A crossover reducer in Drosophila melanogaster due to inversion of a section of the third chromosome

by

A. H. Sturtevant, Columbia University

(With 4 Figures)

A wild stock of *D. melanogaster*, collected at Prague in 1925 by Dr. A. Brozek, was found to contain a crossover reducer for the right half of the third chromosome. This reducer (called C\textsubscript{III}), like those previously described by Sturtevant, Muller, Payne and Ward, lies in the region affected. Females heterozygous for C\textsubscript{III} have been tested for crossing over throughout the chromosome. It is evident from these data that crossing over is substantially normal.
to the left of stripe¹), (locus 62.0), but greatly reduced to the right of that locus. Tests of flies resulting from crossing over have shown that $C_{III\text{B}}$ itself lies to the right of stripe, in the region chiefly affected.

$C_{III\text{B}}$ thus affects crossing over in the same regions as $C_{III}$ (Muller 1916) and $C_{III\text{PR}}$ (Payne 1924). The results of Muller, and results of my own that are still largely unpublished, show that $C_{III}$ and $C_{III\text{PR}}$ each give free crossing over in the region concerned when they are homozygous; but $C_{III}$ over $C_{III\text{PR}}$ gives the reduced crossing over characteristic of either when heterozygous. That is, $C_{III}$ and $C_{III\text{PR}}$ are not allelomorphous. Similar tests show that $C_{III\text{B}}$ is allelomorphous to $C_{III}$ but not to $C_{III\text{PR}}$. The conclusions reached here as to the nature of $C_{III\text{B}}$ thus apply also to $C_{III}$.

Most of the linkage data have been obtained from females that carried one $C_{III\text{B}}$ chromosome and one chromosome with the mutant genes scarlet, stripe, sooty, rough and claret¹). Such females, mated to males carrying all the recessive genes concerned, have given the results shown in Table 1.

<table>
<thead>
<tr>
<th>Wild-type</th>
<th>st sr e⁰ ro ca</th>
<th>st sr e⁰ ro ca</th>
<th>st sr e⁰ ro ca</th>
<th>st sr e⁰ ro ca</th>
<th>st sr e⁰ ro ca</th>
<th>st sr e⁰ ro ca</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>2214</td>
<td>2058</td>
<td>219</td>
<td>238</td>
<td>3</td>
<td>4</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

Tests of these offspring have shown that the wild-type, scarlet, and scarlet stripe individuals carry $C_{III\text{B}}$; the scarlet stripe sooty rough claret, stripe sooty rough claret and sooty rough claret ones do not. That is, $C_{III\text{B}}$ lies to the right of stripe. The single sooty rough individual also carried $C_{III\text{B}}$; it was not present in the scarlet stripe sooty individual. These data are all consistent with the interpretation that $C_{III\text{B}}$ occupies a single locus that lies to the right of claret, though it is then necessary to suppose that the scarlet stripe sooty individual came from a double crossover egg ($e^0\text{-ro, ca-C}_{III\text{B}}$). That is, there were two double crossovers in which one or both of

¹) The mutant genes here discussed are listed and described by Bridges and Morgan (1923) and by Morgan, Bridges, and Sturtevant (1925). There follows a list, showing the name, character affected, symbol, and locus on the standard third chromosome map. Stubble and Minute-g are dominant types; all the others are recessive.

- Scarlet (eye color): st: 44.0.
- Stubble (bristle shape): Sb: 58.2.
- Stripe (thorax shape and pattern): sr: 62.0.
- Sooty (body color): $e^0$ (allelomorph of ebony): 70.7.
- Claret (eye color): ca: 100.7.
- Minute-g (bristle size): Mg: 106.2.
the crossovers were to the right of sooty — but there were no single crossovers in this region. This result seems improbable, and the data now to be described lead to a different and more plausible interpretation of C_{III.B}.

Females homozygous for C_{III.B} were produced by crossing the lines derived from the scarlet stripe and sooty rough crossovers just discussed. When such females were tested, the results showed clearly, in several different experiments, that the sequence was now scarlet stripe rough sooty instead of the usual scarlet stripe sooty rough. Figures 1 and 2 show the intervals of the usual map (from Bridges and Morgan 1923) and of that based on homozygous C_{III.B} data. Scarlet (locus 44 on the standard map) is arbitrarily taken as the zero point for this comparison, since loci to the left of scarlet have not yet been studied in homozygous C_{III.B}.

![Fig. 1](image1)

![Fig. 2](image2)

The natural conclusion from these data is that C_{III.B} is not a gene but is itself simply an inverted section including the loci of sooty and rough. I have suggested (Sturtevant 1921) that such an inversion should produce a crossover reducer effective only when heterozygous; and Sturtevant and Plunkett (1926) have shown the existence of an inverted section in the third chromosome of D. simulans as compared to that of D. melanogaster.

In the present case such an interpretation may be elaborated as follows. The original C_{III.B} chromosome was $+st +sr +ca +ro +e^s$, instead of the usual $+st +sr +e +ro +ca$ (the reason for including claret in the inverted section will appear below). The females whose offspring are recorded in Table 1 thus may be represented as in Figure 3,

![Fig. 3](image3)

where $+1^2$ and $+3^2$ represent the end loci of the inverted section. In these females the chromosomes failed to conjugate normally in the
region between $+^1$ and $+^2$, because like parts were not opposed. Crossing over consequently failed to occur. The reduction in crossing over between stripe and sooty may mean that the inverted section actually reaches almost to stripe, or it may mean that there is a reduction in crossing over adjacent to the inverted section.

From such a female we must, on the hypothesis suggested, suppose that double crossing over gave a chromosome that was $+^{st} +^{sr} +^{ca} +^{ro} e^s$. A glance at Figure 3 will show that such a result demands an additional hypothesis; for, as the formula stands, double crossing over would give $+^{st} +^{sr} e^s +^{ro} +^{ca} +^{ro} e^s - i.e.$ the normal sequence, for these four loci. The observed result may be accounted for if we suppose that the chromosomes in question happened, in this one egg, to conjugate so that the inverted section was opposed to the corresponding genes in the normal chromosome, as in Figure 4. Double crossing over (between $+^1$ and $+^o$, $+^{ro}$ and $+^{ca}$) would then give the observed combination. The scarlet stripe sooty individual of Table 1, that did not carry $C_{III}$, was due to double crossing over in the intervals $+^{st} +^{ro}$ and $+^{ca} +^{sr}$.

It may be noted further that single crossing over anywhere in the region where like is opposed to like would now give rise to chromosomes that would have the genes proper to one end of a normal chromosome represented twice, and those proper to the other end entirely lacking. In diploid Drosophilae such chromosomes would presumably be lethal; but in the cases observed a second crossover restored the normal complement of genes and made the new chromosome capable of forming part of a normally functioning zygote. In fact, tests show that the sooty rough $C_{III}$ chromosome does not even have a recessive lethal effect, so that it must be supposed to contain one and only one complete set of genes characteristic of the third chromosome.

A comparison of Figures 1 and 2 shows that the directly comparable values st Sb, Sb sr, and $e^s +^{ro}$ are not strikingly different. The only real discrepancy occurs in the case of st Sb, which is furthest from the inverted section and is also well known (Bridges and Morgan 1923) to be more variable in frequency of crossing over than are regions further to the right. If one supposes that the inversion has not seriously affected crossing over in the component parts of the right end, analysis of these maps leads to the conclusion that the inverted section extends to the end of the normal chromosome.
Not more than 9 of the 32 units between sr and ro in Figure 2 can represent normal unchanged material, since the sr e* value in Figure 1 is 9, and e* is known to be in the inverted piece. At least 23 units that lie to the left of ro in Figure 2 must thus be supposed to lie to the right of it in Figure 1; but the locus furthest to the right among those known (Mg) is only 15 units beyond ro. One is tempted to predict that the standard map will ultimately be lengthened by about 8 units through the finding of new loci; but it is equally probable that some or all of these 8 units are to be accounted for by supposing slight changes in frequency of crossing over. In any case, it seems certain that claret, the most commonly used locus near the right end, lies in the inverted section; since only on this assumption can the sr e* crossover of Table 1 be simply explained.

The two crossovers in the presence of heterozygous C_{III} that were described by Muller (1918, pp. 444 and 449) can both be explained as coming from chromosomes that conjugated as in Figure 4. Both were then double crossovers within the inverted section. One of them was also a crossover in some region to the left of the inverted section, indicating that the free ends shown in Figure 4 may bend around and conjugate with each other accurately enough to allow crossing over. The second case reported by Muller was interpreted by him as resulting from two independent crossings over in different individuals, but the present interpretation seems to fit the facts as reported better than does that view, and is in fact necessitated by the discovery that C_{III} is an inversion.

There are indications in the literature which suggest that some of the other crossover reducers may also be due to inversion of sections of chromosomes. Payne (1924), for C_{III PL} and C_{III PR}, and Ward (1923), for C_{III CB} and C_{III CYB}, report a few double crossovers in regions where single crossovers are rare or absent. These crossovers seem not to have been carefully tested; but the experiments are now being repeated, in order to see if such rare double crossovers are of the same nature as those obtained from C_{III B}.

Literature cited


