No black, wingless flies appeared which seemed due to close linkage between the factors in question. Yet, when  $F_2$  gray, wingless females were tested by breeding to black, winged males quite a number of black flies were obtained in the first generation (15 to 125). The explanation offered was that "crossing-over" or breaking the linkage occurred so rarely that in the production of the  $F_2$  generation no two wingless black gametes had happened to meet.

In order to test how often crossing-over occurred, the experiment was repeated, but this time the  $F_1$  females and males were tested for cross-overs by mating them to black wingless flies. Thus, black, winged females were mated to gray, wingless males and gave  $F_1$  gray, winged flies. The  $F_1$  males were tested with black wingless females and gave:

These results show that there has been no crossing-over in the  $F_1$  heterozygous males.

The converse cross was as follows: Gray, winged females were bred to black, wingless males and produced gray, winged males and females. The F<sub>1</sub> males were bred, as before, to black, wingless females, and gave:

Here again the combination that went into the  $F_1$  male remained intact.

Similar crosses in which the F<sub>1</sub> females were tested gave a different result: When F<sub>1</sub> gray, winged females (out of black, winged females by gray, wingless males) were bred to black, wingless males there were obtained:

 $BW \color BW \color GW \color GW \color BW \color BW \color GW \color GW \color GW \color BW \color GW \$ 

The converse cross, viz.,  $F_1$ , gray, winged females (out of gray, winged females by black, wingless males) were bred to black, wingless males and gave:

COMPLETE LINKAGE IN THE SECOND CHROMOSOME OF THE MALE OF DROSOPHILA

It has been shown recently that the non-sex-linked factors that give black and wingless flies are linked to each other. In the  $F_2$  generation (from  $P_1$  black winged by gray wingless) there were produced:

Morgan and Lynch, Biol. Bull., Vol. XXIII., p. 174, August, 1912.

found that the percentage of "crossing-over" in the female is 21.9.

These experiments make clear, first, that there is no crossing-over in the male (at least for the number of cases here recorded); second, that in the female the gametic ratio is about one to four.

The bearing of the results on the explanation of the absence of crossing-over of sexlinked characters in the male is obvious. In that case the presence of only one sex chromosome in the male made crossing-over impossible, and this was the explanation offered. But the factors concerned with black and wingless lie in a different chromosome (in the sense that they are linked to each other and not to any sex-linked factor) which is present in duplex in both sexes, yet crossing over occurs in one sex only. Whether this second chromosome is the one to which in *Drosophila* the sex chromosome is attached can not be stated, and the question must be left unsettled until we have tested the crossing-over of other factors in this and in other chromosomes.

As Mr. A. H. Sturtevant has pointed out to me, the case here recorded offers apparently an explanation of cases in plants recently described by Bateson and others.<sup>2</sup> When the two dominants enter from different sides no crossing over is apparent, as seen in the first case recorded above ("complete repulsion"). When the two dominants enter from the same side there is evidence of crossing over ("partial coupling"), as shown by the following example. Gray, winged females were mated to black, wingless males, and gave gray, winged F<sub>1</sub> offspring. These inbred produced the following F<sub>2</sub> classes:

These results in the F<sub>2</sub> generation are of the same kind as those that Bateson and Punnett have recorded for peas, etc. Back-crossing has shown in the flies that the results are due to failure of "crossing-over" in the males. If the same tests, when applied to peas, give

the same result there will be no longer any need to assume, as Bateson and Punnett have done, that there is (A) a system of partial coupling, (B) a system of complete repulsion, or "spurious allelomorphism" or to assume (C) a system of special dichotomous ratios for coupling, such as 3:1 and 7:1, etc.

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<sup>&</sup>lt;sup>2</sup> Proc. Roy. Soc., Vol. 84, 1911.