CROSSOVER MODIFIERS IN THE THIRD CHROMOSOME OF *DROSOPHILA MELANOGASTER*[1]

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In January 1916 I began an experiment to increase the number of bristles on the scutellum of *Drosophila melanogaster* by means of artificial selection. This experiment was carried through 38 generations. At the end of selection the mean bristle number had been increased from four to nine plus. In analyzing these results the strain was crossed to the multiple recessive stock, sepia, spineless, kidney, sooty, rough (all third-chromosome characters), and the F_1 flies inbred. Instead of the standard values, only 17 crossovers occurred among 3327 flies. Fifteen of these were between sepia and spineless and two were double crossovers between sepia spineless and spineless kidney (see PAYNE 1918, table 8). Of the 3327 flies 2701 were wild-type and 609 were s_e s_s k e^s r_o, a ratio of 4.4 to 1. These linkage results were explained by assuming that a crossover modifier was present in the third chromosome of the selected strain. The results show that the strain was probably homozygous for this factor and that the flies used were free from lethals. BRIDGES called this factor C_{IIIP}.

The present paper is not an analysis of the selected strain, but of lance, a second-chromosome recessive mutant which appeared December 5, 1916, within the selected strain. The term "lance" refers to the shape of the wing. In most of the females the wings are pointed instead of rounded at the tips. The character is very variable, however, and the males show it less marked than the females. In fact, the males are difficult to distinguish from the wild-type males. See figure 1 for some of the variations in wing shape and for a comparison with the wild-type. Lance has been maintained in mass cultures since its appearance, and at the present time is not the same with respect to these crossover modifiers as the selected line at the end of selection. In one third chromosome there are now two modifiers, l C_{IIIPL} and l C_{IIIPR}, which cut out nearly all crossing over in the third chromosome. The nomenclature here is slightly cumbersome, but an explanation will make it clear. C_{III} locates the crossover-modifying genes in the third chromosome; P refers to the author; while L and R place the two genes in the left and right ends of the chromosome, respectively;

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l means that a lethal gene is present in the vicinity of each crossover modifier and remains closely associated because of the suppression of crossing over. The other third chromosome of lance may carry a crossover modifier. At least, the modified ratios may be explained in this way; or, as we shall see later, they may be explained by assuming the modifier to be in the "IIIple" strain. The effect on crossing over is not very pronounced, however, except between roughoid and hairy, where the standard percentage is lowered from 26.0 to 18.9. There is a lethal in this chromosome which balances the lethals associated with C_{IIIPL} and C_{IIIPR}. The evidence for this lethal is found in the fact that of several hundred lance flies which have been out-crossed, all have been found to be heterozygous for $l\ C_{\mathrm{IIIPL}}$ and $l\ C_{\mathrm{IIIPR}}$. If this balancing lethal were not present, some of the lance flies would be free from $l\ C_{\mathrm{IIIPL}}$ and $l\ C_{\mathrm{IIIPR}}$. It would seem that C_{IIIP} in the selected lines was the same as $l\ C_{\mathrm{IIIPL}}\ l\ C_{\mathrm{IIIPR}}$ without the lethals. Because of the ratio of 4.4 wild-type flies to 1 $s_e\ s_s\ k\ e^s\ r_o$, when the selected line was crossed to $s_e\ s_s\ k\ e^s\ r_o$, and the F_1 flies inbred, C_{IIIP} was known not to be lethal, and probably did not carry an associated lethal. If there had been a lethal we would have expected a 2 : 1 ratio. Further, the flies used from the selected line must have been homozygous for C_{IIIP}. The balancing lethal in the other third chromosome of lance must have been acquired since its separation from the selected line. The selected strain was started from a single pair of parents taken at Bloomington. Since both the wild-type strain from which the selected strain was started and a second strain taken in Bloomington in 1923, carried the same or similar

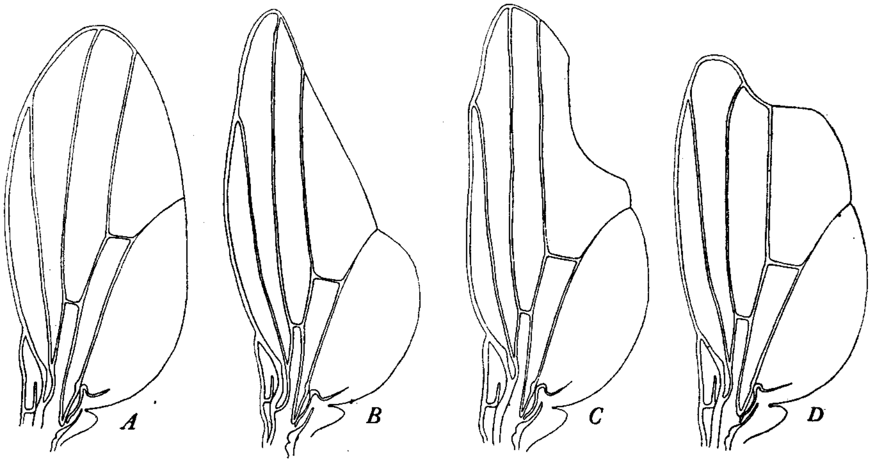

FIGURE 1.—A, wing of wild-type female. B, typical lance-shaped wing of female of lance strain. C and D, two of the variations in wing shape in the lance strain.

crossover modifiers, it seems probable that they were widely or uniformly present in the parental wild strain.

Other crossover modifiers have already been described in Drosophila. STURTEVANT (1913) was the first to discover them. He reported C_{III} at that time, though without analysis or description. This same factor, or another having the same effect and allelomorphic to it, has since been found by MULLER (1916) in spread and beaded, and by BRIDGES (1923) in maroon dwarf and in eosin. C_{III}, when heterozygous, shows its greatest inhibiting effect in the region of sooty. Between e^s and r_o no crossing over occurs; between s_s and e^s, 0.2 percent occurs. Crossing over between spineless and the left end of the chromosome approaches standard values. When C_{III} is homozygous, approximately standard values obtain in both ends of the chromosome.

BRIDGES and MORGAN (1923) report another modifier, C_{IIIM}, in the third chromosome. This was present in a wild stock from Camp Jackson, South Carolina. When heterozygous, C_{IIIM} gives the following crossover values: s_e-s_s, 28.1; s_s-e^s, 0.0; e^s-r_o, 0.5; r_o-M, 0.5. These values are very close to those for C_{III}. No tests were made for homozygous C_{IIIM}, nor to see whether C_{IIIM} might be allelomorphic to C_{III}.

BRIDGES and MORGAN (1923) also mention the presence of a modifier in the region of hairy, which increases crossing over in the hairy-scarlet section. Based upon data collected since this publication, BRIDGES writes me that this value may reach 22 ±. He calls this modifier C_{III}-s_t, because it seems to be carried usually with scarlet. He also thinks there may be a slight reducer ($C_{\text{IIIL-S}}$) in the left end of the third chromosome of "IIIple," and that what he has been calling "standard" may be an interaction of the two.

In the second chromosome several modifiers have been reported. The first was by STURTEVANT (1919). From a stock collected in Nova Scotia he found two modifiers, one in each end of the second chromosome. Each gene, in females heterozygous for it, cuts out nearly all crossing over in the region in which it lies. C_{IIL} is located to the left of purple and reduces the S-b section to 0.5. C_{IIR} is located between purple and speck. It reduces the p_r-c section to 1.6 and the c-s_p section to 0.0. Homozygous C_{IIR} gives standard crossover values. In this same stock, STURTEVANT also reports a modifier, $C_{\text{III, II}}$ which lies in the third chromosome, but which, in the presence of C_{IIR}, increases crossing over in the p_r-c section. This same gene, when heterozygous, also reduces crossing over in the third chromosome. Its effect is similar to, but not identical with, that of C_{III}.

WARD (1923) in a stock of curly-wing flies finds two dominant second-chromosome modifiers, C_{CL} and C_{CR}, which inhibit all crossing over along the entire length of the second chromosome under normal temperature conditions. When the flies are subjected to a higher temperature (30°C ±) crossing over frequently takes place in the right half. WARD also believes these modifiers may affect crossing over in the first and third chromosomes. Her data here, however, are far from convincing. Curly is homozygous for these modifiers.

In order to analyze the peculiar results in lance, I have made use primarily of two groups of third-chromosome linked genes, roughoid, hairy, scarlet, peach, spineless, sooty, called "IIIple," and sooty, rough, claret. For these stocks and others similar to them I am indebted to the Genetical Laboratory of COLUMBIA UNIVERSITY. I also used at times a stock made up by Doctor MULLER in which $l\,C_{IIIPL}$ and $l\,C_{IIIPR}$ were balanced against r_u h s. p^p s_s H e^s. I am indebted to Doctor C. B. BRIDGES for helpful suggestions and criticisms.

When lance is crossed to r_u h s_t p^p s_s e^s, and the F_1 females are back-crossed to r_u h s_t p^p s^s e^s males, about one-half of the females show very little crossing over, while the other half show percentages slightly reduced from standard, except the region between r_u and h, which is reduced more than the others, from 26.0 to 18.9. These two classes of females have been studied separately. The complete data for every pair of parents are not given to save expense of printing. Instead, a summary of the data for each particular kind of cross is given.

TABLE 1

P_1, ♀ *lance* × ♂ "*IIIple*"; F_1 ♀ $\frac{l\,C_{IIIPL}\ l\,C_{IIIPR}}{r_u\ h\ s_t\ p^p\ s_s\ e^s}$ × ♂ "*IIIple*."

Back-cross types	r_u	+	r_u	r_u	r_u		r_u				r_u	r_u	r_u	r_u	
	h			h	h		h			h	h	h	h		h
	s_t				s_t		s_t			s_t	s_t	s_t	s_t	s_t	s_t
	p^p					p^p	p^p			p^p			p^p		p^p
	s_s					s_s		s_s			s_s				
	e^s					e^s		e^s	e^s		e^s	e^s	e^s		e^s
Totals	12,261	15,151	1	2	26	34	19	43	1	1	1	4	4	1	1

TABLE 2

Recombination percents computed from table 1.

Crossing-over section	r_u-h	h-s_t	s_t-p^p	p^p-s_s	s_s-e^s
Total recombinations	4	3	66	69	10
Percent of recombination	0.014	0.010	0.239	0.250	0.036
Standard percents[2]	26.0	16.4	4.2	10.2	12.2

Using the F_1 females in which little crossing over occurs we get the results shown in tables 1 and 2. Table 1 shows the different classes of individuals and the number in each class. Table 2 gives the recombination percentages for the component sections of r_u h s_t p^p s_s e^s computed from table 1. These are as follows: r_u-h, 0.014; h-s_t, 0.010; s_t-p^p, 0.239; p^p-s_s 0.250; and s_s-e^s, 0.036. While nearly all crossing over is cut out, the greatest reduction is between r_u and h, and h and s_t. This is probably the locus of $l\,C_{IIIPL}$. Sooty lies at 70.7. In order to test the extreme right end of the third chromosome, tests similar to those just recorded were made with sooty, rough, claret. A lance female was crossed to an e^s r_o c_a male and the F_1 females were back-crossed to e^s r_o c_a males. The results for the little-crossover class are given in table 3. No crossing over occurred between e^s and r_o, and the r_o-c_a section was cut from 9.6 to 0.78. The influence of these two factors, then, extends from end to end of the third chromosome. In the right end the region of greatest reduction is between e^s and r_o, where we get no crossing over. This is probably the locus for $l\,C_{IIIPR}$. It is interesting in this connection that C_{III} and C_{IIIM} also exert their greatest restriction between e^s and r_o.

TABLE 3

P_1, ♀ *lance* × ♂ $e^s\, r_o\, c_a$; F_1 ♀ $\dfrac{l\,C_{IIIPL}\;\; l\,C_{IIIPR}}{e^s\, r_o\, c_a}$ × ♂ $e^s\, r_o\, c_a$.

$e^s\, r_o\, c_a$	+	$e^s\, r_o$	c_a	e^s-r_o Re.[3]	e^s-r_o Sd.	r_o-c_a Re.	r_o-c_a Sd.
570	695	3	7	0.0	20.2	0.78	9.6

In comparison with the standard percentages the section between s_t and p^p is the least affected. The standard value of 4.2 is reduced to

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[2] These and subsequent standard percentages of recombination for chromosome III were obtained from the curves of figures 1 and 2, pages 12 and 13 of BRIDGES and MORGAN (1923).

[3] Wherever the abbreviations Re. and Sd. occur they refer to the recombination percent observed in the experiment and to the standard percent of recombination.

0.239. A higher percentage, 0.250, of recombination actually occurs for p^p and s_s, but the standard value here is 10.2. So, relatively, there is less effect of the crossover modifiers between s_t and p^p. BRIDGES and MORGAN (1923) point out that the effects of C_{III} and C_{IIIM} grow less in the region of peach. They believe this region to be the middle of the chromosome. Because of the lethal effect it has been impossible to get a strain of flies homozygous for C_{IIIPL} and C_{IIIPR}. This was attempted for many generations by mating wild-type flies to wild-type flies obtained in the F_2 generation from lance × "IIIple."

As crossing over occurs, occasionally, it has been possible to separate $l\,C_{\text{IIIPL}}$ from $l\,C_{\text{IIIPR}}$ and to study their effects, separately. When lance or $\frac{l\,C_{\text{IIIPL}}\ l\,C_{\text{IIIPR}}}{r_u\ h\ s_t\ p^p\ s_s\ H\ e^s}$ is mated to "IIIple" it is possible, because of a small amount of crossing over, to get F_2 flies of the following constitution: $\frac{l\,C_{\text{IIIPL}}\ p^p\ s_s\ e^s}{r_u\ h\ s_t\ p^p\ s_s\ e^s}$. If we take a male of this sort, which will be $p^p\ s_s\ e^s$ in external appearance, and mate to a wild-type stock female, by a further back-cross of the F_1 female to a "IIIple" male we can study the effect of $l\,C_{\text{IIIPL}}$ on crossing over between p^p and s_s and between s_s and e^s. The results of such a cross are summarized in table 4, which gives the actual number of individuals and the percentages of recombination. For the p^p-s_s section we obtained a recombination percent of 13.4, contrasted with standard 10.2; for s_s-e^s, 13.8 contrasted with 12.2. For both sections the recombination percents are higher than the standard values. This same type of cross has been made a second time with recombination percents of 13.9 and 14.8. Here again the values are higher than standard. Whether the differences are really significant I am unable to say.

TABLE 4

P_1, ♂ $\frac{l\,C_{\text{IIIPL}}\ p^p\ s_s\ e^s}{\text{“}III\,ple\text{”}}$ × ♀ +; F_1 ♀ $\frac{l\,C_{\text{IIIPL}}\ p^p\ s_s\ e^s}{}$ × ♂ "*IIIple.*"

$p^p\ s_s\ e^s$	+	p^p	$s_s\ e^s$	$p^p\ s_s$	e^s	$p^p\ e^s$	s^s	p^p-s_s Re.	p^p-s_s Sd.	s_s-e^s Re.	s_s-e^s Sd.
542	682	113	103	115	107	4	5	13.4	10.2	13.8	12.2

A cross similar to that just recorded was made with an F_2 female of the following constitution: $\frac{l\,C_{\text{IIIPL}}\ s_s\ e^s}{r_u\ h\ s_t\,|\,p^p\ s_s\ e^s}$. She was mated to a wild-type male from stock and the females from this cross mated back to "IIIple" males. The offspring of the $\frac{l\,C_{\text{IIIPL}}\ s_s\ e^s}{}$ females only were counted and tabulated in table 5. The recombination percent for the s_s-e^s section was 10.3, slightly less than the standard value of 12.2. The numbers given in table 5 are the sums of two separate experiments performed at widely different times. In one the value for s_s-e^s was 10.2 and other 10.3. If the increased values in table 4 are significant, it would seem strange that we should get a reduced value here. Certainly $l\,C_{\mathrm{IIIPL}}$ is present in both cases. The only difference is in the absence or presence of the region of the chromosome including p^p. Pink, spineless, sooty flies of the following constitution, $\frac{l\,C_{\mathrm{IIIPL}}\;p^p\;s_s\;e^s}{r_u\;h\;s_t\;p^p\;s_s\;e}$, have been mated *inter se*, in an attempt to produce flies homozygous for the crossover modifier. The result of such a cross was 370 $p^p\;s_s\;e^s$ flies to 102 $r_u\;h\;s_t\;p^p\;s_s\;e^s$. The $p^p\;s_s\;e^s$ flies were not homozygous, however. When inbred they again threw $p^p\;s_s\;e^s$ and $r_u\;h\;s_t\;p^p\;s_s\;e^s$ flies. This clearly demonstrates the presence of a lethal associated with the crossover modifier.

TABLE 5

P_1, ♀ $\frac{l\,C_{\mathrm{IIIPL}}\;s_s\;e^s}{r_u\;h\;s_t\;p^p\;s_s\;e^s}$ × ♂ +; F_1 ♀ $\frac{l\,C_{\mathrm{IIIPL}}\;s_s\;e^s}{}$ × ♂ "*IIIple.*"

$s_s\;e^s$	+	s_s	e^s	s_s-e^s Re.	s_s-e^s Sd.
1175	1423	142	157	10.3	12.2

I also crossed F$_2$ $\frac{r_u\;h\;s_t\;l\,C_{\mathrm{IIIPR}}}{r_u\;h\;s_t\;p^p\;s_s\;e^s}$ males to wild-type females from stock and back-crossed the females to "IIIple" males. The offspring of the $\frac{r_u\;h\;s_t\;l\,C_{\mathrm{IIIPR}}}{}$ females have been tabulated in table 6, which gives the numbers of individuals and the percentages of recombination. Between r_u and h I found 23.8 and between h and s_t, 24.5 percent. The value for the roughoid-hairy section is slightly low but probably not significantly so. The value for the hairy-scarlet section is very much increased, from 16.4 to 24.5. This is certainly a significant difference. It has been obtained in separate experiments. It would seem, then, that $l\,C_{\mathrm{IIIPR}}$ in the absence of $l\,C_{\mathrm{IIIPL}}$ increases crossing over between hairy and scarlet. It is probable, however, that the modifier is in the "IIIple" strain, and that it is the same as, or similar in its action to, C_{III}-s_t.

TABLE 6

P_1 ♂ $\frac{r_u\;h\;s_t\;l\,C_{\mathrm{IIIPR}}}{r_u\;h\;s_t\;p^p\;s_s\;e^s}$ × ♀ +; F_1 ♀ $\frac{r_u\;h\;s_t\;l\,C_{\mathrm{IIIPR}}}{}$ × ♂ "*IIIple.*"

$r_u\;h\;s_t$	+	r_u	$h\;s_t$	$r_u\;h$	s_t	$r_u\;s_t$	h	r_u-h Re.	r_u-h Sd.	h-s_t Re.	h-s_t Sd.
689	805	333	281	294	340	27	23	23.8	26.0	24.5	16.4

A similar cross was made with a $\frac{r_u\ h\ s_t\ p^p\ l\ C_{\text{IIIPR}}}{r_u\ h\ s_t\ p^p\ s_s\ e^s}$ male. The only difference here is the addition of p^p to the chromosome with $l\ C_{\text{IIIPR}}$. The results are given in table 7. Here we get practically standard values for the r_u-h and s_t-p^p sections, 26.7 against 26.0, and 4.8 against 4.2. On the other hand, we get the increased value for the h-s_t section, 25.8 against 16.4. This experiment also shows that the inhibiting effect of $l\,C_{\text{IIIPR}}$ does not extend to the left of pink. $\frac{r_u\ h\ s_t\ l\ C_{\text{IIIPR}}}{r_u\ h\ s_t\ p^p\ s_s\ e^s}$ flies have been inbred in an attempt to produce homozygous $l\,C_{\text{IIIPR}}$ flies. The result is to produce flies of the same heterozygous constitution. The strain cannot be made homozygous for $l\,C_{\text{IIIPR}}$.

TABLE 7

P_1 ♂ $\frac{r_u\ h\ s_t\ p^p\ l\ C_{\text{IIIPR}}}{\text{“}III\,ple\text{”}}$ × ♀ +; F_1 ♀ $\frac{r_u\ h\ s_t\ p^p\ l\ C_{\text{IIIPR}}}{}$ × ♂ “*IIIple.*”

r_u h s_t p^p	+	r_u	h s_t p^p	r_u h	s_t p^p	r_u h s_t	p^p	r_u s_t p^p	h	r_u p^p	h s_t	r_u h p^p	s_t	r_u h Re.	r_u h Sd.	h s_t Re.	h s_t Sd.	s_t p^p Re.	s_t p^p Sd.
463	514	210	186	227	226	36	35	26	26	6	13	2	3	26.7	26.0	25.8	16.4	4.8	4.2

To test the further effects of these modifiers, $\frac{r_u\ h\ s_t\ l\ C_{\text{IIIPR}}}{r_u\ h\ s_t\ p^p\ s_s\ e^s}$ flies were crossed to $\frac{l\ C_{\text{IIIPL}}\ p^p\ s_s\ e^s}{r_u\ h\ s_t\ p^p\ s_s\ e^s}$ flies. The result was four kinds of flies: wild-type 227, $r_u\ h\ s_t$ 166, $p^p\ s_s\ e^s$ 194, and $r_u\ h\ s_t\ p^p\ s_s\ e^s$ 162. This is what we would expect from previous results.

One third chromosome then, contains two crossover modifiers which are associated with lethals. One of these genes, $l\,C_{\text{IIIPL}}$ lies in the left end in the region of hairy and restricts crossing over in this end as far as peach and perhaps for a few units to the right of peach. The other modifier, $l\ C_{\text{IIIPR}}$, lies in the right half of the chromosome in the region of sooty. It restricts crossing over in this end as far to the left as spineless and perhaps for some units beyond spineless. The increased crossing over between roughoid and hairy is perhaps best explained by assuming that the modifier lies in the third chromosome of “IIIple.”

As previously stated, the two third chromosomes of lance are not alike. The one which we have just analyzed cuts out nearly all crossing over. When lance is crossed to “IIIple,” half of the F_1 females will have the third chromosomes as follows: $\frac{l}{r_u\ h\ s_t\ p^p\ s_s\ e^s}$. When these females are back-crossed to "IIIple" males, crossing over between all the genes is reduced a small amount, but the section between roughoid and hairy is reduced more than the others, from 26.0 to 18.9 (tables 8 and 9). This type of cross has been made five different times, with results very similar to those in tables 8 and 9. I have been rather reluctant to admit that the

TABLE 8

P_1, ♀ lance × ♂ "IIIple"; F_1 ♀ $\frac{l}{r_u\ h\ s_t\ p^p\ s_s\ e^s}$ × ♂ "IIIple."

Control, ♀ "Texas wild" × ♂ "IIIple"; F_1 ♀ × "IIIple" ♂.

Back-cross types	$r_u\ h\ s_t\ p^p\ s_s\ e^s$	+	r_u	$h\ s_t\ p^p\ s_s\ e^s$	$r_u\ h$	$s_t\ p^p\ s_s\ e^s$	$r_u\ h\ s_t$	$p^p\ s_s\ e^s$	$r_u\ h\ s_t\ p^p$	$s_s\ e^s$	$r_u\ h\ s_t\ p^p\ s_s$	e^s	$r_u\ s_t\ p^p\ s_s\ e^s$	h	$r_u\ p^p\ s_s\ e^s$	$h\ s_t$	$r_u\ s_s\ e^s$	$h\ s_t\ p^p$	$r_u\ e^s$	$h\ s_t\ p^p\ s^S$
l	809	1031	284	249	249	206	20	24	54	94	28	134[4]	1	4	1		26	13	44	12
Control	767	928	353	280	225	207	28	20	74	66	42	117	6	12	4	7	26	18	38	35

TABLE 8 (continued)

$r_u\ h\ p^p\ s_s\ e^s$	s_t	$r_u\ h\ s_s\ e^s$	$s_t\ p^p$	$r_u\ h\ e^s$	$s_t\ p^p\ s_s$	$r_u\ h\ s_t\ s_s\ e^s$	p^p	$r_u\ h\ s_t\ e^s$	$p^p\ s_s$	$r_u\ h\ s_t\ p^p\ e^s$	s_s	$h\ p^p\ s_s\ e^s$	$r_u\ s_t\ p^p$	$h\ s_s\ e^s$	$r_u\ s_t\ p^p\ s_s$	$h\ e^s$	$h\ s_t\ e^s$	$r_u\ s_s$	$h\ s_t\ p^p\ e^s$	$r_u\ h\ p^p$	$s_t\ e^s$	$s_t\ p^p\ e^s$
	2	13	20	33	6		1	1	1	5			2			1		2	1		1	1
2	2	21	31	24	15	6	5	1	5	3	2	1	3	1	1	3	4		1	3	1	1

TABLE 9

Recombination percents computed from table 8.

Crossing-over sections	r_u-h	h-s_t	s_t-p^p	p^p-s_s	s_s-e^s
Total recombinations, *l*	639	539	51	232	270
Percent of recombinations, *l*	18.9	15.9	1.5	6.8	8.0
Total recombinations, "control"	793	558	109	261	293
Percent of recombinations, "control"	23.4	16.4	3.2	7.7	8.6
Standard percentages	26.0	16.4	4.2	10.3	12.2

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[4] At times difficulty has been encountered in the identification of sooty, hence some errors are probably present in the recombination values for the s_s-e^s section. Since I have drawn no conclusions concerning this section the errors in no way obviate my general results. It is possible that sooty intensifiers have caused the trouble.

reductions, except that between roughoid and hairy, were significant, and I am not at all sure that they are. Another reason why I am somewhat skeptical as to these reduced values is that I have crossed "IIIple" to a wild-type strain from Texas and back-crossed the F_1 females to "IIIple" males. This ought to give standard values. The results are given in table 8 as a control. All values are low. It is true, they are slightly higher than those in the cross with lance, but the differences are not large except in the case of the roughoid-hairy section. In the control this value approaches the standard.

Lance was also crossed to $e^s\ r_o\ c_a$ and the F_1 $\frac{l}{e^s\ r_o\ c_a}$ females back-crossed to $e^s\ r_o\ c_a$ males. The results are given in table 10. The recombination values are 17.8 and 10.2, against standard values of 20.2 and 9.6. The e^s-r_o section is slightly low, the r_o-c_a section slightly high. It would seem there were no effects of a modifier upon the extreme right end.

TABLE 10

P_1, ♀ $e^s\ r_o\ c_a$ × ♂ *lance*; F_1 ♀ $\frac{e^s\ r_o\ c_a}{l}$ × ♂ $e^s\ r_o\ c_a$.

$e^s\ r_o\ c_a$	+	e^s	$r_o c_a$	$e^s\ r_o$	c_a	$e^s\ c_a$	r_o	e^s-r_o Re.	e^s-r_o Sd.	r_o-c_a Re.	r_o-c_a Sd.
508	580	136	131	77	75	2	0	17.8	20.2	10.2	9.6

In a further study of this same third chromosome, lance was mated to "IIIple" and the F_1 females back-crossed to "IIIple" males. Some of the F_1 females show crossing over. From this group F_2 males were selected with different sections of the third chromosome from lance. When an F_2 $\frac{r_u\ h\ s_t\ \ ?}{r_u\ h\ s_t\ p^p\ s_s\ e^s}$ male is crossed out to a wild-type female there will be two types of individuals produced, since there is no crossing over in the male. One type will be $\frac{r_u\ h\ s_t\ \ ?}{}$, and it is this type which we mated back to "IIIple" males. The left end of one third chromosome comes from "IIIple," the right end from lance. The other third chromosome comes from the wild stock. This experiment gives a reduced value of 19.8 for the r_u-h section (similar to that of table 8), and an increased value of 21.2 for the h-s_t section (table 11). This h-s_t value is similar to that obtained with $l\ C_{\text{IIIPR}}$ in the absence of $l\ C_{\text{IIIPL}}$ (tables 6 and 7).

When we use the left end of this same chromosome combined with $p^p\ s_s\ e^s$ and $s_t\ p^p\ s_s\ e^s$ we get approximately standard values for p^p-s_s and

TABLE 11

$$P_1,\ ♂\ \frac{r_u\ h\ s_t\quad ?}{r_u\ h\ s_t\ p^p\ s_s\ e^s} \times ♀\ +;\ F_1\ ♀\ \underline{r_u\ h\ s_t\quad ?} \times ♂\ \text{“}III\text{ple.”}$$

$r_u\ h\ s_t$	+	r_u	$h\ s_t$	$r_u\ h$	s_t	$r_u\ s_t$	h	r_u-h Re.	r_u-h Sd.	h-s_t Re.	h-s_t Sd.
338	478	114	137	140	129	9	8	19.8	26.0	21.1	16.4

s_s-e^s (tables 12 and 13). The s_t-p^p region is reduced, but again it is doubtful whether the reduction is significant.

TABLE 12

$$P_1,\ ♀\ \frac{?\quad p^p\ s_s\ e^s}{r_u\ h\ s_t\ p^p\ s_s\ e^s} \times ♀\ +;\ F_1\ ♀\ \underline{?\quad p^p\ s_s\ e^s} \times ♂\ \text{“}III\text{ple.”}$$

$p^p s_s\ e^s$	+	p^p	$s_s\ e^s$	$p^p\ s_s$	e^s	$p^p\ e^s$	s_s	p^p-s_s Re.	p^p-s_s Sd.	s_s-e^s Re.	s_s-e^s Sd.
348	439	60	42	49	61	1	1	10.3	10.3	11.1	12.2

TABLE 13

$$P_1,\ ♂\ \frac{?\ \ s_t\ p^p\ s_s\ e^s}{r_u\ h\ s_t\ p^p\ s_s\ es} \times ♀\ +;\ F_1\ ♀\ \underline{?\ s_t\ p^p\ s_s\ e^s} \times ♂\ \text{“}III\text{ple.”}$$

s_t p^p s_s e^s	+	s_t	p^p s_s e^s	s_t p^p	s_s e^s	s_t p^p s_s	e^s	s_t p^p e^s	s_s	s_t s_s e^s	p^p	p^p s_s	s_t p^p Re.	s_t p^p Sd.	p^p s_s Re.	p^p s_s Sd.	s_s e^s Re.	s_s e^s Sd.
647	831	19	12	126	128	124	168	1	15	1	1	2	1.6	4.2	13.1	10.3	14.9	12.2

As indicated in tables 6 and 7, $l\,C_{\text{IIIPR}}$ in the absence of $l\ C_{\text{IIIPL}}$, seems to increase crossing over between hairy and scarlet; but, as previously stated, this result can be explained by assuming that the modifier is in the "IIIple" strain. In table 11, where we use the right end of the second third chromosome of lance, we get both a decrease in the r_u-h section and an increase in the h-s_t section. Here, then, we get in the same experiment, what seemed to be the effect of $l\,C_{\text{IIIPR}}$, and of a modifier in the other third chromosome of lance. These results would seem to make it practically conclusive that the modifiers lie in the "IIIple" strain and that they are similar in their action to C_{III}-s_t and C_{IIIL}-S.

Considerable difficulty has been experienced in analyzing these crossover modifiers, due to the fact that two wild-type stocks used in outcrosses, and taken in Bloomington at widely different times, have either the same crossover factors or others which have about the same influence. These strains were not the same as lance with respect to these factors, for they give different results when crossed to "IIIple". When lance is crossed to "IIIple" and the F_1 females back-crossed to "IIIple" males, we find there are two types of F_1 females. In one type very little crossing over occurs; in the other, crossing over approaches standard values. When one of these wild-type strains, called B1, is crossed to "IIIple" and the F_1 females back-crossed to "IIIple" males, we again find two types of F_1 females, but they are not the same as in the lance cross. In one type we find very little crossing over in the left end (tables 14 and 15); in the second type very little crossing over in the right end (tables 14 and 15). Evidently the crossover modifiers are in the wild strain and the probability is that we have C_{IIIPL} in one and C_{IIIPR} in the other.

When the second wild-type strain, B2, was crossed to "IIIple" and the F_1 females back-crossed to "IIIple" males, we found there were three kinds of F_1 females. In one group very little crossing over occurs (tables 14 and 15). These results are similar to those obtained when $l\,C_{\text{IIIPL}}$ and $l\,C_{\text{IIIPR}}$ are present. In the second group crossing over is restricted in the right end and increased between hairy and scarlet (tables 14 and 15). The results are similar to those obtained with $l\,C_{\text{IIIPR}}$. In the third group crossover values approach the standard, except possibly between roughoid and hairy, where it is reduced by 4.5 percent (tables 14 and 15).

TABLE 14

+ ♀ (*B1 wild-type stock*) × ♂ "*IIIple*"; F_1 ♀ × ♂ "*IIIple.*"
+ ♀ (*B2 wild-type stock*) × ♂ "*IIIple*"; F_1 ♀ × ♂ "*IIIple.*"

Back-cross types	r_u h s_t p^p s_s e^s	+	r_u	h s_t p^p s_s e^s	r_u h	s_t p^p s_s e^s	r_u h s_t	p^p s_s e^s	r_u h s_t p^p	s_s e^s	r_u h s_t p^p s_s	e^s	r_u s_t p^p s_s e^s	h	r_u p^p s_s e	h s_t
B1, CL	178	180					2	1	9	30		41				
B1, CR	331	538	147	189	110	123	11	12		1			8	12	6	6
B2, CL CR	652	888					2	2	1	7						
B2, CR	533	657	261	195	233	220	37	43	9	12			8	10	12	8
B2,	484	470	146	178	123	138	20	17	49	58	40	76	7	11	3	2

TABLE 14 (continued)

r_u s_s e^s	h s_t p^p	r_u e^s	h s_t p^p s_s	r_u h p^p s_s e^s	s_t	r_u h s_s e^s	s_t p^p	r_u h e^s	s_t p^p s_s	r_u h s_t s_s e^s	p^p	r_u h s_t e^s	p^p s_s	r_u h s_t p^p e^s	r_u s_t p^p	h s_s e^s	r_u s_t p^p s_s	h e^s
				1								2		4				
				3	1													
6	7	6		8	11	3	8	1	6	2	2	8	1	2				
19	18	20	14	3	3	14	13	24	16	2	2	2	3	7	2	1	1	1

TABLE 14 (continued)

r_u p^p s_s	h s_t e^s	r_u s_t	h p^p s_s e^s	h s_t p^p e^s	h s_t s_s e^s	r_u h p^p	h s_t e^s	r_u p^p	r_u s_s	s_t p^p e^s	p^p e^s	r_u s_t p^p e^s	h p^p
		1	1	1		1	1			5		1	1
1	2			2	1			1	1	1	1		1

TABLE 15

Recombination values computed from table 14.

Crossing-over sections	r_u-h	h-s_t	s_t-p^p	p^p s_s	s_s-e^s
Total recombinations, B1, CL	0	1	6	39	47
Percent of recombinations, B1, CL	0.0	0.2	1.3	8.7	10.4
Total recombinations, B1, CR	368	257	39	1	0
Percent of recombinations, B1, CR	24.5	17.1	2.6	0.06	0.0
Total recombinations, B2, CL CR	0	0	4	8	0
Percent of recombinations, B2, CL CR	0.0	0.0	.25	.51	0.0
Total recombinations, B2, CR	519	518	137	60	31
Percent of recombinations, B2, CR	22.3	22.3	5.9	2.5	1.3
Total recombinations, B2	434	359	64	193	212
Percent of recombinations, B2	21.7	17.9	3.2	9.6	10.6
Standard percentages	26.0	16.4	4.2	10.3	12.2

In an attempt to see whether the modifiers present in lance have any effect upon crossing over in the second chromosome, lance was mated to black, purple, curved, plexus, speck, and the F_1 females back-crossed to $b\ p_r\ c\ p_x\ s_p$ males. The results of this cross are given in table 16, cross A. The recombination values for b-p_r, $p_r\ c$, and c-s_p are 9.6, 23.5 and 25.5, against standard values of 6.0, 21.0 and 31.5. The first two values are high, the third one low. I doubt whether the differences are significant. By using Doctor MULLER's stock of $\frac{l\,C_{\mathrm{IIIPL}}\ l\,C_{\mathrm{IIIPR}}}{r_u\ hs_t\ p^p\ s_s\ H e^{s}}$, it was possible to test the effects of $l\,C_{\mathrm{IIIPL}}$ and $l\,C_{\mathrm{IIIPR}}$. This stock was crossed to $b\ p_r\ c\ p_x\ s_p$ and the F_1 not-hairy females back-crossed to $b\ p_r\ c\ p_x\ s_p$ males. The results are given in table 16, cross B, and the percentages of recombination approach very closely standard values. They are 4.6 against 6.0; 22.8 against 21.0; and 33.5 against 31.5. It would seem there was certainly no influence here, and no conclusive evidence in the former case.

TABLE 16

Cross A. F_1 ♀ $\frac{l\,C_{\mathrm{IIIPL}}\ l\,C_{\mathrm{IIIPR}}}{}\ \frac{b\ p_r\ c\ s_p}{}$, *or* $\frac{}{l}\ \frac{b\ p_r\ c\ s_p}{}$ × ♂ $b\ p_r\ c\ s_p$.

Cross B. F_1 ♀ $\frac{l\,C_{\mathrm{IIIPL}}\ l\,C_{\mathrm{IIIPR}}}{}\ \frac{b\ p_r\ c\ s_p}{}$ × ♂ $b\ p_r\ c\ s_p$.

Back-cross types	$b\ p_r\ c\ s_p$	+	b	$p_r\ c\ s_p$	$b\ p_r$	$c\ s_p$	$b\ p_r\ c$	s_p	$b\ c\ s_p$	p_r	$b\ s_p$	$p_r\ c$	$b\ p_r\ s_p$	c	$b\ c$	$p_r\ s_p$	$b\ p_r$ Re.	$b\ p_r$ Sd.	$p_r\ c$ Re.	$p_r\ c$ Sd.	$c\ s_p$ Re.	$c\ s_p$ Sd.
Cross A	425	522	63	41	199	187	195	263	3	14	26	39	43	50	7	9	9.6	6.2[5]	23.5	19.9	25.5	30.2
Cross B	466	682	39	8	113	215	225	322	7	2	20	22	50	125	15	1	4.6	6.2	22.8	19.9	33.5	30.2

To test whether there were any effects upon crossing over in the first chromosome, lance was also crossed to a stock having the first-chromosome characters eosin and miniature, and the F_1 females were back-crossed to eosin miniature. The result was 31.3 percent of recombination against the standard value of 33.2 (table 17). There was no effect on this region of the first chromosome.

TABLE 17

P_1, ♀ *lance* × ♂ *eosin miniature*; F_1 ♀ × ♂ *eosin miniature*.

$w^e m$	+	w^e	m	$w^e m$ Re.	$w^e m$ Sd.
413	395	166	203	31.3	32.2[6]

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[5] The standard percentages were taken from table 140, page 298, of BRIDGES and MORGAN (1919).

[6] This standard recombination percentage was taken from table 65, page 84, of MORGAN and BRIDGES (1916).

At the beginning it was taken for granted that the gene for lance was in the third chromosome. Tests with star dichaete, however, show it to be in the second. Lance was mated to *S D*, and the F_1 *S D* males backcrossed to lance females. The result was 286 *S D* flies, 116 *D* lance, 158 lance, and 178 *S*. No attempt was made to locate lance within the chromosome. Because of the great variability of lance and the fact that these variations when inbred do not breed true, leads me to suspect that lance may be due to more than one gene.

When lance is mated to wild-type flies from stock and the F_1 flies inbred we do not get a 3 : 1 ratio. By actual count we obtained 1923 wild-type flies to 240 lance, a ratio of 8 : 1. This extreme ratio may be due, in part, to failure to recognize all lance flies; to the poor viability of lance; or again if lance is the effect produced by several genes, to the separation of these genes.

SUMMARY

1. Lance is a second-chromosome character and highly variable. The wing is pointed.
2. One of the third chromosomes of lance carries two crossover modifiers, C_{IIIPL} and C_{IIIPR}, each associated with a lethal. $l\,C_{IIIPL}$ lies in the region of hairy and scarlet and restricts crossing over in the left half of the chromosome. $l\,C_{IIIPR}$ lies in the region of ebony and restricts crossing over in the right half. The high h-s_t value obtained with $l\,C_{IIIPR}$ can be best explained by assuming the presence of a modifier in the third chromosome of "IIIple."
3. The second third chromosome of lance may carry a crossover modifier which reduces the roughoid-hairy value from 26.0 to 18.9. The change is perhaps better explained by assuming the crossover modifier to be in the left end of the third chromosome of "IIIple." The reduced values in other regions are of doubtful significance. There is a lethal gene in this chromosome.
4. The modifiers produce no noticeable effect upon crossing over either in the first or second chromosomes.
5. Because the two third chromosomes carry different lethals, and also linkage modifiers that prevent these lethals from crossing over with another, the stock is maintained as a balanced lethal stock.
6. In the original stock C_{IIIPL} and C_{IIIPR} were not associated with lethals.

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