

COINCIDENCE OF CROSSING OVER IN *DROSOPHILA MELANOGASTER* (*AMPELOPHILA*)¹

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TABLE OF CONTENTS

	PAGE
INTRODUCTION	135
Coincidence of widely separated regions.....	138
Coincidence in the second chromosome.....	146
Coincidence in the third chromosome.....	148
Coincidence in other forms.....	148
The mechanism of crossing over.....	148
Triple crossing over	149
Maximum and minimum coincidence.....	153
The distance between the breaking points in double crossing over.....	154
Mutations observed	156
SUMMARY	158
LITERATURE CITED	158
TABLES	160

The present investigation was undertaken in the hope of throwing some light on the behavior of the chromosomes during crossing over. The problem was considered from the point of view of genetics by studying the effect of crossing over in one region of the chromosome on crossing over in another region, and by considering how this effect varies with variation of the distance between the regions involved. The phenomena have a bearing on the method of twisting of the chromosomes and the mechanism of crossing over.

According to the theory of linear arrangement and the chiasmatype, Mendelian genes are disposed in linear series in the chromosomes, and the separation of linked genes (crossing over) is due to breaks in homologous chromosomes (which have come together during synapsis) and recombinations between the resulting pieces (JANSSENS 1909, MORGAN 1910, STURTEVANT 1913, 1915, MULLER 1916). The percentage of cases in which two linked genes separate (amount of crossing over between them) is necessarily proportional, other things being equal, to

¹ Contribution from Zoölogical Laboratory of COLUMBIA UNIVERSITY.

the distance between the genes. Hence the distance on a chromosome map is measured by this percentage of crossing over. But this percentage is also affected by other conditions than actual morphological distance; for example, the age of the female, definite Mendelian factors, etc. (STURTEVANT 1913, 1915, BRIDGES 1915, MULLER 1916). Moreover, different regions may be, and in some cases are known to be, affected to different extents. The distances on chromosome maps are, therefore, not necessarily to be interpreted as actual morphological distances, for it is possible that the amount of crossing over in the morphologically shorter of two distances is greater than in the morphologically longer. Therefore, when the term *distance* is used in this paper, it should be interpreted as *percentage of crossing over*.

Breaks may occur simultaneously at more than one point of a chromosome. For example, in the disjunction of two chromosomes of which one contains the factors $M N P Q$ and the other the allelomorphous factors $m n p q$ (see figure 1), when a break occurs between M and N a break may also occur between P and Q . If the pieces recombine, the resulting chromosomes will contain respectively the factors $m N P q$ and $M n p Q$.

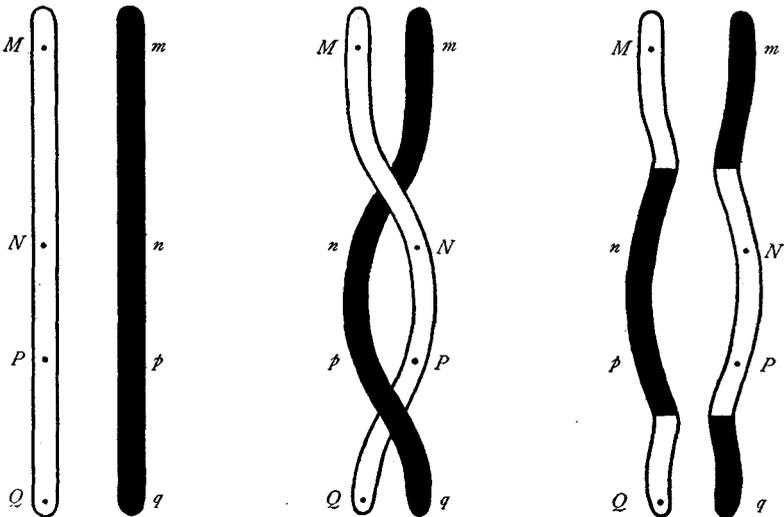


FIGURE 1

It was evident, however, from the data on which the theories above referred to were based, that when a break occurs in one region of a chromosome, neighboring regions are much less likely to undergo a break

than would otherwise be the case. If, in the above example, the regions *M N* and *P Q* are not far apart, a break between *M* and *N* will tend to prevent the occurrence of a break between *P* and *Q* (STURTEVANT 1913, 1915, MORGAN, STURTEVANT, MULLER and BRIDGES 1915, pp. 63-64, MULLER 1916).

This phenomenon, which has been termed *interference*, is well illustrated by an unpublished cross carried out by BRIDGES. The cross involved four sex-linked factors in *Drosophila*: vermilion (eye color), sable (body color), garnet (eye color) and forked (bristles). The relative positions of these factors are shown in the diagram (figure 2).

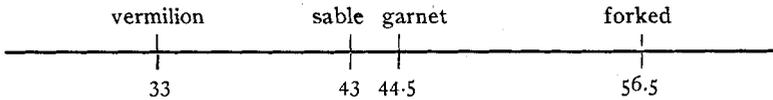


FIGURE 2

The amount of crossing over in the vermilion sable region is about 10 percent; in the garnet forked region about 12 percent. That is, if we take all the offspring from this cross, about 10 percent will be crossovers between vermilion and sable, and about 12 percent will be crossovers between garnet and forked. But if instead of taking all the flies we take only those which have already resulted from a crossing over between vermilion and sable, we find that in this sample the proportion that are also crossovers between garnet and forked is not 12 percent but only 1.2 percent. That is, these crossovers are only one-tenth as numerous as in a random sample. Or, if we count only the crossovers between garnet and forked, the number that are also crossovers between vermilion and sable is not 10 percent, but only 1.0 percent—again only one-tenth as many as in a random sample.

The actual data are as follows:¹

TABLE I

————	<u>1</u>	<u>2</u>	<u>3</u>	<u>1 2</u>	<u>1 3</u>	<u>2 3</u>	<u>1 2 3</u>	Total
2651	313	47	380	0	3	0	0	3394

Since the total amount of crossing over in the vermilion sable region is 0.093 and in the garnet forked region 0.113, the amount of crossing

¹ In this and other tables the non-crossover class is denoted by a line, ——— without numerals. The crossover classes are denoted by a line and numerals referring to the regions in which the crossing over took place, the regions being numbered from left to right. In the present case, the vermilion sable region is 1, the sable garnet region is 2, the garnet forked region is 3. 1 indicates a crossing over in the vermilion sable region, 1 3 indicates a double crossing over involving the vermilion sable and garnet forked regions, etc. In the text, crossover classes may be indicated by the numbers of the regions in which crossing over has occurred. For example, the 1, 3 crossover class is the class involving crossing over in both the first and third regions.

over involving both regions simultaneously (if they were independent of each other) would be $0.093 \times 0.113 = 0.01$. The observed proportion of crossing over involving both regions is only 0.001. The ratio of the actual amount to the amount expected if the regions did not affect each other is $\frac{0.001}{0.01} = 0.10$. This ratio is termed the *coincidence of crossing over* of the two regions (BRIDGES 1915, MULLER 1916).² That is, the coincidence of crossing over of two regions is the ratio of the actual amount of crossing over involving both regions to the amount that would occur if crossing over in one region did not affect crossing over in the other.³

It is evident that in a double crossing over involving the regions $M N$ and $P Q$ (see figure 3), the distance between the two points at which



FIGURE 3

the breaks occur may be just greater than $N P$ or just less than $M Q$; or it may have any intermediate value. It can be shown that the average distance between the breaking points is the mean of $N P$ and $M Q$, or the distance from the mid-point of $M N$ to the mid-point of $P Q$. This was pointed out by MULLER (1916). The proof of this and a discussion of the assumptions on which it rests will be given later in this paper; I wish here merely to call attention to the formula.

COINCIDENCE OF WIDELY SEPARATED REGIONS

In the vermilion garnet sable forked cross above cited, the intermediate distance (sable garnet) is very short—only about two units. The work on *Drosophila* has shown that in general the coincidence of two regions increases as the distance between them increases (STURTEVANT 1915, MULLER 1916). The present investigation was undertaken to determine the value of coincidence when the intermediate distance becomes very long. Two crosses were made involving factors in the sex chromosome. The relative positions of these factors are shown in figure 4.

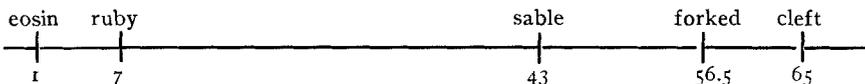


FIGURE 4

² This phenomenon was originally referred to in terms of interference. The index of interference used was the reciprocal of coincidence (STURTEVANT 1913, 1915, BRIDGES 1915, MULLER 1916).

³ MULLER has preferred to state this ratio as a percentage; but for greater ease in calculation it is better expressed as a decimal fraction. The latter usage will be adopted in this paper.

One cross involved the factors eosin (eye color), ruby (eye color), sable (body color) and forked (bristles); and the other cross involved eosin, ruby, forked and cleft (venation). Practically the entire length of the sex chromosome (so far as known) is involved in the latter cross, since eosin is only one unit from the extreme left-hand end and cleft is (with the possible exception of lethal *sc*) the extreme right-hand factor. The farthest right-hand factor hitherto worked with in determinations of coincidence has been bar, which is only half a unit to the right of forked.

In choosing the factors to be worked with, it was necessary (for reasons that will be explained later) to make the regions whose coincidence was to be determined short enough to prevent the occurrence of double crossing over within them. This made the percentage of crossing over within each region small and necessitated making large counts to get significant results.

The results indicate that the coincidence of the eosin ruby region and the sable forked region (a mean intermediate distance of about 46) is about 1.00 (possibly a little more), and that the coincidence of the eosin ruby region with the forked cleft region (a mean intermediate distance of about 57) is only 0.68. That is, when the intermediate distance increases beyond a certain value, coincidence instead of rising or remaining at the value it has reached, falls again. This means that crossing over at the extreme left-hand end of the chromosome interferes with crossing over at the right-hand end, but has practically no effect on crossing over in the region just to the left of the right-hand end.

In each cross, females heterozygous for the particular combination of factors under consideration were bred singly. Since the factors involved are sex-linked, the proportion of the different classes of sons is a direct index of the frequency of crossing over in the different regions of the chromosome. The daughters were counted in order to keep track of the sex ratios, but were not classified, because it is often impossible to distinguish eosin from ruby in the female, and because it is impossible to backcross by cleft males, which are sterile. The mothers, therefore, instead of being backcrossed, were in most cases mated to bar males. Bar is a dominant sex-linked character; hence it was possible to distinguish non-disjunction in both male and female offspring (BRIDGES 1916). Cultures giving non-disjunction were excluded from the totals in both crosses, because of the possibility that non-disjunction might affect coincidence.

Each cross was made so that the factors involved entered in several different combinations in different matings. In this way any particular crossover class is represented by several different combinations of characters, so that if the viability of any particular combination of characters is poor, it may be counterbalanced by the good viability of another combination and *vice versa* (MORGAN and BRIDGES 1916). Moreover, cultures giving less than 40 males were excluded because a small number of offspring is often due to poor culture conditions, which may entail differential inviability.

The data for the eosin ruby sable forked cross are as follows:

TABLE 2

♀ ♀	♂ ♂	1	2	3	1 2	1 3	2 3	1 2 3	Total ♂ ♂
15298	6363	579	3638	1208	128	115	350	6	12387

The total proportionate amount of crossing over in the eosin ruby region is here 0.0668. The total amount of crossing over in the sable forked region is 0.1355. If crossing over in one region does not affect crossing over in the other, the amount of crossing over involving both regions simultaneously would be $0.0668 \times 0.1355 = 0.00905$. The actual amount of double crossing over involving both regions (the triple crossovers are excluded for reasons that will be explained later) is 0.00928. The coincidence is $\frac{0.00928}{0.00905} = 1.025$.⁴ The two regions are

therefore independent. If anything, a crossing over between eosin and ruby makes crossing over between sable and forked slightly more likely to occur.

The counts of the eosin ruby forked cleft cross are given in the following table:

TABLE 3

♀ ♀	♂ ♂	1	2	3	1 2	1 3	2 3	1 2 3	Total ♂ ♂
17584	6894	530	5307	828	203	47	352	14	4175

⁴ The actual calculation of coincidence can be made somewhat more simply. For if the total number of flies involved is n , the total number of crossovers in the two regions respectively a and b , and the total number of double crossovers involving both regions x , then

$$\text{the coincidence} = \frac{\frac{x}{n}}{\frac{a}{n} \times \frac{b}{n}} = \frac{xn}{ab}$$

This makes it possible to calculate the coincidence of two regions without calculating their lengths.

The total amount of crossing over in the eosin ruby region is 0.0560; the amount of crossing over in the forked cleft region is 0.0875. The amount of double crossing over involving both regions (if they do not affect each other) should be $0.0560 \times 0.0875 = 0.004904$. The actual amount of double crossing over involving both regions is 0.003316. The coincidence is $\frac{0.003316}{0.004904} = 0.6761$. This indicates that crossing over in the eosin ruby region hinders crossing over in the forked cleft region.

The value obtained for the coincidence in each case is, of course, subject to a probable error of random sampling. But the applicability of the ordinary formula is doubtful in cases where the class under consideration (here the 1, 3 double crossover class), forms as small a proportion of the total as in the present case. PEARL (1917) has therefore suggested another method. DR. PEARL was kind enough to undertake a calculation of the significance of the present data, which was published in the paper referred to. This calculation, based on all the data in the eosin ruby sable forked cross, but only 9017 flies in the eosin ruby forked cleft cross, gives a probability of 0.0421; that is, the chances are about 23 to 1 against obtaining in the eosin ruby sable forked cross a coincidence as low as, or lower than, that obtained in the eosin ruby forked cleft cross.⁵

Since more data are now available, a recalculation on the basis of all the data has been made. This gives for the lower quartile of the 1,3 double crossover class in the eosin ruby sable forked cross, the value 65.3951, which is considerably higher than 47. But the probability to which this value corresponds cannot be determined from the table given by PEARL, since the latter is based on only part of the data involved.

On the Gaussian hypothesis, the observed deviation would correspond to odds of about 105 to 1 that the two values are different. But since the Gaussian method is supposed to be inapplicable to cases where p is very small and since statisticians are not in agreement on the validity of the other method (PEARSON 1917; compare also WRIGHT 1917), it seems best to suspend judgment on the statistical significance of the data.

There is, moreover, an objection to calculating the coincidence, as has just been done, on the basis of all the data lumped together. This is due to the fact that in any series of matings (such as the eosin ruby sable

⁵ In the data submitted to DR. PEARL, I did not take into account the difference between the values of the eosin ruby distance obtained in the two crosses; hence the probability arrived at by DR. PEARL is different from that given here. This fact, of course, in no way affects the validity of the method used.

forked cross) the coincidence might be the same in all the cultures; and yet if the coincidence were calculated from the total data instead of for each culture separately, the value derived might be different from that for each separate culture, if the amount of crossing over varied in the separate bottles.

This will be evident from a simple numerical example. Let us take two imaginary cultures of 100 flies each. Let us suppose that in one culture the number of crossovers in each of the two regions involved is 10 (or 0.10 of the total) and the number of double crossovers involving both regions is 1 (or 0.01 of the total). Let us suppose that in the second culture the number of crossovers in each of the regions is 20 (or 0.20 of the total) and the number involving both regions at once

is 4 (or 0.04 of the total). The coincidence in the first case is $\frac{0.01}{0.01} = 1.00$; in the second case it is $\frac{0.04}{0.04}$, which is also 1.00; but if we calculate

the coincidence on both cultures together it is $\frac{5}{200} = 1.11$.

$$\frac{30}{200} \times \frac{30}{200}$$

We can state this in more general terms. In one culture let m be the total number of flies, a and b the number of crossovers involving respectively the two regions under consideration, and x the number of double crossovers involving both regions simultaneously. In another culture let the corresponding values be n , p and q , and y . Then the coincidence in the first case (see footnote 4, p. 140) is $\frac{xm}{ab}$ and in the second case $\frac{yn}{pq}$. The average of these two values is $\frac{1}{2} \left(\frac{xm}{ab} + \frac{yn}{pq} \right) = \frac{xmpq + ynaab}{2abpq}$. The coincidence calculated on the total data is $\frac{(x+y)(m+n)}{(a+p)(b+q)}$. It is evident that these two values are not necessarily equal.

The coincidence in each cross was therefore calculated by considering each culture separately. The values obtained are given in the tables at the end of the paper. (In a few cultures there was no crossing over in

one of the two regions involved. In such cases the value of the coincidence is $\frac{0}{0}$, which is indeterminate. These cultures are consequently omitted from the calculation.)

The average value of the coincidence of eosin ruby and sable forked calculated in this way is 1.0238. The average value of the coincidence of eosin ruby and forked cleft is 0.6064. If the values are weighted according to the number of individuals in each culture, the averages are practically the same; namely, 1.0081 and 0.6049 respectively. These values agree very well with the values obtained in the previous calculation.

In table 4 the values of coincidence are grouped by intervals of 1.00, and the accompanying curves (figures 5 and 6) show these distributions graphically.

TABLE 4

Coincidence	0	1	2	3	4	5	6	7	8	9	10	Total broods
Number of broods, eosin ruby sable forked cross	91	41	12	6	2	4	1	0	0	0	0	157
Number of broods, eosin ruby forked cleft cross	141	13	7	4	3	2	1	1	0	0	1	173

It is noticeable that there is a comparatively smaller number of cultures whose coincidence is zero and a greater number of cultures whose coincidence is between 1 and 2 in the eosin ruby sable forked cross than in the eosin ruby forked cleft cross. This is partly at least due to the fact that the expected number of double crossovers involving the particular regions under consideration would (quite apart from considerations of coincidence) be greater in the former cross than in the latter, because the distance between sable and forked is greater than that between forked and cleft, and also because the eosin ruby distance in the first cross is slightly longer than in the second. However, this is counterbalanced to some extent at least by the fact that when a double crossover does occur in the second cross it raises the coincidence relatively more than in the first cross. It is in accordance with this that the highest values for coincidence are found in cultures of the second cross, not of the first, although the average coincidence in the first is higher.

Bearing in mind the possibilities of error due to these facts, we may

apply the χ^2 test (PEARSON 1911) to these two distributions. We obtain for χ^2 a value of 29.166. By referring to ELDERTON'S tables (ELDERTON 1901, p. 159) we find that this value for $n=9$ corresponds to a chance

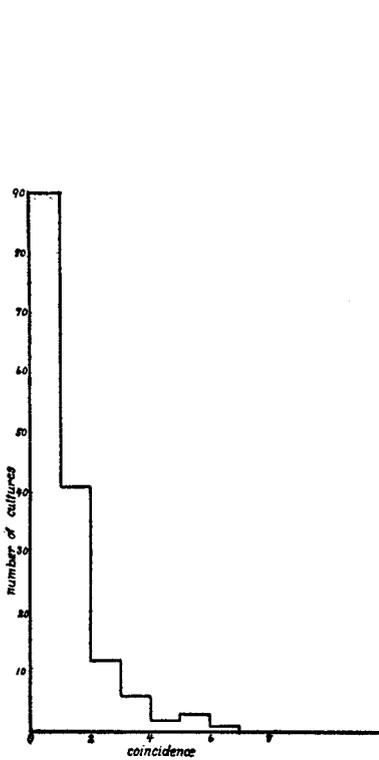


FIGURE 5.—Distribution of the values of coincidence of eosin ruby and sable forked.

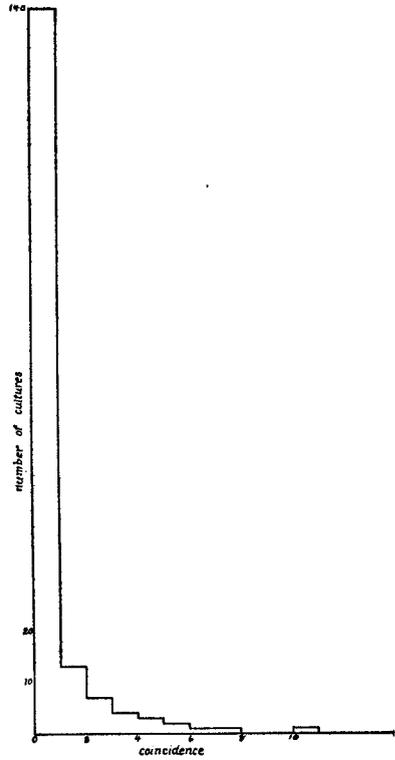


FIGURE 6.—Distribution of the values of coincidence of eosin ruby and forked cleft.

of 0.000299. Since this is equivalent to only one chance in 3344, the chance that the two distributions are the same is statistically negligible.

In some of the matings involving eosin, ruby, forked and cleft, a fifth factor, lozenge (eye), was also followed. Figure 7 indicates the location of this factor with respect to the others.



FIGURE 7

The intermediate distance between the ruby lozenge and the forked cleft regions is about the same as that between the eosin ruby and the

sable forked regions. Hence we might expect the coincidence of ruby lozenge and forked cleft to be about the same as that of eosin ruby and sable forked, and greater than that of eosin ruby and forked cleft. The actual counts in the present cross are as follows:

TABLE 5

♀ ♀	♂ ♂															Total ♂ ♀
		1	2	3	4	12	13	14	23	24	34	123	124	134	234	
3409	1217	96	321	599	164	3	31	4	53	34	44	1	1	3	1	2572

While these data are not sufficiently extensive in themselves to be significant, it may be instructive to compare them with the data already considered. The coincidence of ruby lozenge and forked cleft is here 0.866; that of eosin ruby and forked cleft is 0.295. Both values are lower than those obtained for the similar distances in the other crosses; but the disproportion between them is in the same direction and is even more marked.

A cross was also made with the factors eosin, ruby, forked and fused (wing). Since fused is between forked and cleft (figure 8), the co-

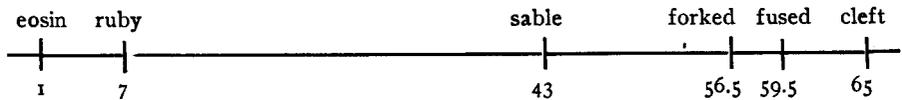


FIGURE 8

incidence of eosin ruby and forked fused might be expected to be intermediate between that of eosin ruby and sable forked and that of eosin ruby and forked cleft. The data obtained were as follows:

TABLE 6

♀ ♀	♂ ♂								Total ♂ ♀
		1	2	3	1 2	1 3	2 3	1 2 3	
8220	3889	290	3027	103	130	7	59	1	7506

Here the proportion of crossing over between eosin and ruby is 0.5702; between forked and fused the proportion is 0.0226. The coincidence of these two regions is 0.7221. This agrees with the expectation.

The cultures included above, as in the other crosses, were only those which contained at least 40 males, but since the number was too small to be significant another table was made in which all the other available cultures were also added in. The resulting distribution is as follows:

TABLE 7

♂ ♂								Total ♂ ♀
	1	2	3	1 2	1 3	2 3	1 2 3	
4260	326	3367	118	145	10	69	3	8298

The coincidence of eosin ruby and forked fused is now 1.1144.* The

* See note on page 159.

disagreement of the calculations with each other may be due to the poor viability of the cultures containing less than 40 individuals. In any case, the small numbers involved render the results insignificant statistically.

But even if the second value obtained represents the true value of the coincidence, the result can be harmonized with that of the crosses involving eosin, ruby, sable, forked and cleft. For the coincidence of eosin ruby and forked cleft is a composite value; and the coincidence of eosin ruby and forked fused might be over 1.00 and of eosin ruby and fused cleft might be correspondingly less than 0.68. Thus the coincidence of eosin ruby and forked cleft might be 0.68, which is intermediate between the other two values. Why there should be a sudden drop of coincidence from more than 1.00 to 0.68 is hard to see. It might conceivably be connected with the fact that the fused cleft region is at the end of the chromosome. It is easy to see why the proportion of crossing over should be less in a given morphological distance at the end of a chromosome than in an equal morphological distance further in; for it might be supposed that the twisting of chromosomes at the end is not as tight as in regions further in. But since map distances are calculated on the basis of proportion of crossing over, any such decrease in the amount of crossing over must already have been taken into account in the calculation of the map distance; and it is hard to see why coincidence should be affected.

For distances less than 46, the best data for the calculation of coincidence in the sex chromosomes are MULLER'S (1916). MULLER'S curve shows a steady rise of coincidence from 0 to a little over 1.00, as the distance increases from 0 to 45. STURTEVANT'S (1915) data, which gave a value of 2.88 for the coincidence of yellow eosin and vermilion miniature (a mean intermediate distance of about 33) are too small to be significant. MULLER'S curve also shows a fall and a second rise in coincidence when the distance rises above 45; but as MULLER himself stated, this part of the curve is not significant because the data were insufficient.

We may, therefore, conclude that in the sex chromosomes of *Drosophila* the coincidence rises to about 1.00 as distance increases to about 46, and that coincidence declines as distance increases further.

COINCIDENCE IN THE SECOND CHROMOSOME

In the second chromosome of *Drosophila*, only a few determinations of coincidence have been published. STURTEVANT (1915) obtained a co-

incidence of 0.307 in a cross involving black, purple, and curved (a total map distance of about 25.5), and a coincidence of 0.599 for a cross involving black, curved and speck (a total distance of about 55) (see figure 9). The data in both cases were too small to be significant. BRIDGES (1915) obtained a coincidence of 1.11 (first broods) and of 1.00 (second broods) for black, purple and curved. This variation of coincidence with the age of the female may not be significant; but even if these figures do not represent values significantly greater than 1.00, it is evident that there must be values of coincidence greater than 1.00 in the second chromosome. For the figures obtained represent average values, including the coincidence of adjacent regions, which is generally low (less than 1.00) when the regions are short. Therefore, the coincidence of the more widely separated portions of the regions involved is probably greater than 1.00.

Dr. BRIDGES has kindly placed at my disposal the data (as yet unpublished) of a cross involving the factors star, purple, curved and speck, whose relative positions are shown in figure 9.

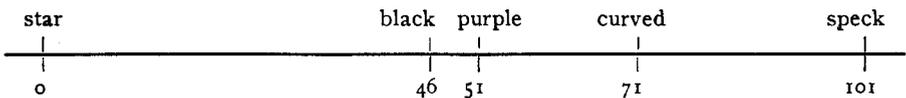


FIGURE 9

The data for this cross are as follows:

TABLE 8

	1	2	3	1 2	1 3	2 3	1 2 3	Total	
	1929	1487	687	1005	601	837	135	85	6766

The coincidences of the various regions are as follows:

TABLE 9

Regions	Total length	Coincidence
Purple curved and curved speck	53	0.4787
Star purple and purple curved	67	1.0226
Star purple and curved speck	99	0.9124

These figures resemble those obtained for the first chromosome in that the coincidence first rises and then falls with increase of distance, but the figures are not consistent with the figures of the black purple curved cross, which gave a coincidence of about 1.00 for a total distance of

about 20. These inconsistencies may be partly due to the variability of linkage in the second chromosome; they are probably also due to the fact that each of the regions involved (except black purple) is long enough to allow a considerable amount of double crossing over (which remains undetected) within it. It should be recalled in this connection that double crossing over for a given distance is more frequent in the second chromosome than in the first.

COINCIDENCE IN THE THIRD CHROMOSOME

The only published third chromosome data from which coincidence can be calculated are those of MULLER (1916). The counts are, however, very small. Some unpublished crosses made by MULLER and BRIDGES give results somewhat more extensive, but still too small to be significant. The coincidence does not rise much above 1.00, except in two cases in which it is over 2.00; but in both cases larger counts might change the results.

COINCIDENCE IN OTHER FORMS

In *Primula* ALTENBURG (1916) has obtained a coincidence of 0.64 (possibly, as he explained, this may represent a value as high as 1.00) for two adjacent regions whose lengths are 11.62 and 34.02 units respectively. The only other crosses hitherto reported involving more than two pairs of linked Mendelian genes at the same time have been carried out by GREGORY (1911) with *Primula* and PUNNETT (1913) with sweet peas. In PUNNETT'S crosses it is not possible to calculate the coincidence, since he worked with an F_2 instead of a backcross; and GREGORY'S results as reported give the linkage of only two pairs of factors at a time. Even so, coincidence could be calculated for GREGORY'S data had he not been unable to follow one of the factors in all the plants. For given AB , BC and AC in any one cross, the doubles may be deduced (STURTEVANT 1914, BRIDGES 1914).

THE MECHANISM OF CROSSING OVER

It has been pointed out that during crossing over the chromosomes might be either loosely or tightly twisted about each other (MORGAN, STURTEVANT, MULLER and BRIDGES 1915, p. 64, MULLER 1916).

If crossing over occurs when the chromosomes are loosely twisted, i.e., when there are a few long loops, the low coincidence of crossing over of neighboring regions may be explained on the supposition that a twist in one region tends to prevent twisting in near-by regions. If the longer

loops are more frequent than the shorter ones, coincidence will rise with increase of distance between the points at which crossing over takes place. If there is a tendency to form loops of a particular length and if loops of greater or lesser length are less frequent, coincidence will rise to a maximum for an intermediate distance corresponding to the most frequent length of loop, and will then decline. The maximum coincidence might be greater than 1.00, but it might also be less. If the most frequent length of loop is sufficiently short to allow more than one to be formed in the same chromosome, there may be more than one maximum value for coincidence corresponding to the several intermediate distances. It is evident, therefore, that on the supposition of loose twisting all the known facts of coincidence may be explained.

On the other hand, let us suppose that during crossing over the chromosomes are tightly twisted; i.e., that there are many short loops instead of a few comparatively long ones. The low coincidence of crossing over of neighboring regions is then to be explained on the hypothesis that a break in one region loosens the twisting and thus prevents breaks in neighboring regions. If, however (owing to friction, adhesion or what not), more distant regions are loosened less quickly or not at all, we should expect the coincidence of widely separated regions to rise and even to reach 1.00. MULLER has pointed out that coincidence on this scheme might also rise above 1.00. MULLER's scheme could be used to explain a decline in coincidence after it had once risen above 1.00; but it is hard to see how it could explain a decline in coincidence after it had risen to only 1.00. For since a crossing over in the eosin ruby region does not affect crossing over in the sable forked region, it can not affect the coincidence of sable forked and the region to the right of forked.

If, therefore, the determinations of coincidence in this paper are valid and comparable with each other, they seem to show that *the twisting of the chromosomes during crossing over is loose; or, if it is tight, that the distance between the places of crossing over depends on other conditions than the mere tension due to the twisting.*

TRIPLE CROSSING OVER

In the above calculations of coincidence, triple crossovers were excluded from the double crossover class under consideration, in spite of the fact that the triples involve crossing over in the same regions as the doubles. Of course, coincidence might be arbitrarily defined so as to exclude the triples. While it is neither necessary nor desirable to limit the definition in this way for all cases (since the word may be applied

in any sense, provided the sense in which it is applied is stated), it should be observed that triple crossing over involves conditions different from those involved in double crossing over. For in double crossing over the intermediate region remains unbroken, while in triple crossing over the intermediate region breaks. If the chromosomes are tightly twisted at this stage, the intermediate region is loosened up in triple, but not in double crossing over. If the chromosomes are loosely twisted, a double crossing over need involve only a single loop, whereas a triple crossing over necessarily involves at least two shorter loops within the same distance, as indicated in figure 10.



FIGURE 10

The coincidence as calculated in the data given (that is, omitting the triples from the double crossover class) measures the tendency of a second break to occur without the interposition of an intermediate break. If coincidence be calculated by including the triples in the double crossover class, it would measure the tendency of a break to occur without regard to whether or not the intermediate region remains intact. If the chromosomes twist loosely during crossing over, it is obvious that for the calculation of the most frequent length of loop the value of the coincidence should be obtained by omitting the triples from the double crossover class.

In the eosin ruby sable forked cross, the amount of triple crossing over is so small that its inclusion would make no appreciable difference. The value of the coincidence of eosin ruby and sable forked would be raised from 1.025 to 1.078. In the eosin ruby forked cleft cross, however, the coincidence would be appreciably raised, namely, from 0.676 to 0.878. This still leaves the coincidence of eosin ruby and forked cleft markedly less than that of eosin ruby and sable forked, but it suggests that in crosses involving a larger proportion of triple crossovers—as in the second chromosome of *Drosophila*—the inclusion of the triples in the double crossover class might disguise the results. For while in one cross the double crossovers might be significantly lower than in the other, the triple crossovers might in the first cross be sufficiently more numerous than in the second to make the coincidence (calculated by including both classes) equal in one case to that in the other. This would hide the fact

that coincidence in each case is a composite made up of two respectively different values.

Triple crossing over in the sex chromosome is comparatively rare, and only six cases have hitherto been observed: one by STURTEVANT (1915), one by MULLER (1916), and four by BRIDGES. If, as the variation of coincidence with distance suggests, the distance between the two breaking points of a double crossing over tends to be greater than half the length of the chromosome, the chromosome is not long enough to allow two such loops to occur and we should expect the percentage of triple crossing over to be low. It is in accordance with these facts that relatively more triple crossovers were obtained in the eosin ruby forked cleft cross (a total distance of 65.5) than in the eosin ruby sable forked cross (a total distance of 57).

It is possible to calculate the coincidence of triple crossing over in a manner similar to that of calculating coincidence of double crossing over.

In the latter case it will be recalled the formula is $\frac{x}{ab}$, where a and b

are the respective proportions of crossing over in the regions involved, and x is the proportion of double crossing over involving both regions simultaneously. In the case of triple crossing over, if a , b and c are the proportions of crossing over in the regions involved, the expected amount of triple crossing over is abc , provided the regions do not affect one another. If x is the actual proportion of triple crossing over, the coincidence is $\frac{x}{abc}$.

ence is $\frac{x}{abc}$.

The coincidence of triple crossing over of eosin ruby, ruby sable, and sable forked is 0.16; the coincidence of triple crossing over of eosin ruby, ruby forked and forked cleft is 0.4858. In the second chromosome the coincidence of triple crossing over in the star purple curved speck cross is 0.4157.

The phenomenon of triple crossing over raises the question of how to calculate the coincidence of distances of which at least one is sufficiently long to allow double crossing over to occur within it. Let us suppose that in the diagram (figure 11) the distance PQ is long enough to



FIGURE 11

allow double crossing over to take place within it. Should these doubles be included in the calculation of coincidence? The question is really a

matter of definition. Perhaps the simplest way would be to disregard entirely the double crossovers within PQ and to calculate crossing over between P and Q on the basis of the individuals which are only single crossovers in this region. This is mathematically self-consistent; for if the proportion of single crossing over within MN is a ; and within PQ is b , the proportion of crossovers which are singles within MN and at the same time singles within PQ will be (on chance alone) ab .

But the interpretation of such calculations of coincidence may be misleading. For suppose that a crossing over in MN prevents crossing over near P . Then it would lower the amount of double crossing over within PQ , since the total distance within PQ available for double crossing over would be decreased. To look at it in a slightly different way, the occurrence of a crossover in MN would move a double crossover within PQ further to the right, so that one of the breaks involved might fall to the right of Q . This would obviously increase the frequency of single crossing over within PQ at the expense of double crossing over within the same region. Consequently, the apparent coincidence of crossing over of MN and PQ might be high; but this would mean only that crossing over within MN helps *single* crossing over within PQ , for the *total* amount of crossing over within PQ would be cut down.

This suggests that it might be best to include the doubles within PQ in the calculation. We can not always in practice do this, since there may not be an intermediate factor between P and Q which can be followed. The choice still remains, however, of counting each double as one crossing over or as two. The matter is again a question of how we choose to define coincidence.

The shortest distance in the sex chromosome within which a double crossing over has been observed to occur is 13.5. Hence, the considerations just mentioned do not call into question the validity of the calculations of coincidence of eosin ruby and forked cleft or of eosin ruby and sable forked. For the eosin ruby and forked cleft distances are too short to allow double crossing over to occur within them; and while the sable forked distance is just sufficiently long, the frequency of such double crossing over is so small (only one case has been observed in all the *Drosophila* work) that the result would not be appreciably affected. The ruby lozenge distance, which is 16 units long, is also too short to be appreciably affected.

In the second and third chromosomes of *Drosophila* the shortest distance within which double crossing over has been observed to occur is shorter than for the sex chromosome. Moreover, as has been pointed

out, the distances in the second chromosome for which coincidence has been calculated are so long as to allow a great amount of double crossing over within them. Consequently, the interpretation of these data should be attended with caution.

MAXIMUM AND MINIMUM COINCIDENCE

It may be interesting to compare the observed values of coincidence with the maximum values mathematically possible under the circumstances. The latter values can be calculated as follows:

If a and b are respectively the lengths of (proportions of crossing over within) the regions under consideration, the amount of double crossing over involving both regions simultaneously is abx , where x is the coincidence. Now, the maximum number of double crossings over will occur when every crossing over in one region is also a crossing over in the other. That is, when coincidence is at a maximum,

$$abx = a, x = \frac{1}{b} \text{ where } a < b$$

$$abx = a = b, x = \frac{1}{b} = \frac{1}{a}, \text{ where } a = b$$

That is, the greatest possible coincidence of two regions is the reciprocal of the frequency of crossing over in the greater region (if the regions are unequal), or of either region (if the regions are equal).

The greatest significant coincidence observed in the sex chromosome was 1.025, in the case of eosin ruby and sable forked. The maximum possible coincidence in this case is $\frac{1}{0.1355} = 7.3776$. The coincidence actually obtained falls far short of this.

The formula for maximum possible coincidence can be extended to any case of multiple crossing over. For example, in the case of triple crossing over, where a , b and c are the distances involved and x the coincidence, $abcx = a$, $x = \frac{1}{bc}$ where a is the shortest distance involved.

If a equals b , $x = \frac{1}{bc} = \frac{1}{ac}$. If $a = b = c$, $x = \frac{1}{ab} = \frac{1}{bc} = \frac{1}{ac}$.

The minimum possible value of coincidence is obviously 0; but this is true only when the sum of the proportions of single crossing over within each of the regions involved is not greater than 1.00. For it is evident that if this sum is greater than 1.00, some crossovers in one

region must also be crossovers in the other and the coincidence must be greater than 0.

THE DISTANCE BETWEEN THE BREAKING POINTS IN DOUBLE CROSSING OVER

Given the factors $M N P Q$ in the order mentioned (see figure 12)



FIGURE 12

the average length of a double crossover involving the regions MN and PQ is $NP + \frac{MN}{2} + \frac{PQ}{2}$. For every such crossover necessarily in-

cludes NP , and it has an equal chance of involving in addition any length from 0 to the entire distance NM on one side, and 0 to PQ on the other. It would on the average, therefore, involve half of NM and half of PQ . This value is obviously the mean between the longest and the shortest possible distances, or it is the distance from the mid-point of NM to the mid-point of PQ . Where only three factors are involved, NP is 0; hence the value of the mean intermediate

distance becomes $\frac{MN}{2} + \frac{NQ}{2} = \frac{MQ}{2}$, or one-half the total distance.

This proof rests (as has been mentioned) on the assumptions that a break is just as likely to occur at any point as at any other, and that the distance between breaks (length of a double crossing over) is no more likely to be of any particular length than would occur as the result of pure chance. The first of these assumptions is justified, since the term *distance* is used to represent the frequency of crossing over and not necessarily morphological distance. The second assumption, however, is not true in general; for, as we have seen, coincidence varies with the intermediate distance, and only for some distances (where coincidence is 1.00) are double crossovers as frequent as they would be on pure chance. Hence, in any case the true average value will be a weighted mean. Since we do not know accurately how coincidence varies with short increments of distance, we cannot judge just how accurate the formula is in any case. But if variation in coincidence is gradual, the formula must be a good index of the mean intermediate distance when MN and PQ are short.

Double crossing over within short distances is very rare, and in the sex chromosome has never been observed to occur within distances shorter than 13.5. If, therefore, in any sex-linked cross in *Drosophila* the intermediate distance is less than 13.5, allowance can be made in the formula for the mean intermediate distance for the absence of the

shorter double crossovers by substituting 13.5 for NP provided that $MQ > 13.5$.

When the distance NP is longer than 13.5, double crossing over may occur within it, and if no factors in this region are followed the double crossing over can not be observed. Hence the apparent amount of crossing over in the intermediate region will be less than the true value. For example, the value obtained for the distance between ruby and sable in the eosin ruby sable forked cross was 0.333; and the value obtained for the distance between ruby and forked in the eosin ruby forked cleft cross was 0.415. The map values for these regions are respectively 36.5 and 51.5.

It is, of course, possible, though unlikely, that the amount of undetected double crossing over within the ruby sable region in the first cross was sufficiently greater than the amount of double crossing over within the ruby forked region in the second cross to make the ruby sable region in the first case greater than the ruby forked region in the second case. This is further suggested as a possibility by the fact that the crossing over in the eosin ruby region is slightly greater in the first case (0.0668) than in the second (0.0560). And this might be held to explain why the coincidence of eosin ruby and forked cleft is lower than that of eosin ruby and sable forked. But even if we increase the map value of the ruby sable distance in the ratio of $\frac{0.0668}{0.0560}$, the distance will

be only 41.61. This is still considerably less than the map distance of ruby forked and is almost exactly equal to the apparent length of the latter distance in the eosin ruby forked cleft cross. Since the true length in the latter case must have been greater than 41.61 because of the occurrence of (unobserved) double crossing over within it, the suggestion that the ruby sable region was genetically longer cannot be considered probable, though it remains as a rather remote possibility.

To dispose of this possibility absolutely it would be necessary either to follow enough factors in the intermediate region so that no double crossing over remains unobserved, or to make a cross involving simultaneously all the regions whose coincidences are sought. The former method has the disadvantage that a great number of mutant factors tends to cause differential non-viability and that it is not always feasible to obtain properly spaced factors which can be worked together. The second method was actually tried by making crosses involving simultaneously eosin, ruby, sable, forked and cleft. But it was found that sable cleft flies were

almost always non-viable and the cross was abandoned. The method was, however, successfully used in the cross involving simultaneously eosin, ruby, lozenge, forked and cleft. Here the ruby forked distance is necessarily longer than the lozenge forked distance, since the former consists of the latter plus the ruby lozenge distance. It will be recalled that the results of this cross, while not numerically great, were in accordance with those of the two main crosses.

MUTATIONS OBSERVED

Several mutations were observed in the course of this work.

1. *Yellow body color.* Three yellow males appeared in a cross of a female carrying the factors eosin ruby forked in one sex chromosome and the factor fused in the other, by a bar male. The other offspring fell into the expected classes. Of the three yellow flies, one was also eosin fused, a second eosin ruby fused, and the third eosin forked; so that they also (except for the yellow character) fell into expected classes. This, together with the fact that the amount of crossing over between yellow and eosin is only one percent, and that no other yellow eosin flies were then, so far as known, in existence, makes it quite unlikely that the three yellow flies were the result of contamination. The yellow factor must therefore have arisen by mutation in the sex chromosome of the mother, for the mutants were all males and did not arise by non-disjunction.

The new yellow was ascertained to be sex-linked and recessive to wild, like the old yellow. When it was mated to the old yellow the daughters produced were yellow; hence the two factors must be the same.

2. *Achete.* The laboratory stock of yellow was discovered to be pure for a factor causing a reduction in number, and sometimes a total absence of, the dorso-central bristles. This factor, termed achete, is a sex-linked recessive. No crossovers between it and yellow were observed in over 200 flies; hence it is either closely linked to yellow or an effect of the yellow factor itself. If the latter turns out to be true, the yellow locus may furnish a case of quadruple allelomorphism, for another yellow stock (containing also white eyes) and the yellow which arose independently (as reported above) have the normal number of dorso-central bristles (four), and there are besides two other allelomorphs, spot and normal.

3. *Lethal.* Two females in the eosin ruby sable forked cross gave lethal ratios. The lethal in each case is about one unit from yellow; in one case it is known to be to the left of yellow. It is, therefore, the

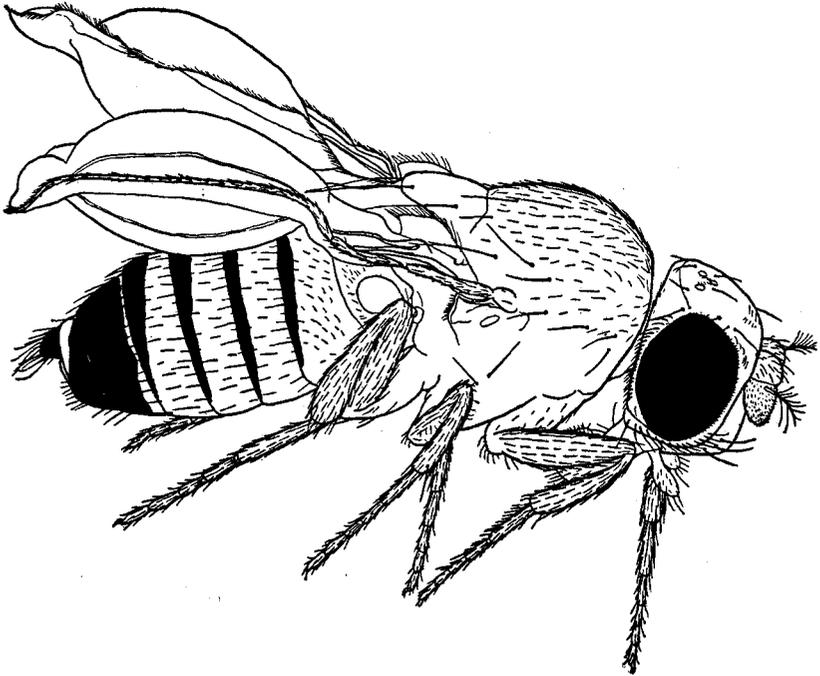


FIGURE 13.—Fly with inflated wings.

farthest to the left of any factor known in the sex chromosome. Since the females were sisters, the same factor is probably involved in both cases.

4. *Inflated*. In several of the cultures of the eosin ruby forked cleft cross there appeared flies whose wings were inflated (figure 13). As the flies grow older the wings collapse and look blistered. This variation was ascertained to be sex-linked and to be located about 1 or 2 units to the left of forked, in approximately the same locus as the factor for rudimentary wing. But the two factors are not allelomorphic to each other, since the F_1 females of the cross between them are long-winged.

In several of the cases reported above, more than one individual displaying the same mutant character appeared in the same brood. It seems unlikely that the character arose independently in each individual; more probably the individuals in each case were derived from a single mutated germ cell. If this is true, the yellow mutation must have occurred at least before the next to the last oögonial division, since it arose in the female; the lethal factor must have arisen at least before the first maturation division if it occurred in the mother of the females tested, but it may have originated between the first and second maturation divisions if it arose in the father.

SUMMARY

It has been known that the coincidence of crossing over of two regions increases in general as the distance between them increases. The evidence presented in this paper indicates that, for the sex chromosome of *Drosophila melanogaster*, when the intermediate region reaches a value of about 46, coincidence is approximately 1.00; and as the intermediate distance increases still further, coincidence decreases again. In other words, crossing over in one region of the chromosome interferes with crossing over in neighboring regions. But this influence decreases as the distance between the regions increases, until when the distance is about 46 units the interference has practically disappeared. For regions more than 46 units apart, interference reappears again.

It is pointed out that if the data presented are statistically significant, either the twisting of the chromosomes during the process of crossing over is loose, or the distance between the places of crossing over in the chromosome is dependent on other conditions than the mere tension due to the twisting.

I wish to thank Professor T. H. MORGAN and Dr. H. J. MULLER, Dr. C. B. BRIDGES and Dr. A. H. STURTEVANT for helpful suggestions made in the course of this work. I wish also to thank Dr. RAYMOND PEARL, Dr. J. A. HARRIS, and Mr. J. W. GOWEN for help with the statistical aspects of the problem.

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NOTE ADDED IN THE PAGE PROOFS.

At the bottom of page 145 the value of the coincidence of eosin ruby and forked fused (for all the broods, including those containing less than 0 males) should be 0.8572 instead of 1.1144 as given. (The latter value represents the coincidence calculated by including the triples in the double crossover class.) The suggestion made on page 146 in connection with the value 1.1144 is rendered unnecessary, since the correct value agrees with the expectation and is consistent with the other results obtained.

A. WEINSTEIN, COINCIDENCE OF CROSSING OVER IN *Drosophila melanogaster* (*ampetophila*)

TABLE 10
Individual culture counts of crosses involving eosin (w^e), ruby (r_b), sable (s), and forked (f).
(1) $\frac{w^e \cdot sf}{r_b}$

Culture No.	Females		Males										Total males	Coincidence of $w^e r_b$ and sf			
	$w^e sf$	r_b	1		2		3		1 2		2 3				1 2 3		
			$w^e r_b$	sf	w^e	$r_b sf$	$w^e s$	$r_b sf$	$w^e r_b sf$	+	$w^e r_b s$	$w^e f$			$r_b s$	$w^e r_b s$	f
125	110	20	3	18	11	2	2	1	1	1	1	1	1	1	1	89	0
126	98	28	2	19	14	8	9	1	1	1	1	1	1	1	1	114	0
127	49	13	3	15	11	1	1	1	1	1	1	1	1	1	1	62	1.7714
105	89	15	4	18	9	3	4	1	1	1	1	1	1	1	1	71	0
200	100	16	2	15	10	1	3	1	1	1	1	1	1	1	1	74	4.1111
225	68	13	1	13	6	4	5	1	1	1	1	1	1	1	1	50	4.1667
226	100	20	2	12	6	4	5	1	1	1	1	1	1	1	1	92	1.5333
227	91	17	1	11	4	2	4	1	1	1	1	1	1	1	1	69	2.5556
228	104	12	1	17	5	1	4	1	1	1	1	1	1	1	1	72	0
241	88	19	4	17	7	1	4	1	1	1	1	1	1	1	1	69	0
196	64	16	1	12	7	2	1	1	1	1	1	1	1	1	1	59	0
108	71	16	1	10	10	4	4	1	1	1	1	1	1	1	1	52	0
203	77	14	1	10	6	3	5	1	1	1	1	1	1	1	1	60	0
224	96	15	3	12	3	1	5	1	1	1	1	1	1	1	1	58	0.9667
220	100	23	3	21	11	1	5	1	1	1	1	1	1	1	1	97	1.2436
231	83	10	4	11	11	2	1	1	1	1	1	1	1	1	1	54	1.9286
233	87	13	2	17	9	4	5	1	1	1	1	1	1	1	1	71	0.7396
234	90	19	1	17	11	1	7	1	1	1	1	1	1	1	1	79	0
236	76	14	2	16	6	5	4	1	1	1	1	1	1	1	1	69	0
239	105	10	3	14	7	5	4	1	1	1	1	1	1	1	1	83	1.6600
240	97	27	7	15	15	7	7	1	1	1	1	1	1	1	1	101	0
245	74	21	2	9	10	4	4	1	1	1	1	1	1	1	1	62	0
246	75	13	3	13	5	1	1	1	1	1	1	1	1	1	1	54	1.8000
128	91	20	1	13	16	4	4	1	1	1	1	1	1	1	1	82	2.2778
104	71	13	1	9	2	2	4	1	1	1	1	1	1	1	1	49	0
202	70	7	2	8	5	1	1	1	1	1	1	1	1	1	1	40	0
137	88	18	2	18	10	3	5	1	1	1	1	1	1	1	1	85	0

* The symbol + indicates wild type.

A. WEINSTEIN, COINCIDENCE OF CROSSING OVER IN *Drosophila melanogaster* (*ampelophila*)

TABLE 10 (continued)
(1) $\frac{w^o sf}{r_h}$ (continued)

Culture No.	Females	Males											Total males	Coincidence of $w^o r_h$ and sf			
		I		2		3		I 2		I 3		2 3			I 2 3		
		$w^o r_h$	sf	w^o	$r_h sf$	$w^o s$	$r_h f$	$w^o r_h sf$	+	$w^o r_h f$	s	$w^o f$			$r_h s$	$w^o r_h s$	f
138	70	11	18	12	11	2	4	1	1	1	1	1	1		62	3.8750	
141	101	26	24	18	11	1	4	1	1	1	1	1	1	2	92	2.0444	
263	88	16	14	13	6	2	1	2	2	2	1	2	2	2	59	0	
267	86	15	24	10	8	4	5	2	1	1	1	2	2	2	81	1.5987	
269	56	14	12	11	7	3	5	3	4	4	3	4	4	2	57	0	
270	104	16	29	16	15	3	3	3	4	4	4	4	4	3	89	0	
275	90	6	22	10	5	2	6	2	2	2	2	2	2	3	59	0	
271	86	11	30	20	11	1	2	1	2	1	2	1	2	2	85	0	
273	92	14	21	15	9	3	3	1	2	1	2	1	2	1	73	1.3036	
129	123	21	23	18	9	3	2	1	1	1	1	1	1	1	80	0	
132	90	14	20	24	11	4	2	1	1	1	1	1	1	2	83	0	
133	50	24	26	15	6	4	4	3	4	4	4	4	4	2	88	1.3538	
134	144	29	19	19	20	8	6	4	4	6	6	4	4	3	120	0.8163	
135	123	20	18	21	13	4	3	1	1	4	3	3	2	2	90	1.8750	
136	96	27	23	21	18	8	9	1	1	9	6	2	2	2	99	1.9800	
144	120	23	20	23	13	3	3	1	2	3	4	1	2	1	101	5.0500	
264	112	22	18	19	11	5	4	4	4	4	4	4	4	1	87	0	
265	95	13	17	11	13	4	4	2	2	4	4	2	2	2	69	0	
262	106	22	22	16	4	4	4	1	1	4	4	1	1	1	78	1.5600	
146	91	12	18	13	14	4	4	1	1	4	4	1	1	1	77	0.70000	
145	101	10	23	11	8	2	3	1	1	1	1	1	1	3	75	1.3889	
295	67	18	11	14	12	1	5	1	1	1	1	1	1	3	67	1.5952	
297	107	22	25	16	16	2	6	1	1	1	6	1	2	5	103	1.7557	
336	87	15	24	0	12	3	5	1	1	1	5	1	1	1	78	1.5758	
130	130	14	18	28	13	3	6	1	1	1	6	1	1	1	88	1.6000	
Totals	4726	904	1030	780	488	145	192	25	31	22	19	66	46	1	3957		

A. WEINSTEIN, COINCIDENCE OF CROSSING OVER IN *Drosophila melanogaster* (*ampelophila*)

TABLE 10 (continued)

$$(2) \frac{w^s r_b f}{s}$$

Culture No.	Females	Males												Total males	Coincidence of $w^s r_b$ and sf						
		1			2			3			I					2 3			I 2 3		
		$w^s r_b f$	$w^s s$	$r_b f$	$w^s r_b s$	f	$w^s r_b$	sf	$w^s f$	$r_b s$	$w^s sf$	r_b	$w^s r_b sf$			+	-	w^e	$r_b sf$		
213	98	26	3	4	8	7	5	3	2	1	2	2	2	1	1	83	1.5062				
214	110	22	11	1	15	10	4	5	1	1	1	2	2	1	1	77	1.4808				
215	108	24	23	1	4	10	1	5	1	2	1	1	1	1	1	79	2.4687				
210	134	12	22	2	11	14	4	6	1	1	1	1	1	1	1	75	0				
218	92	15	17	5	7	7	2	3	1	1	1	1	1	1	1	60	0				
219	107	29	17	3	11	16	1	1	1	1	1	1	1	1	1	80	5.0000				
87	18	18	2	1	3	17	6	1	2	1	1	1	1	1	1	75	0				
302	155	45	40	2	17	21	8	5	1	1	1	1	1	1	1	143	0				
303	149	49	28	2	11	9	5	7	1	1	1	1	1	1	1	116	1.9333				
306	147	33	36	4	12	20	7	6	1	1	1	1	1	1	1	120	1.3333				
310	134	40	24	3	1	18	2	5	1	1	1	1	1	1	1	107	0				
323	105	30	23	3	3	14	3	6	1	1	1	1	1	1	1	85	0				
223	118	20	12	3	10	15	5	6	1	1	1	1	1	1	1	76	2.1714				
305	122	33	31	3	10	12	9	6	1	1	1	1	1	1	1	107	0.1486				
208	103	23	21	3	11	13	6	2	1	1	1	1	1	1	1	86	1.7374				
210	70	23	14	4	5	15	3	3	1	1	1	1	1	1	1	64	0				
211	105	15	21	1	3	14	3	3	1	1	1	1	1	1	1	59	5.9000				
212	88	26	19	3	8	17	3	8	1	1	1	1	1	1	1	93	0.8611				
220	104	18	22	2	13	9	2	2	1	1	1	1	1	1	1	73	2.0857				
221	62	16	17	1	8	11	4	9	1	1	1	1	1	1	1	74	0				
222	85	10	16	3	17	14	5	5	1	1	1	1	1	1	1	87	1.3810				
251	126	28	25	2	7	24	7	3	1	1	1	1	1	1	1	120	0				
252	81	15	10	2	6	7	5	4	1	1	1	1	1	1	1	52	0.9630				
253	70	15	13	2	6	12	2	4	1	1	1	1	1	1	1	58	1.6111				
254	135	27	21	1	14	22	15	7	1	1	1	1	1	1	1	117	1.0833				
256	135	21	23	5	3	11	5	8	1	1	1	1	1	1	1	97	0				
257	58	17	10	1	12	10	3	1	1	1	1	1	1	1	1	58	0				

A. WEINSTEIN, COINCIDENCE OF CROSSING OVER IN *Drosophila melanogaster* (*ampelophila*)

TABLE 10 (continued)

$$(2) \frac{w^s r_b f}{s}$$

Culture No.	Females	Males												Total males	Coincidence of $w^s r_b$ and sf	
		1		2		3		I		2		3				
		$w^s s$	$r_b f$	$w^s r_b s$	f	$w^s r_b$	sf	$w^s f$	$r_b s$	$w^s sf$	r_b	$w^s r_b sf$	+			
		$w^s r_b f$	s													
259	93	21	24	4	13	13	4	4	4	1	1	3	3	1	91	0.8750
260	64	18	15	1	12	11	4	2	2	1	1	3	3	2	70	1.9444
261	83	17	23	3	11	14	3	4	4	1	1	2	1	2	79	0
301	160	41	32	5	23	25	10	11	11	1	1	2	1	3	153	0.8407
309	149	27	24	2	18	20	12	4	4	2	1	1	1	1	112	3.2000
311	120	29	9	1	12	16	6	3	3	2	1	1	2	1	82	0
312	99	22	23	1	13	4	7	4	4	1	1	1	1	5	82	1.5850
314	112	33	23	1	4	19	4	4	5	1	1	1	1	3	94	2.4103
315	116	42	31	1	10	18	10	8	8	1	1	1	1	3	124	0
317	77	33	24	1	5	4	6	4	4	1	1	1	1	1	77	0
318	96	20	30	2	8	11	6	4	4	1	1	1	2	1	82	0
319	52	12	12	1	8	7	2	2	4	1	1	1	2	1	50	0
320	103	17	43	2	11	16	4	4	7	1	1	1	1	2	103	0
321	85	21	15	2	6	11	2	4	4	1	1	1	1	2	64	1.8286
322	102	25	28	2	4	16	8	3	3	1	1	1	1	1	106	0
324	114	27	25	3	9	10	5	2	2	1	1	1	1	2	91	0
325	105	26	29	1	18	20	2	10	10	1	1	1	1	3	112	2.1961
316	66	21	10	1	3	7	1	2	2	1	1	1	1	1	48	0
282	70	19	14	1	8	18	3	4	4	1	1	1	1	3	74	0
283	90	12	13	1	5	9	2	1	1	1	1	1	1	1	51	1.2750
284	84	12	19	1	4	7	1	4	4	1	1	1	2	3	54	1.3500
285	75	12	10	3	11	15	9	6	6	2	1	1	2	2	74	0.4328
286	110	26	13	3	14	17	4	6	6	1	1	1	1	6	96	0.5926
287	71	14	15	2	8	11	2	3	3	1	1	1	1	1	62	1.1071
292	82	20	20	4	16	12	3	2	2	1	1	1	2	1	83	1.3175
357	78	15	19	1	3	7	1	5	5	1	1	1	1	1	52	3.7143
358	82	10	20	3	3	11	4	3	3	1	1	1	1	1	58	0

A. WEINSTEIN, COINCIDENCE OF CROSSING OVER IN *Drosophila melanogaster* (*ampelophila*)

TABLE 10 (continued)
(2) $\frac{w^e r_b f}{s}$ (continued)

Culture No.	Females	Males													Total males	Coincidence of $w^e r_b$ and sf						
		1		2		3		I		2		3		I								
		$w^e r_b f$	s	$w^e s$	$r_b f$	$w^e r_b s$	f	$w^e r_b$	sf	$w^e f$	$r_b s$	$w^e sf$	r_b	$w^e r_b sf$			+	$w^e r_b sf$				
359	77	19	13	1		6	9	3				3				1	2			58	2.90000	
395	107	28	31	5		9	15			1		4					2	1			99	0
405	100	24	26			9	16					8					2	2			92	0
288	72	11	10	1		5	8			1		2					1	1			43	0
352	78	11	15			1	4					3					4	2			40	0/0
330	134	20	30	6		1	20			1		2					3	1			120	0.8333
331	116	35	32	2		2	18					3					2	2			107	0
332	145	21	27	2		1	12					18					1	1			94	1.5667
334	134	28	41	3		1	17					3					3	4			131	0
337	83	20	23			1	2					5					1	1			62	0
338	64	16	11	2		2	14			1		5					2	1			53	0
339	112	30	29	2		2	8					8					2	1			112	0
340	69	10	9	1		5	10					11					3	1			52	2.2941
341	93	21	21	1		6	13					3					2	3			92	0
342	76	28	16	2		2	10					3					1	1			59	0
343	77	14	22	1		12	10					3					2	2			70	3.1818
345	95	29	19	3		11	6					4					2	1			87	1.7400
346	111	22	19	3		1	7					5					3	3			70	0
347	83	16	30	3		2	4					8					2	1			86	0
348	111	27	23	3		2	4					17					1	1			84	0
349	76	20	7	2		4	12					20					2	1			60	0.8333
350	103	21	19			8	20			1		5					1	1			77	0
353	97	24	21			7	12					7					1	1			76	6.3333
355	123	21	26	1		3	22					3					3	1			80	0
360	119	27	24			8	15					5					4	1			90	0
368	141	27	29	1		3	12					4					7	1			84	0
Totals	8022	1821	1693	133	150	734	1078	390	323	31	25	23	32	85	103	1	1	1		6623		

A. WEINSTEIN, COINCIDENCE OF CROSSING OVER IN *Drosophila melanogaster* (*ampelophila*)

TABLE 10 (continued)

$$(3) \frac{w^o s}{r_n} f$$

Culture No.	Females		Males												Total males	Coincidence of $w^o r_n$ and sf		
			1		2		3		$w^o r_{ns}$		$w^o r_n$		$w^o r_{nsf}$				$w^o r_{nsf} +$	
	$w^o s$	$r_n f$	$w^o r_{nf}$	s	$w^o f$	r_{ns}	$w^o sf$	r_n	$w^o r_{ns}$	f	$w^o r_n$	sf	$w^o r_{nsf}$	2				3
328	12	26	3	3	10	7	4	4	2								80	0.5229
329	23	27	1	1	15	17	5	4									96	2.6667
329a	9	12	2	2	13	9	1	1									53	0
329b	15	17	3	3	9	10	2	1									63	0
377	31	31	2	2	19	10	1	8									117	1.6250
383	23	19	3	1	15	13	6	1									81	0
384	8	13	3	3	15	5	2	1									54	1.9286
386	28	31	3	1	19	12	3	6									108	1.2857
390	16	23	4	2	24	11	5	3									98	1.8840
393a	6	30	2	2	12	1	2	2									60	3.3333
369	14	11	4	1	7	4	1	3									46	0
371	6	21	1	1	8	3	3	1									46	0
385	22	1	4		15	3	5	1									48	1.6000
391	0	19			9	3	1	1									42	0/0
393c	8	13	2	1	11	3	1	2									45	0
389	15	34	2	1	12	12	2	5									89	1.4833
382	25	24	2	4	19	12	5	7									102	0.8095
370	3	32	2	2	17	1	1	2									61	0
379	31		3		23		1										60	5.0000
Totals	304	384	46	25	272	142	50	51	5	9	6	23	20				1349	

TABLE II
Individual culture counts of crosses involving eosin (w^e), ruby (r_b), forked (f) and cleft (c_t).

Culture No.	Females	Males											Total males	Coincidence of $w^e r_b$ and $f c_t$		
		(1) $\frac{w^e r_b f}{c_t}$														
		$w^e r_b f$	c_t	I	2	3	$w^e f$	$r_b c_t$	I	2	3	$w^e r_b f c_t$				
4	160	37	37	2	3	22	25	I	I	4	I	I	I	I	134	0
5	95	23	23	I	I	19	12	I	I	I	I	I	I	I	79	0
7	98	21	21	I	I	12	19	I	I	I	I	I	I	I	87	0
9	108	30	20	I	I	15	22	I	I	5	I	I	I	I	96	0
10	97	22	15	I	I	13	15	I	I	2	I	I	I	I	72	6.0000
12	55	12	10	I	I	7	6	I	I	I	I	I	I	I	51	0
16	80	24	10	I	I	12	19	I	I	I	I	I	I	I	70	0
17	106	20	10	I	I	10	17	I	I	4	I	I	I	I	73	1.8250
18	79	21	14	I	I	6	18	I	I	I	I	I	I	I	66	0
19	82	9	11	I	I	8	11	I	I	2	I	I	I	I	54	0
20	81	25	12	I	I	9	22	I	I	I	I	I	I	I	73	0
21	175	34	15	I	I	20	28	I	I	5	I	I	I	I	107	3.8214
22	84	18	13	I	I	8	17	I	I	3	I	I	I	I	65	0
24	146	31	23	I	I	17	24	I	I	4	I	I	I	I	107	0
25	119	41	22	I	I	10	33	I	I	7	I	I	I	I	122	0
32	63	19	11	I	I	9	15	I	I	2	I	I	I	I	63	0
33	58	23	14	I	I	9	10	I	I	3	I	I	I	I	61	0
34	106	20	22	I	I	6	10	I	I	I	I	I	I	I	70	1.6667
35	96	15	23	I	I	2	16	I	I	3	I	I	I	I	82	0
36	83	12	21	I	I	2	12	I	I	I	I	I	I	I	64	0
54	87	16	21	I	I	3	19	I	I	5	I	I	I	I	71	0/0
55	80	22	18	I	I	16	8	I	I	I	I	I	I	I	72	0
56	80	21	14	I	I	7	21	I	I	2	I	I	I	I	69	0
57	96	30	18	I	I	15	17	I	I	6	I	I	I	I	89	5.5625
60	120	20	15	I	I	6	22	I	I	I	I	I	I	I	70	0
65	87	18	6	I	I	2	6	I	I	2	I	I	I	I	58	0
73	89	23	15	I	I	2	16	I	I	2	I	I	I	I	73	0
74	02	10	21	I	I	2	0	I	I	I	I	I	I	I	77	0

TABLE II (continued)
(1) $\frac{w^+r_+f}{c_t}$ (continued)

Culture No.	Females	Males												Total males	Coincidence of w^+r_+ and f_c		
		w^+r_+f		$w^+r_+c_t$		$w^+r_+f c_t$		$w^+r_+f c_t$		$w^+r_+f c_t$		$w^+r_+f c_t$					
		1	2	1	2	1	2	1	2	1	2	1	2				
75	117	33	14	19	5	3											0
8	103	29	18	23	1	1											0
11	83	13	11	10	1	1											0
66	104	21	18	16	2	2											0
70	68	17	14	7	2	1											2.4000
23	124	27	16	14	3	1											0
37	66	24	8	10	1	3											0
39	78	14	6	16	1	1											0
40	100	26	21	14	1	4											0
48	55	25	12	12	2	2											0
49	90	20	4	16	3	2											0
51	78	20	8	18	2	1											0
52	48	12	10	20	2	2											0
53	37	7	11	13	1	1											47333
59	70	26	1	11	1	3											0
62	70	16	10	11	1	2											0/0
63	69	12	13	7	1	1											0
67	77	21	7	14	3	2											0/0
77	62	9	15	20	1	1											0
78	85	17	7	11	1	4											0
81	102	20	17	26	2	2											0
82	93	16	11	16	6	7											0.5000
84	106	27	12	15	3	3											0
86	94	30	14	17	3	5											1.5312
87	129	26	21	24	2	4											1.5515
88	94	23	13	13	2	1											3.0357
89	85	20	15	24	3	3											0
90	60	17	8	20	3	3											5.9000

TABLE II (continued)

(1) $\frac{w^*r_{bf}}{c_t}$ (continued)

Culture No.	Females	Males												Coincidence of w^*r_b and fc_t						
		1		2		3		1-2		1-3		2-3								
		w^*r_{bf}	c_t	w^*c_t	r_{bf}	$w^*r_b c_t$	f	$w^*r_{bf} c_t +$	w^*f	$r_b c_t$	$w^*r_b c_t$	w^*r_b	fc_t		w^*fc_t	r_b				
91	112	27	29	3	2	20	20	3	7	5	1						1	123	0	
94	85	21	29	1	2	20	16	3	3	2	1							1	95	0
95	142	34	23	2	2	23	28	2	5	2	3							1	129	0
96	94	23	20	1	1	13	20	1	1	4	1								86	2.8667
97	156	35	32	6	5	37	23	1	4	1	1								146	0
98	117	18	20	3	1	15	20	1	1	1	1								82	0
99	122	36	30	1	1	27	22	3	3	1	1								126	0
101	100	24	24	2	3	17	18	4	2	1	1								101	1.1477
102	79	16	8	1	2	9	11	1	1	1	1								52	0
104	84	10	16	1	1	13	11	1	1										53	0
105	82	16	14	4	3	13	17	4	3	1	1								81	0
109	104	19	10	1	1	10	11	1	5	1	1								59	0
110	68	19	14	1	1	8	13	2	2										62	0
112	75	19	17	1	1	18	13	1	1	1	1								70	0
113	70	20	17	3	2	5	11	1	4	1	1								66	1.3750
114	100	22	10	2	1	20	13	1	1	1	1								71	0
115	76	16	15	1	1	16	17	2	3	2	2								75	0
116	82	16	23	4	2	10	14	1	1	1	1								71	0
117	81	20	13	2	4	15	9	6	1	1	3								76	0
118	82	25	11	1	2	9	9	1	2	1	1								59	0
120	77	17	20	3	1	14	14	1	1	1	1								72	4.8000
122	99	20	23	1	3	10	16	1	1	1	1								87	0
123	62	14	20	4	1	20	15	1	3	1	1								69	0
23887	113	27	20	6	3	14	21	2	2	1	1								89	0
2389	124	33	20	1	2	22	25	3	4	2	2								112	0
2390	133	31	22	1	3	22	25	3	4	2	2								111	0
2462	169	43	27	1	5	23	23	4	3	2	2								136	0
2463	152	42	32	3	4	30	27	8	3	2	2								158	0
2468	85	27	19	1	1	11	17	4	3	2	2								83	7.5455
2469	135	39	23	1	3	18	31	3	3	1	1								124	0

† Cultures 2388-2505 are from crosses made by BRIDGES.

TABLE II (continued)
(I) $\frac{w^v r_{bf}}{c_t}$ (continued)

Culture No.	Females	Males										Total males	Coincidence of w^v and f_{c_t}											
		$w^v r_{bf}$	c_t	I	$w^v c_t$	r_{bf}	$w^v r_{bf} c_t$	f	$w^v r_{bf} c_t$	2	$w^v r_{bf} c_t$			3	$w^v r_{bf} c_t$	+	$w^v r_{bf} c_t$							
2503	137	28	31	2	2	14	18	3														97	0	
2504	93	21	23	1	1	11	23	2															88	0
2505	156	30	28	2	2	10	20	2															112	1.7500
506	59	16	8	2	2	6	15	1															57	0
508	63	11	7	1	1	3	12	2															56	2.8000
510	84	18	8	2	2	11	11	1															66	0
513	76	14	15	1	1	13	15	3															67	0
532	86	12	14	2	2	17	15	2															57	1.1875
533	75	18	6	3	3	6	14	2															91	0
534	109	23	19	4	4	13	18	3															75	0
535	85	20	18	1	1	6	21	3															77	0
536	98	16	19	1	1	15	18	3															101	0
537	110	28	21	1	1	14	24	8															91	0
538	106	28	15	1	1	13	22	3															62	0
539	88	25	13	2	2	12	20	4															50	0/0
540	92	19	15	1	1	9	9	1															50	0
542	59	14	9	1	1	12	12	1															67	0
543	89	12	12	1	1	17	17	2															62	0
545	75	19	21	1	1	8	12	1															40	0
547	57	13	13	1	1	6	10	5															46	2.8750
503	39	12	8	1	1	8	6	2															47	0
511	65	8	14	1	1	6	11	1															41	0/0
512	64	11	7	2	2	10	11	3															64	0
546	59	17	7	1	1	9	5	1															52	2.6000
548	65	10	10	1	1	5	13	1															82	0
562	60	20	14	2	2	10	14	1															14	0
567	61	21	6	2	2	6	11	3															13	0
Totals	10330	2406	1884	153	163	1440	1854	183	284	80	45	14	13	116	82	2	2	8721						

A. WEINSTEIN, COINCIDENCE OF CROSSING OVER IN *Drosophila melanogaster* (*ampelophila*)

TABLE II (continued)

$$(2) \frac{w^o f}{r_b c_t}$$

Culture No.	Females	Males										Total males	Coincidence of $w^o r_b$ and $f c_t$					
		1		2		3		1 2		1 3				2 3		1 2 3		
		$w^o f$	$r_b c_t$	$w^o c_t$	$r_b f$	$w^o f c_t$	r_b	$w^o r_b f$	c_t	$w^o r_b$	$f c_t$			w^o	$r_b f c_t$	$w^o r_b c_t$	$w^o r_b f c_t +$	
418	84	13	10	2	3	9	7	5	3								53	0
419	61	17	10	2	3	5	12	2	1								47	0/0
422	129	24	10	2	1	2	16	3									59	0
449	132	28	27	3	3	23	29	5	3								132	1.4667
451	53	14	5	3	1	3	8	1									40	0
455	65	17	6		2	13	12	2	2								52	0
466	71	22	6	2		5	10	1	1								50	0
Totals	595	135	74	9	10	60	94	16	14	4	2	6	7	2			433	

A. WEINSTEIN, COINCIDENCE OF CROSSING OVER IN *Drosophila melanogaster* (*ampelophila*)

TABLE 11 (continued)

$$(3) \frac{w^r r_b}{f c_e}$$

Culture No.	Females	Males												Total males	Coincidence of $w^r r_b$ and $f c_e$		
		1		2		3		4		5		6					
		$w^r f c_e$	r_b	$w^r r_b f c_e$	+	$w^r r_b c_e$	f	$w^r r_b f c_e$	$r_b c_e$	$w^r f$	$r_b c_e$	$w^r r_b f c_e$	c_e			$w^r c_e$	$r_b f$
579	73	18	14	2	2	11	13	5	3	3	3	1	1	3	3	71	0
580	109	24	12	2	3	10	16	1	3	3	3	1	1	2	2	75	1.6667
581	122	27	14	3	3	12	17	2	5	1	1	1	1	1	1	83	0
585	87	12	18	2	4	8	12	2	1	1	1	1	1	1	1	63	0
589	71	17	5	2	2	12	12	2	1	1	1	1	1	1	1	51	0
594	80	11	6	2	2	9	16	2	4	1	1	1	1	2	2	54	1.5000
604	76	22	5	1	1	7	10	3	2	1	1	1	1	1	1	54	0
586	73	9	10	1	1	10	8	2	1	1	1	1	1	1	1	45	4.5000
587	64	9	11	1	1	7	13	1	1	1	1	1	1	1	1	43	0
610	56	8	10	1	1	8	10	2	1	1	1	1	1	1	1	42	0.8750
611	91	17	1	1	4	3	15	1	4	1	1	1	1	1	1	40	0
613	93	24	2	1	1	11	11	1	2	1	1	1	1	1	1	43	0
615	68	15	2	1	1	5	18	1	3	1	1	1	1	1	1	45	0
617	65	23	11	1	1	4	11	1	4	1	1	1	1	1	1	58	2.4167
618	72	10	12	1	1	7	21	1	2	1	1	1	1	1	1	66	0
620	83	15	14	1	1	12	12	2	4	1	1	1	1	1	1	64	0
660	68	13	8	1	1	4	18	2	3	1	1	1	1	1	1	52	0
803	120	17	5	1	6	4	23	1	2	2	2	2	2	2	2	61	0
Totals	1471	300	158	13	30	133	256	24	46	18	4	5	2	12	14	1019	

A. WEINSTEIN, COINCIDENCE OF CROSSING OVER IN *Drosophila melanogaster* (*ampelophila*)

TABLE II (continued)

(4) $w^e r_b f c_t$

Culture No.	Females	Males												Total males	Coincidence of $w^e r_b$ and $f c_t$				
				1		2		3		1 2		1 3				2 3		1 2 3	
		$w^e r_b f c_t$	+	w^e	$r_b f c_t$	$w^e r_b$	$f c_t$	$w^e r_b f$	c_t	$w^e f c_t$	r_b	$w^e c_t$	$r_b f$			$w^e r_b c_t$	f	$w^e f$	$r_b c_t$
679	77	13	11	1		11	10	1						2			49	0	
680	44	4	18			14	11	2						2			53	0/0	
681	106	10	28	3	2	25	15	5						2			91	0	
683	84	5	20	2		11	11	2	1					2			54	0	
684	118	11	31	5		22	22	1	1	1			1	2			97	0	
686	79	16	19	2	3	19	7	3						2			71	0	
687	167	24	36	3	1	20	13	3	2				4	1			108	0	
688	59	14	14	1		13	8	2	2	3			1	1			59	0	
689	93	16	25	4	1	12	14	3	3	2	2		1				83	0	
690	101	23	27	1	3	20	12	3	2				2				93	0	
691	90	12	24	3	1	21	11	5	7				1				86	1.2286	
695	101	10	34	2		19	8	1	2	1				1			78	0	
742	159	19	33	2	1	35	18	5	6	1	1	2	1	1			125	3.1250	
750	127	23	20		4	15	13	4	3	1	1		2	3			90	10.9890	
751	124	9	27			26	17	4	3				1				87	10.8750	
752	125	17	22	2		14	12	8	2				1	2			81	0	
753	125	20	32	5	3	28	23	2	6				2	1			125	0.9542	
Totals	1779	246	421	36	19	325	225	52	44	9	9	2	5	14	23		1430		

TABLE II (continued)

$$(5) \frac{w^o l_z^*}{r_n f c_t}$$

Culture No.	Females	Males																		Total males	Coincidence of $w^o r_b$ and fc_t								
		1		2		3		4		1 2		1 3		1 4		2 3		2 4				3 4		1 2 3	1 2 4	1 3 4	2 3 4		
		$w^o l_z$	$r_b fc_t$	$w^o r_b fc_t$	l_z	$w^o fc_t$	$r_b l_z$	$w^o l_z fc_t$	r_b	$w^o l_z c_t$	$r_b f$	$w^o r_b l_z$	fc_t	$w^o r_b$	$l_z fc_t$	$w^o r_b f$	$l_z c_t$	w^o	$r_b l_z fc_t$			$w^o f$	$r_b l_z c_t$	$w^o l_z f$	$r_b c_t$	+	$w^o r_b l_z c_t$	$l_z f$	$r_b l_z f$
702	142	37	17	4	3	7	9	16	16	2	7					1	1											120	0
703	154	35	24	1	2	7	5	9	11	1	1			1		2	2			1		1	1				105	3.5000	
704	115	20	12	1		4	9	14	16	1	4					4		1	1								91	0	
705	95	13	14	2	2	3	5	8	12	1	2			1		3									1		67	0	
706	161	30	29		3	9	8	13	20	4	2			1						2							121	0	
743	97	31	6	2	3	4	8	8	13										1								76	0	
745	82	22	17	2	1	4	9	5	10	1	3					1		1	1								77	0	
797	139	36	11	2	3	7	9	1	12	4	7			1				2	1								96	0	
812	194	42	19	4	3	6	13	12	24	1	7			2	3			3		2							143	0	
813	148	25	26	1	4	8	2	13	12			3								2						1	96	0	
835	116	26	11	1	1	5	3	2	12																		69	0	
836	128	28	15			8	6	9	12	4	6					1				1							93	0/0	
845	80	22	17	1		3	5	9	11	1	4								1								77	0	
890	85	18	10		4	3	2	6	13											1							65	0	
892	67	13	11	1	1	1	2	6	10	3	2			1					1								55	0	
901	125	33	19	1	11	5	12	6	19	2	4			1					2	1	3						113	0	
913	148	22	22	4	6	10	12	11	21	3	6		1	3	4	2			7	2	3	1	7	2	1	1	151	0.5491	
914	73	21	12	1	2	1	6	2	10										2		1						65	0	
919	142	32	16		1	5	6	9	10										2		1						87	0	
921	117	29	17			2	6	11	14	4	3								1		1						90	0/0	
922	143	40	18	3	4	5	6	6	15	2	3			2													108	0	
923	173	36	35	4	2	3	5	10	17	5	8		1						1								128	0	
925	176	30	23	1	1	4	10	5	23	4	5			3													116	1.4872	
927	137	19	27	2	3	9	3	4	14	1	7										2		3	3			100	0	
928	151	26	13	2		6	8	6	12	3	4														1		84	0	
943	82	14	17	1	3	3	4	7	5	2	6			1													70	0	
947	139	37	22	2		8	8	11	16	1	2			1													109	0	
Totals	3409	737	480	43	53	140	181	219	380	50	114	2	1	23	8	4		40	13	22	12	26	18	1	1	3	1	2572	

* l_z = lozenge.