THE LINKAGE DISTURBANCE INVOLVED IN THE CHROMOSOME TRANSLOCATION I. OF DROSOPHILA, AND ITS PROBABLE SIGNIFICANCE.

G. W. DELUZ HAMLETT,

DEPARTMENT OF ZOÖLOGY, UNIVERSITY OF TEXAS.

The chromosomal abnormality in *Drosophila* known as "translocation I." was found by Bridges in 1917, and was first referred to by Morgan (1919); a preliminary account of it was given by Bridges in 1923. The case is a very remarkable one, unique in the literature to date, and it raises certain new problems concerning the arrangement which genes may have in a chromosome as well as concerning the changes in arrangement which they may undergo. The abnormality arose by a portion of the right hand end of chromosome II. breaking off and becoming attached near the middle of the right half of chromosome III. Bridges' data showed the size of the transposed piece and its approximate point of attachment on the third chromosome. It was known that the break in chromosome II. was between arc (ar) and plexus (pl), making the fragment about 8 units long, and that the transposed piece was attached somewhere between ebony (e) and rough (ro) in chromosome III. The deficient second chromosome was known as "Pale," from its effect on eosin-eyed flies, and the deficiency was lethal unless accompanied by translocation.

In the hope of getting further light on the chromosome change involved, the writer undertook to test more extensively the third chromosome linkage values in flies which carried the translocation. I wish to take this opportunity to express my indebtedness to Dr. H. J. Muller, who suggested the work, and whose aid and suggestions have made it possible. In these experiments the homozygous as well as the heterozygous condition of translocation was studied, and all of the left hand end of Chromosome III. was under genetic observation. Bridges had already shown that crossing over was greatly reduced in the region close to the locus of translocation; but his data included

only flies heterozygous for the transposed piece. The comparison of the homozygous and the heterozygous conditions with each other is of especial interest because of its bearing on the problem of the mode of attachment of the second chromosome fragment, as will be shown later.

The third chromosome mutant genes used in the experiments are, in their order from left to right along the chromosome: roughoid (ru), hairy (h), scarlet (st), pink (p), spineless (ss), delta (Δ), hairless (H), ebony (e), rough (ro), and claret (ca). Their locations are shown in the map of Fig. 1. Translocation is represented by Tr, and the deficient second chromosome by Pl. Curly (Cy) is a second chromosome gene used in balancing stocks. The linkage in flies homozygous for Tr was tested in two experiments. The summarized results for these crosses are given below, in Tables I. and II.

TABLE I.

$$\frac{Cy}{Pl}\ \frac{\Delta\ H\ e\ Tr}{ru\ h\ st\ p\ ss\qquad Tr}\ \text{♀} \times ru\ h\ st\ p\ ss\ e\ \text{♂}.$$

Regional Crossover Frequencies.						Total.
ru–h.	h–st.	st–p.	p–ss.	ss–Δ.	Δ–H.	
285	202	45	86	61	10	1,097
26.0%	18.4%	4.1%	7.8%	5.6%	.9%	

TABLE II.

$$\frac{Cy}{Pl}\ \frac{\Delta\ H\ e\ Tr}{Tr\ ro\ ca}\ \text{♀} \times e\ ro\ ca\ \text{♂}.$$

Regional Crossover Frequencies.				Total.
Δ–H.	H–e.	e–ro.	ro–ca.	
8	13	27	16	463
1.7%	2.8%	5.9%	3.5%	

These figures show a remarkable drop below normal in the crossover values as the locus of translocation is approached. This may be seen by comparing their map values (see Fig. 1,

b and *c*) with the normal third chromosome map (Fig. 1, *a*). The map length of the left-hand third will be seen to be slightly increased, but the genes between pink and claret are crowded much closer together. There is an apparent lengthening of the

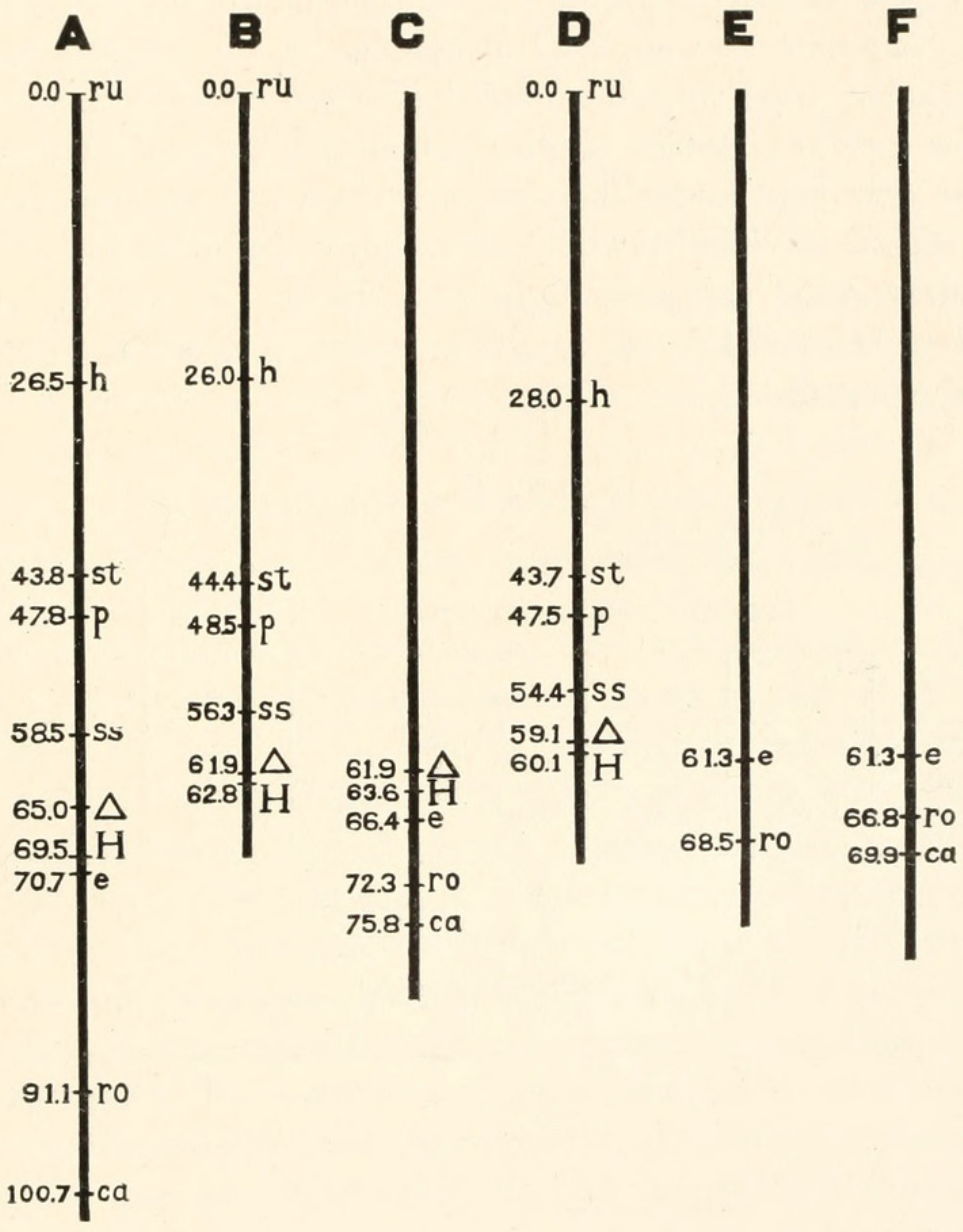


FIG. 1. (*a*) The normal third chromosome map. (*b*) and (*c*) Maps of third chromosome homozygous for translocation. (*d*), (*e*) and (*f*) Maps of third chromosome heterozygous for translocation.

distance between hairless and ebony, but this distance is so short, and the probable error so large, that the increase is probably not significant. Between ebony and rough, the region where the second chromosome fragment is attached, the per cent. of crossing over is less than one third of the normal value. These

relations are shown in Fig. 2, *a*, which shows the ratios of the values obtained in these experiments to the standard values of each of the major regions studied.

At the same time that these crosses were being made, the linkage in flies heterozygous for the abnormality was being tested. The same stocks were used in making up the crosses, and the characters used were introduced into the cross in as near the same way as possible. Both the homozygous and heterozygous lines were kept under the same conditions, so that any possible variations in viability would affect both lines alike and allow us to draw valid comparisons between them. As will be seen in Tables III. and IV., the results were almost identical with those of the first tests.

TABLE III.

$$\frac{}{\text{Pl}}\ \frac{\Delta\ \text{H e Tr}}{\text{ru h st p ss}\qquad\text{e}}\ \text{♀} \times \text{ru h st p ss e ♂}.$$

Regional Crossover Frequencies.						Total.
ru–h.	h–st.	st–p.	p–ss.	ss–Δ.	Δ–H.	
162	91	22	40	27	6	578
28.0%	15.7%	3.8%	6.9%	4.7%	1.0%	

TABLE IV.

$$\frac{}{\text{Pl}}\ \frac{\text{ru h st p ss}\quad\text{Tr}}{\text{p ss e}\qquad\text{ro}}\ \text{♀} \times \text{p ss e ro ♂}.$$

Crossovers.		Total Flies.
(ru h st) p ss e	(ru h st) p ss ro	
42	41	
Total Crossovers	83	1,155
	7.2%	

In Table V. are results for a test involving the ebony-rough and rough-claret distances. Only those flies which did not show delta hairless could be used in computing crossover values in this experiment. This cross also gave data on the exact location of translocation, as will be discussed later.

TABLE V.

$$\frac{Cy}{\quad}\ \frac{ru\ h\ st\ p\ ss\quad Tr}{e\quad ro\ ca}\ \text{♀} \times \frac{Cy}{Pl}\ \frac{\Delta\ H\ e\ Tr}{e\quad ro\ ca}\ \text{♂}.$$

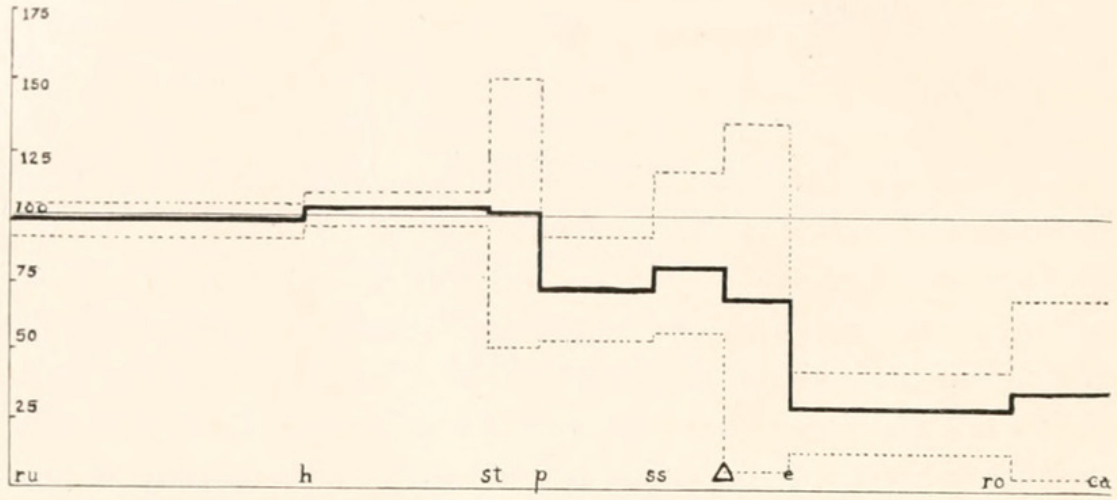
Regional Crossover Frequencies.		Total Utilizable Count.
e–ro.	ro–ca.	
50	28	902
5.5%	3.1%	

The results given in the last three tables are summed up in the chromosome maps shown in Fig. 1, *d*, *e*, and *f*, and Fig. 2, *b* shows the ratios of these values to the standard values. It will be seen on comparing these results with those based on the homozygous Tr flies that there is no noticeable difference in the crossover effects produced by the homozygous and by the heterozygous conditions.

The chief significance of the results probably lies in their bearing on the mode of attachment of the translocation. There are two conceivable ways in which the translocated piece might be attached between ebony and rough: it might be interpolated within this length, thus causing a prolongation of the thread between ebony and rough, or it might be attached somehow to the side of the original thread, thus resulting in a configuration of genes and of chromatin different from what had previously been regarded as normal, and not entirely in one line. The present results clearly disprove the first alternative, for if it were true, crossing over between ebony and rough should be increased when the flies were homozygous for the interpolated fragment. We must therefore conclude that the chromosome carrying translocation is branched or doubled in the region where the latter is attached.

The second point of significance is that the presence of translocation does not reduce crossing over throughout the chromosome. Beginning at the left-hand end of the chromosome, we find that the number of crossovers is practically normal until we reach the locus of pink, one third of the distance along the chromosome. From this point on, the map distance is markedly

shortened until the locus of translocation is reached. In this interval, between ebony and rough, the per cent. of crossing over is less than one third that of the normal. Between rough and



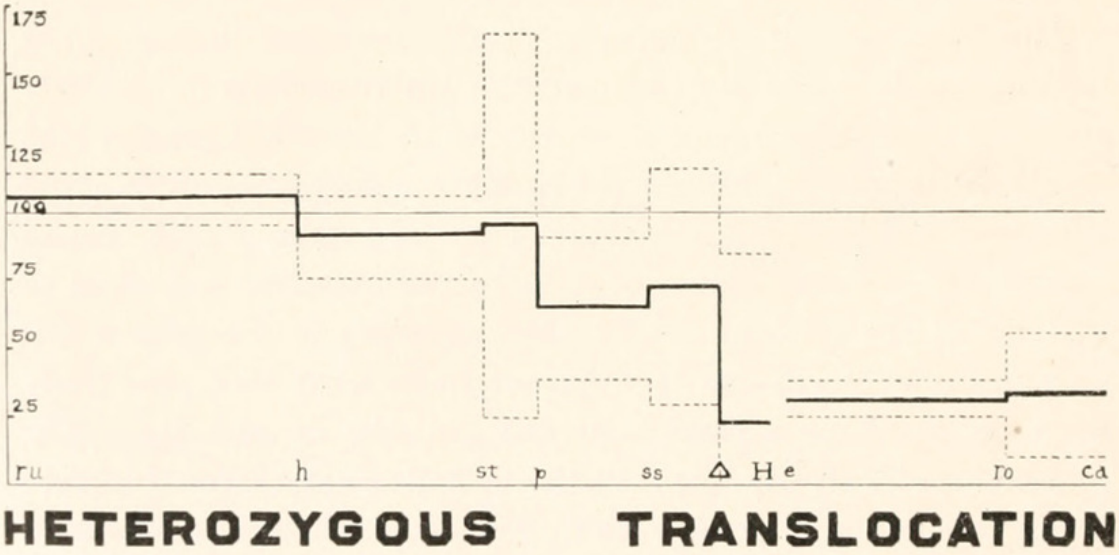


FIG. 2. Chart showing the ratios (in percentages) of the observed crossover values to the standard. The abscissa represents the length of the III. chromosome from roughoid to claret; the ordinate represents the percentage which the observed crossovers form of the standard value in each region. The heavy line represents the percentage observed; the dotted lines mark the limits of the probable error of this percentage, calculated for each interval.

claret the amount of crossing over rises again, approaching half the normal value. The number of flies involved was not large enough to yield reliable data on the coincidences, but as far as they went they agreed well with the normal.

If crossing over takes place at a stage in synapsis in which the chromosomal threads are twisted about each other, we can readily see why the presence of the attached fragment in either one or both of the third chromosomes should produce the effects that it does. Either by stiffening the threads so that they could not twist as tightly as in the rest of the chromosome, or by an actual interference with the loops, the transposed piece should tend to prevent the close association between the homologous chromosomes necessary for that interchange of genes which constitutes crossing over. This interference would produce its maximum effect at the point of attachment, and the effect would decrease to either side. This gradual decrease in the interference is well shown to the left of ebony. The locus of translocation is too close to the right-hand end of the chromosome to show any marked diminution of its effect toward that side. The rough-claret crossovers are, however, nearer to the normal percentage than those in the ebony-rough interval.

In the cross shown in Table V., 36 crossovers between ebony and rough were observed in which it was possible to follow the behavior of the translocation. The results are shown below.

TABLE VI.

$$\frac{Cy}{\quad}\ \frac{ru\ h\ st\ p\ ss\quad Tr}{e\qquad ro\ ca}\ \text{♀} \times \frac{Cy}{Pl}\ \frac{\Delta\ H\ e\ Tr}{e\qquad ro\ ca}\ \text{♂}.$$

Crossovers between (e) and (Tr) $\frac{\quad}{Pl}\ \frac{e\ Tr}{e\qquad ro\ ca}$	Crossovers between (Tr) and (ro) $\frac{\quad}{Pl}\ \frac{(ru\ h\ st\ p\ ss)\quad Tr\ ro\ (ca)}{e\qquad ro\ ca}$
11	25
36	

Translocation is, according to these figures, located at approximately 11/36 of the distance between ebony and rough, or at 76.9 on the chromosome map. The data given in Bridges and Morgan's monograph on the III. chromosome characters also show translocation to be between ebony and rough, but their figures show the locus of translocation to be closer to rough than to ebony. Also, the amount of crossing over in the ebony-

rough interval is even lower than in the experiments here reported. These differences may be due to a differential viability in the two cases; there may also be differences in genes influencing crossing over, but such differences in ratios do not affect the principal conclusion of this paper. The important point is that the effect of the translocation is the same whether it is heterozygous or homozygous.

Summary.

1. The chromosomal abnormality in *Drosophila*, known as translocation I., is located at approximately 76.9 on the third chromosome.

2. The presence of translocation does not affect the crossover values for the first 45 units in the left-hand end of the chromosome. To the right of this point, the per cent. of crossing over progressively decreases as the locus of translocation is approached, reaching its minimum of less than one third normal value in the region between ebony and rough.

3. The same results are obtained no matter whether the translocation is homozygous or heterozygous.

4. The fact that the results are the same in both heterozygous and homozygous flies shows that the attached fragment is not interpolated in the third chromosome, but is attached to its side. The resulting chromosome is thus of a type which has hitherto not been reported: that is, one in which the genes are not in a single linear series.

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