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Genetic Factors Affecting the Strength of Linkage in *Drosophila*

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in two days. This number of eggs therefore has not received the exposure necessary to produce the change in crossing over. The culmination of the two days exposure is to be expected in those eggs so situated that 125 to 175 eggs will be laid before them. Such an interpretation makes it extremely likely that the change in the amount of crossing over is finally affected in the earliest oocytes, that is, at the beginning of the growth period. The above evidence on the time of applying the new temperature and the time when the change in crossing over occurs, suggests that the crossing over process takes place in the stage when the chromosomes of *Drosophila* are known to be finely drawn out threads.

The decrease in the strength of linkage caused by temperature in no way weakens the chromosome interpretation of linkage. It rather adds to it considerable support, for it localizes the process of crossing over at a period in oogenesis when twisting between homologous threads seems possible. The evidence positively establishes the fact that crossing over does not take place during the early oogonial divisions, and makes it extremely improbable that it occurs at so late a stage in the growth period as the thick thread stage favored by Janssens as the chiasmatype.

<sup>1</sup>Bridges, C. B., *J. Exp. Zool., Wistar Inst., Philadelphia*, 19, No. 1, July, 1915.

<sup>2</sup>Sturtevant, A. H., these PROCEEDINGS, 3, 1917, (555-558).

<sup>3</sup>Cf. Snyder, C. D., *Amer. J. Physiol.*, 22, 1908, (309).

## GENETIC FACTORS AFFECTING THE STRENGTH OF LINKAGE IN *DROSOPHILA*

By A. H. Sturtevant

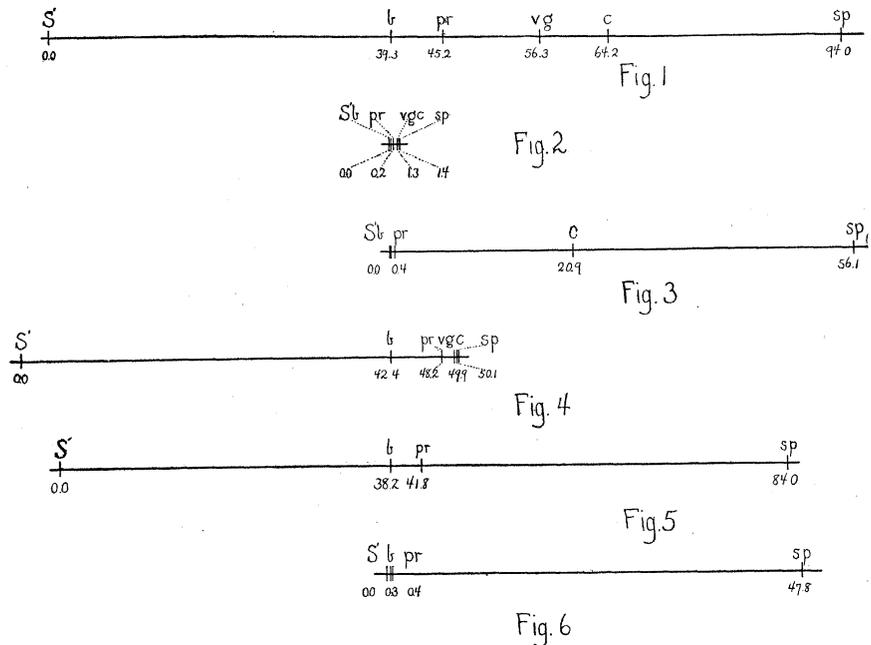
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Communicated by T. H. Morgan, July 5, 1917

In September, 1913, a wild female *Drosophila* of a stock from Liverpool, Nova Scotia, was crossed to a male bearing the second chromosome mutant characters vestigial and speck. A single daughter of this mating was tested, and gave no crossovers among 99 offspring, though vestigial and speck usually show about 37% crossing over. This strain has since been bred in very large numbers, and the experiments are being continued; but it has seemed advisable to report briefly on some of the results obtained.<sup>1</sup>

It has become clear that the original result was due to something in the second chromosome derived from the Nova Scotia female. Two of her granddaughters and all of her later descendants that were known, from linkage, to have received the second chromosome in question gave

similar results; but those descendants known not to have received it gave the 'usual' result. This was true whether the chromosome came from the mother (as above) or from the father. And when other second chromosome genes were substituted for vestigial and speck, unusual ratios still appeared; but for any combination the result was relatively constant, and the combined 'unusual' results give as consistent a scheme as the 'usual' results. The first column of table 1 shows the percentage of crossing over in the ordinary females for various combinations of second chromosome genes.<sup>2</sup> The second column gives similar data for tests of females that carry a Nova Scotia chromosome. Figures 1 and 2 are chromosome maps constructed on the basis of these two columns.



A large number of these experiments have been made with females having one Nova Scotia chromosome, and its mate bearing the mutant genes black, purple, and curved. Numerous tests have been made in order to determine the nature of the crossovers produced. It has been found that those crossovers that receive the part of the original Nova Scotia chromosome lying to the left of the purple locus still give unusual results and transmit the peculiarity to all of their descendants that receive this piece. The results produced by such females are not, however, the same as those produced when all the Nova Scotia chromosome

is present, as is shown in column 3 of table 1 and in figure 3. When the other piece of the Nova Scotia chromosome, lying to the right of purple (and, in many experiments, that part of it that is also to the left of speck) is tested, a still different result is obtained, as shown in column 4 and figure 4.

TABLE 1

GENES	PERCENTAGE OF CROSSING OVER					
	Normal	$\frac{C_{III} C_{IIR}}{C_{IIR}}$	$\frac{C_{III}}{C_{IIR}}$	$\frac{C_{IIR}}{C_{IIR}}$	$\frac{C_{IIR}}{C_{IIR}}$	$\frac{C_{III} C_{IIR}}{C_{IIR}}$
Star black.....	39.3	0.0	0.0	42.4	38.2	0.3*
Star purple.....	40.2	0.0	×	45.4	40.6	0.3*
Star curved.....	46.5	×	25.9	47.3	×	×
Star speck.....	48.3	0.4	49.0	46.0	49.0	47.4
Black purple.....	5.9	0.2	0.4	5.8	3.6	0.1
Black vestigial.....	16.9	1.2	×	8.9	×	×
Black curved.....	22.7	1.3	25.6	7.5	×	×
Black speck.....	49.3	1.1	48.8	9.3	43.5	47.0
Purple vestigial.....	11.1	1.2	×	0.6	×	×
Purple curved.....	19.0	1.1	20.5	1.7	×	×
Purple speck.....	46.5	1.2	47.4	2.8	42.2	47.4
Vestigial speck.....	36.7	0.2	×	0.0	×	×
Curved speck.....	29.8	0.1	35.2	0.2	×	×
†Total length.....	94.0	1.4	56.1	50.1	84.0	47.8

\* These few (6) crossovers are doubtful. None of them were tested; and there is apt to be a small percentage of error in classifying Star flies.

† Calculated as Star black + black purple + purple curved + purple speck in all but the last two columns, where purple speck is used. In no case further corrected for double crossing over.

It follows from these results that the original Nova Scotia chromosome contained at least two factors causing reduced crossing over, and each affecting chiefly the region in which it lies. We may call these two factors 'C<sub>III</sub>' and 'C<sub>IIR</sub>' (C for crossing over, after Muller,<sup>3</sup> II to distinguish them from similar factors affecting other chromosomes, *l* and *r* for left hand and right hand).

By appropriate matings it has been possible to obtain females homozygous for C<sub>IIR</sub>, and a surprising result has been observed: the effect produced by C<sub>IIR</sub> when heterozygous disappears when it becomes homozygous (see columns 5 and 6, figures 5 and 6). There can be no doubt of this result, as it has been obtained repeatedly, and has often been checked by tests of the offspring. It has also been paralleled more recently by results obtained by Muller<sup>3</sup> (1916) and by me<sup>4</sup> with C<sub>IIR</sub>. Similar tests of homozygous C<sub>III</sub> have not been possible since no chromo-

some has yet been obtained that contains both that factor and any mutant factor within its "sphere of influence."

Backcross tests have shown that males of all the above types with respect to  $C_{III}$  and  $C_{IV}$  resemble "normal" males in giving no cross-overs at all.

Included in the above tables are a considerable number of data involving three or more loci at once; and these agree with the table in showing clearly that the linear order of the factors established for the usual second chromosome is unchanged by the factors under discussion. The amount of crossing over is altered, often markedly, and not usually proportionately in different regions; but the factors keep their same sequence. This result serves to emphasize the importance of considering the distances on chromosome maps as only diagrammatic, not as representing actually proportionate distances between the genes, although actual distance is evidently an important factor influencing the end result. It does not, I think, in any way weaken the case for the chromosome hypothesis, but merely shows, together with the results of Bridges<sup>5</sup> (1915) and Plough<sup>6</sup> (1917), that any chromosome map is available for purposes of numerical prediction only when the conditions under which it was made are duplicated.

<sup>1</sup> Some of the early results were reported at the 1913 meeting of the American Naturalists, and brief references have been published by me (1915) and by Muller (1916).

<sup>2</sup> Much of this data has not hitherto been published. It has been collected mainly by Dr. C. B. Bridges, to whom I am indebted for permission to use it.

<sup>3</sup> Muller, H. J., *Amer. Nat., Lancaster, Pa.*, **50**, 1916, (193, 284, 350, 421).

<sup>4</sup> Sturtevant, A. H., *Zs. Abst. Vererb.*, **13**, 1915, (234).

<sup>5</sup> Bridges, C. B., *J. Exp. Zool., Wistar Inst. Philadelphia*, **19**, 1915, (1).

<sup>6</sup> Plough, H. H., these PROCEEDINGS, **3**, 1917, (553-555).

## FURTHER EVIDENCE ON THE CONCENTRATION OF THE STARS TOWARD THE GALAXY

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Communicated by G. E. Hale, July 9, 1917

In a previous communication<sup>1</sup> attention was directed to the striking difference in the results for the distribution of the stars with respect to the galactic plane found by Kapteyn<sup>2</sup> and by Chapman and Melotte.<sup>3</sup> An analysis of the counts of stars on photographs of 88 Selected Areas, made at Mount Wilson with the 60-inch reflector, gave preliminary values for the variation in the totals to magnitude 17.5 which agree well with those of Kapteyn.