}* (1110-436) and 626 *Bl V4* (824-198) represent the number of noncrossovers which came from no-exchange tetrads. The results of applying this method of correction for orthoploid and aneuploid noncrossover classes are given in table 4-7 in the column headed "Correction". The ratios of

TABLE 6

Progeny of V4 ve h th / stw³ females by V4 D^{l3} stw³ c st / Bl stw³ c st males

| Composition of gametes | | Progeny phenotype | Number | Regrouped classes | Correction |
|---------------------------------------|-----------|--|--------|-------------------|------------|
| Male | Female | | | | |
| non-c.o. orthoploid | | | | | |
| 2S + 3 | 2S + 3 | <i>Bl stw³</i> | 913 | 1116 | 757 |
| 2'L' + 3' | 2S + 3 | <i>V4 stw³ D^{l3}</i> | 908 | 1102 | 752 |
| 2S + 3 | 2'L' + 3' | <i>Bl V4</i> | 942 | 1027 | 886 |
| 2'L' + 3' | 2'L' + 3' | <i>V4/V4</i> | 40 | | |
| non-c.o. aneuploid I | | | | | |
| 2'L' + 3 | 2S + 3' | <i>V4 stw³ st</i> | 626 | 782 | 428 |
| 2S + 3' | 2'L' + 3 | <i>Bl V4 D^{l3}</i> | 378 | 527 | 397 |
| c.o. orthoploid | | | | | |
| 2S + 3 | 2'S + 3 | <i>Bl</i> | 203 | | |
| 2'L' + 3' | 2'S + 3 | <i>V4 D^{l3}</i> | 194 | | |
| 2S + 3 | 2'L' + 3' | <i>Bl V4 stw³</i> | 85 | | |
| c.o. aneuploid I | | | | | |
| 2'L' + 3 | 2'S + 3' | <i>V4 st</i> | 156 | | |
| 2S + 3' | 2'L' + 3 | <i>Bl V4 D^{l3} stw³</i> | 45 | | |
| c.o. in L' | | | | | |
| 2S + 3' | 2'L' + 3 | <i>Bl V4 D^{l3} ve..</i> | 93 | | |
| c.o. in interstitial region and in L' | | | | | |
| 2S + 3' | 2L' + 3 | <i>Bl V4 D^{l3} stw³ ve..</i> | 11 | | |

individuals in the complementary aneuploid I classes which came from no-exchange tetrads are 142/116 (table 4), 674/626 (table 5), 428/397 (table 6), and 442/399 (table 7). It may be seen that the effect of the correction on the relative frequencies of complementary noncrossover orthoploids for those coming from exchange tetrads is less striking since the number of crossovers relative to that of the noncrossovers is considerably less than that for the aneuploid classes. However, the data given in tables 6 and 7 that there is a statistically significant difference between the classes *V4 stw³ D^{l3}* and *Bl stw³* on the one hand, and *Bl V4* on the other, of some importance being the approximate 16% excess of *Bl V4* as compared with *V4 stw³ D^{l3}*. Since this probably reflects a difference in the relative viabilities of the two classes, it would mean that the frequency of individuals from the class *V4 stw³ D^{l3}* in tables 4 and 5 which came from no-exchange tetrads should be increased by 16%. It may be shown, however, that this correction is not sufficient to effect a difference between these complementary aneuploid classes and those from tables 6 and 7. (A comparison

TABLE 7
Progeny of V4 st / stw³ c females by V4 Dl³ stw³ c st / Bl stw³ c st males

| Composition of gametes | | Progeny phenotype | Number | Regrouped classes | Correction |
|-------------------------|-----------|---|--------|-------------------|------------|
| Male | Female | | | | |
| non-c.o. orthoploid | | | | | |
| 2S + 3 | 2S + 3 | <i>Bl stw³ c</i> | 857 | 957 | 747 |
| 2'L' + 3' | 2S + 3 | <i>V4 Dl³ stw³ c</i> | 832 | 953 | 722 |
| 2S + 3 | 2'L' + 3' | <i>Bl V4 st</i> | 882 | 943 | 845 |
| 2'L' + 3' | 2'L' + 3' | <i>V4/V4</i> | 7 | | |
| non-c.o. aneuploid I | | | | | |
| 2'L' + 3 | 2S + 3' | <i>V4 stw³ c st</i> | 553 | 663 | 442 |
| 2S + 3' | 2'L' + 3 | <i>Bl V4 Dl³</i> | 460 | 497 | 399 |
| c.o. orthoploid Reg. I | | | | | |
| 2S + 3 | 2'S + 3 | <i>Bl c</i> | 84 | | |
| 2'L' + 3' | 2'S + 3 | <i>V4 Dl³ c</i> | 101 | | |
| 2S + 3 | 2L' + 3' | <i>Bl V4 stw³ st</i> | 54 | | |
| c.o. orthoploid Reg. II | | | | | |
| 2S + 3 | 2'S + 3 | <i>Bl</i> | 16 | | |
| 2'L' + 3' | 2'S + 3 | <i>V4 Dl³</i> | 20 | | |
| 2S + 3 | 2L' + 3' | <i>Bl V4 stw³ c st</i> | 7 | | |
| c.o. aneuploid Reg. I | | | | | |
| 2'L' + 3 | 2'S + 3' | <i>V4 c st</i> | 91 | | |
| 2S + 3' | 2L' + 3 | <i>Bl V4 Dl³ stw³</i> | 29 | | |
| c.o. aneuploid Reg. II | | | | | |
| 2'L' + 3 | 2'S + 3' | <i>V4 st</i> | 19 | | |
| 2S + 3' | 2L' + 3 | <i>Bl V4 Dl³ stw³ c</i> | 8 | | |

of the results in table 4 with those in tables 6 and 7 give χ^2 values of 3.87 and 3.17, 2 d.f., *P* values of 0.2–0.1 and 0.3–0.2, respectively; a comparison of results in table 5 with those in tables 6 and 7 gives χ^2 values of 28.2 and 1.82, 2 d.f., *P* values of 0.3–0.2 and 0.5–0.3, respectively).

FREQUENCIES OF THE VARIOUS RECOVERED CLASSES

In comparing our results with those obtained by GLASS insofar as the relative frequencies of orthoploids and aneuploids are concerned, the gametic frequencies of the two classes were calculated from the present data by taking the square root of the average number of individuals in each class, that is, by assuming that the frequency of the two types of gametes are equal in the male and the female, and applying the appropriate correction for the viability difference between the complementary

TABLE 8

Summary of crossover types and frequencies from the tables indicated. The classes bearing identical symbols in each table have been combined

| Symbol | Disjunction | Chromatid | Tables | | | |
|---------------------|-----------------------|-----------|--------|-----|-----|-----|
| | | | 4 | 5 | 6 | 7 |
| 2'L' + 3 / 2'S + 3' | exchange alternate | short | 25 | 331 | 156 | 110 |
| 2S + 3' / 2L' + 3 | exchange alternate | long | 11 | 125 | 56 | 37 |
| 2S + 3 / 2'S + 3 | exchange adjacent | short | 40 | 466 | 203 | 110 |
| 2'L' + 3' / 2'S + 3 | exchange adjacent | short | 24 | 406 | 194 | 121 |
| 2S + 3 / 2L' + 3' | exchange adjacent | long | 20 | 198 | 85 | 61 |

aneuploid classes in tables 4 and 5. These ratios from the columns headed "Re-grouped classes" are as follows: 1.0:0.75 (table 4), 1.0:0.72 (table 5), 1.0:0.77 (table 6), and 1.0:0.78 (table 7). Calculated in the same way, the ratio of orthoploids to aneuploids from the results obtained by GLASS from crosses involving heterozygous V4 females in the absence of inversions (see table 1a), is 1.0:0.74. As has been shown, however, these classes are composed of a mixture of noncrossover and crossover types, each of these types coming from a different kind of disjunction; that is, crossover individuals identified as orthoploids come from adjacent I disjunction while crossover aneuploids come from alternate disjunction. Therefore, the ratio of the recovered (i.e., not gametic) frequencies of orthoploids to aneuploids from no-exchange tetrads and from exchange tetrads was calculated. From no-exchange tetrads, the ratios of orthoploids to aneuploids are: 1.0:0.49 (table 4); 1.0:0.39 (table 5); 1.0:0.52 (table 6); and 1.0:0.55 (table 7). It is clear that orthoploids coming from no-exchange tetrads following alternate disjunction appear considerably more frequently than do aneuploids from no-exchange tetrads following adjacent I disjunction. Since following an exchange, crossover aneuploids come from alternate disjunction, and crossover orthoploids from adjacent disjunction the terms "exchange alternate" and "exchange adjacent" have been used to designate the types of disjunction giving rise to aneuploid and orthoploid crossovers, respectively. From the summary given in table 8 of the results from tables 4-7, the ratios, in that order, of the total crossover orthoploids (exchange adjacent) to crossover aneuploids (exchange alternate) are: 1.0:0.64, 1.0:0.64, 1.0:0.66, and 1.0:0.76. These ratios indicate that, after an exchange in the interstitial region, the crossover classes identified as having come from adjacent I disjunction are recovered with a greater frequency than those which came from alternate disjunction. The ratios of complementary crossover products for each of the crossover types are as follows: (1) for crossover orthoploids, the ratios of individuals carrying the shorter crossover chromatid to those carrying the longer are 1.0:0.63, 1.0:0.45, 1.0:0.43, and 1.0:0.55 (2) for crossover aneuploids, the comparable ratios are 1.0:0.44, 1.0:0.38, 1.0:0.36, and 1.0:0.34.

CONCLUSIONS

The results from these experiments show that the discrepancy between complementary aneuploid I classes is not related to the elimination of individuals carrying a lethal in the homozygous condition, since, as indicated by comparing the results from two types of experiments designed specifically to test this, there is no evidence for the presence of a lethal in the translocation stocks used. It is evident, however, that a discrepancy as large as that reported by GLASS was not found. The hypothesis of non-random disjunction is supported by these results since this phenomenon was demonstrated as operating in exchange tetrads. It was shown that adjacent I disjunction may take place following an exchange in the interstitial region, and that the great majority of aneuploid individuals come from no-exchange tetrads. Disagreements between the data presented here and those presented previously by GLASS (1933) are at least partially resolvable if the following argument is made, based on the assumption of different crossover rates in the two experiments. The extent to which non-random disjunction may contribute to the discrepancy between complementary aneuploid I classes will depend not only on the degree of nonrandomness but also on the frequency of crossing over in the interstitial region. A higher crossover value would have the effect of increasing the difference between complementary aneuploid classes and reducing the frequency of noncrossover aneuploids coming from no-exchange tetrads. As the simplest approximation, a direct relationship of the following sort may be set up to arrive at a value for the discrepancy to be expected between the complementary aneuploid classes after regrouping assuming a higher frequency of crossing over: the observed difference between complementary aneuploid non-crossovers/the difference after regrouping = the expected difference between complementary aneuploid noncrossovers resulting from a higher crossover rate/ x , the value for the expected difference after regrouping. The crossover value used was 21.9%, given by GLASS (1933). The results of these calculations, after applying the viability correction in tables 5 and 6, give the following values for x : 53.0% (table 4), 49.4% (table 5), 42.5% (table 6), and 37.8% (table 7); the average difference observed by GLASS was 42.9%. The general agreement of these calculated values suggests that the apparent differences in the frequency of adjacent disjunction, and the extent of non-randomness may be the result of some change, with the effect of simply altering crossover values, taking place in the lines used between the time of the early experiments (1933), and those reported on here.

It was pointed out that whereas no-exchange orthoploids coming from alternate disjunction appeared appreciably more frequently than the no-exchange aneuploids coming from adjacent disjunction, the orthoploid crossovers, identified as coming from adjacent I disjunction appeared more frequently than aneuploid crossovers identified as having come from alternate disjunction. An explanation which can be proposed to explain these results involves a shift in the relative positions of centromeres 2 and 2' after an exchange in the interstitial region such that each would occupy the position of the former. This would have the effect of placing in an alternate position the dyads which were originally arranged in an adjacent fashion and *vice versa*. If alternately disposed chromosomes disjoin more frequently to the same pole than those arranged adjacently, then the gametes arising from this kind of

disjunction (and which carry orthoploid crossover products) would be recovered more often than those coming from adjacent disjunction (containing aneuploid crossover products). The results might equally well be interpreted, however, assuming a shift prior to the time of crossing over. The data do not permit distinguishing between these possibilities.

SUMMARY

Female *Drosophila* heterozygous for certain kinds of translocations do not produce complementary types of gametes with the expected equal frequencies. A genetic analysis has shown that the inequality of frequencies arises after an exchange occurs in the interstitial region, which forms asymmetric dyads consisting of a short and a long chromatid. Non-random disjunction is responsible for the recovery of the shorter chromatid in preference to the longer, thereby causing a deviation from the simple one-to-one expectations for the frequency of complementary types. Other aspects of disjunction in this particular kind of translocation heterozygote are discussed.

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