CHAPTER VII

CROSSING OVER

THE correlative aspect of linkage is crossing over, and inasmuch as it involves a change in the mechanism that gives linkage, it is entitled to rank as one of the fundamental principles of heredity.

In the illustration of complete linkage given in the preceding chapter, the cases chosen were ones in which entire chains of genes remained intact during the reduction divisions. The male of *Drosophila* exhibits this phenomenon, as does also the female of the silk-worm moth. On the other hand, there is an interchange of blocks of genes between homologous pairs of chromosomes in other cases, as in the females of *Drosophila,* in the males of moths and fowls, and in both egg-cells and sperm-cells of the plant *Primula.*[1] This interchange is called crossing over, and the evidence shows that it is not haphazard, but gives numerical results of extraordinary constancy. A few examples will suffice to illustrate crossing over.

When a black fly with vestigial wings is crossed to a wild-type ("gray") fly with long wings (Fig. 33) the offspring are, as we have already seen, "gray," long. If one of the F_1 *females* is back-crossed to a black vestigial male there are four kinds of offspring produced, *viz.,* the two original combinations, black vestigial, and gray long; and in addition two recombinations of these, *viz.,* black long, and gray vestigial. The two latter classes are called the crossover classes, or more briefly, crossovers. The percentage of crossovers is definite for a given stock,

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[1] Crossing over in both sexes in the rat has been reported by Castle and Wright, and in the male and female grasshopper by Nabours.

of a given age and under given environmental conditions. In this case the percentages are as follows:

Non-crossovers		Crossovers	
Black vestigial	Gray long	Black long	Gray vestigial
41.5 per cent	41.5 per cent	8.5 per cent	8.5 per cent
83 per cent		17 per cent	

If a pair of chromosomes in the F_1 fly is represented as carrying the genes of the characters here involved, one member of such a pair carries both a gene for black and a gene for vestigial (Fig. 36); the homologous member of the pair of chromosomes carries both of the normal allelomorphs, *viz.*, a gene for gray and a gene for long wings. When crossing over takes place so that a gene for black goes over into the other chromosome, the converse phenomenon takes place, a gene for gray goes over into the chromosome that gave up its black gene. It is the constancy of this interchange that makes the phenomenon reducible to exact mechanical treatment.

The interchange is independent of the way in which the genes enter the cross. For example, if a black long-winged fly is crossed to a gray vestigial fly (Fig. 37), the F_1 offspring will be, as before, gray long. If an F_1 female (gray long) is back-crossed to a black vestigial male, there will be four kinds of offspring, namely, the two original combinations black long, and gray vestigial; and the two crossover combinations, black vestigial, and gray long, in the following proportions:

Non-crossovers		Crossovers	
Black long	Gray vestigial	Black vestigial	Gray long
41.5 per cent	41.5 per cent.	8.5 per cent	8.5 per cent
83 per cent		17 per cent	

The interchange in the last cases is in the reverse order of that in the first case, but it is numerically identical. In other words, it makes no difference whether the gene for black and for vestigial enter the cross together, *i.e.*,
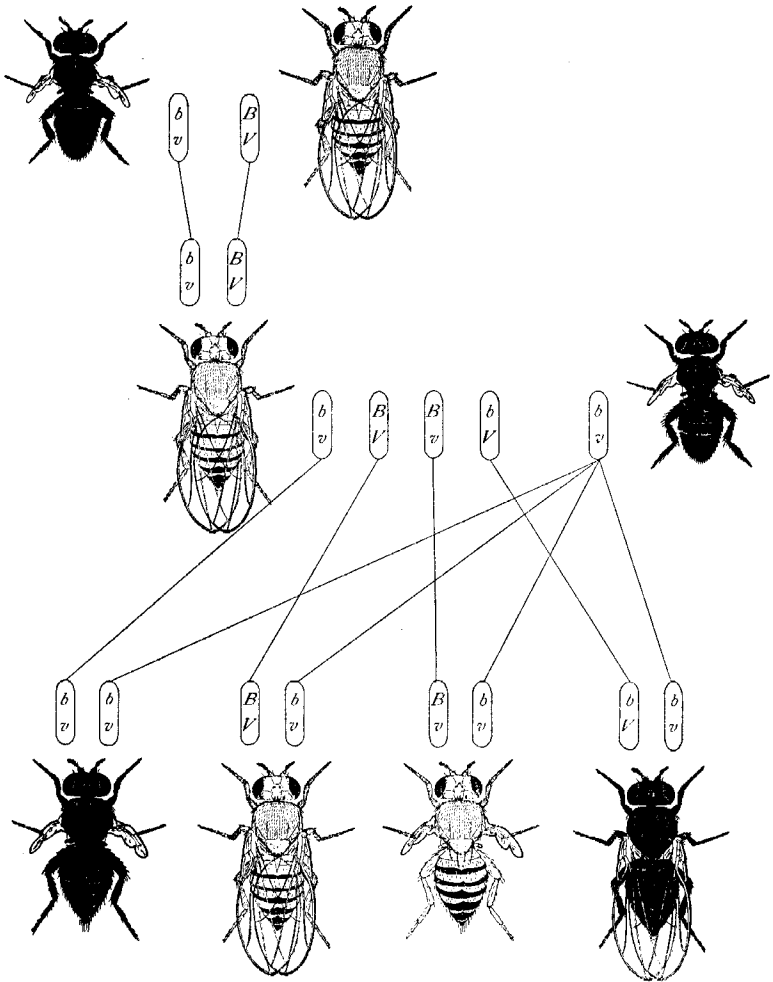
Fig. 36.—Back-cross of F_1 female (out of black vestigial by wild) to black vestigial male.

in the same chromosome, or whether they enter the cross in opposite chromosomes—their likelihood of interchange is exactly the same. If the F_1 male had been back-crossed (Fig. 34) only two kinds of offspring would have been
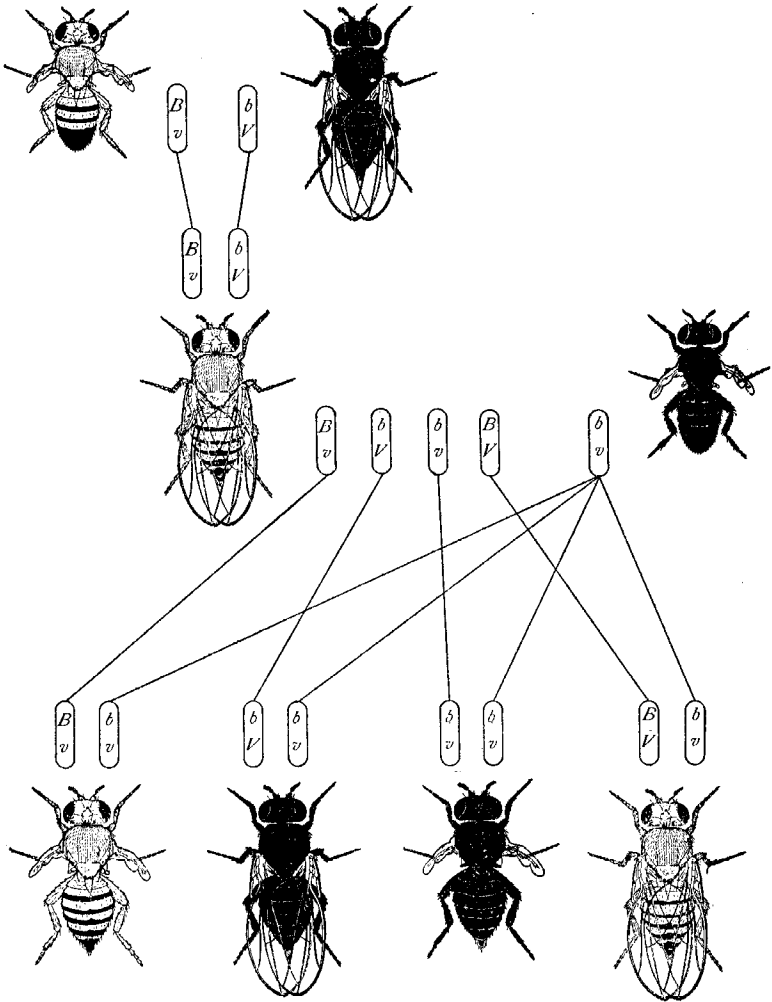
Fig. 37.—Back-cross of F_2 female (out of gray vestigial by black) to black vestigial male.

produced because, as was shown, there is no crossing over in the male.

It should be pointed out here, that the interchange (or crossing over) can of course only be recorded when two

òr more pairs are involved, for, obviously, unless a character that enters the cross comes in with some other known one that is recognizable as such, there is no way of determining whether interchange between the homologous chromosomes has taken place. As will be pointed out later, there is every reason to suppose, and practically a demonstration of the fact, that the interchange goes on irrespective of the presence of other genes by which it can be observed.

Experiments with different pairs of characters show that for each two pairs there is a definite numerical ratio. For instance, if a female fly with yellow wings and white eyes is crossed to a fly with gray wings and red eyes (wild type) the daughters will have gray wings and red eyes (wild type). If the F_1 female is back-crossed to a male with yellow wings and white eyes, four classes of offspring will be produced in the following proportions:

Non-crossovers		Crossovers	
Yellow white	Gray red	Yellow red	Gray white
49.5 per cent	49.5 per cent	0.5 per cent	0.5 per cent
99 per cent		1 per cent	

Here, crossing over takes place in only one case out of a hundred. If the characters enter in a different combination, viz., yellow red and gray white, the crossover percentage is the same as before, viz.,

Non-crossovers		Crossovers	
Yellow red	Gray white	Yellow white	Gray red
49.5 per cent	49.5 per cent	0.5 per cent	0.5 per cent
99 per cent		1 per cent	

Another combination of white eyes with a different character shows a different linkage. If a female fly with white eyes and miniature wings is crossed to a male with red eyes and long wings (wild type), the F_1 daughters will have red eyes and long wings. If one of these F_1 females

is back-crossed to a white miniature male the four classes
of offspring appear in the following proportions:

Non-crossovers		Crossovers	
White miniature	Red long	White long	Red miniature
33.5 per cent	33.5 per cent	16.5 per cent	16.5 per cent
67 per cent		33 per cent	

Here crossing over takes place in 33 out of 100 flies,
whereas in the former crosses between white eyes and
another mutant character (yellow) crossing over took
place only once in a hundred times. Based on these
numerically different ratios of crossing over, and on other
related phenomena, a theory of crossing over has been
formulated that will be discussed later. For the present
we are concerned only with the data.

When more than two pairs of characters are involved
new phenomena of crossing over make themselves evident.
Some of these are more related to principles that are dis-
cussed in later chapters, but a few results may be pointed
out here. When, for example, three pairs are involved,
two may cross over, while the third does not. A female
with white eye color, miniature wings, and forked bristles
crossed to a wild-type male gives wild type in F_1. An
F_1 daughter back-crossed to a white miniature forked male
will give, in the next generation, not only the two original
combinations but recombinations also. As we have seen,
33 per cent. of all the offspring will be crossovers between
white and miniature; there will also be 20 per cent. of
crossing over between miniature and forked. In other
words, there will be both red miniature and white long
flies, and there will also be crossovers between white and
miniature, *i.e.*, miniature wings straight spines, and long
wings forked spines. It follows that there may also be
cases in which crossing over has taken place between both
of the above combinations at the same time (Fig. 38),
that is, there will be some flies that are white long-winged
and forked and others that are red miniature and straight

spines. A list of these classes with the expectation based on the results from a single experiment is given below.

Non-crossover	Single crossover		Double crossover	
$\begin{cases} w\ m\ f\ \ \ 23.2 \\ W\ M\ F\ 23.2 \end{cases}$	in 1st region	$\begin{cases} w\ M\ F\ 13.2 \\ W\ m\ f\ \ 13.2 \end{cases}$	in both regions	$\begin{cases} w\ M\ f\ \ 3.3 \\ W\ m\ F\ 3.3 \end{cases}$
	in 2nd region	$\begin{cases} w\ m\ F\ \ \ 6.7 \\ W\ M\ f\ \ \ 6.7 \end{cases}$		

Inasmuch as this subject and certain peculiarities in the results can be better understood after the evidence for
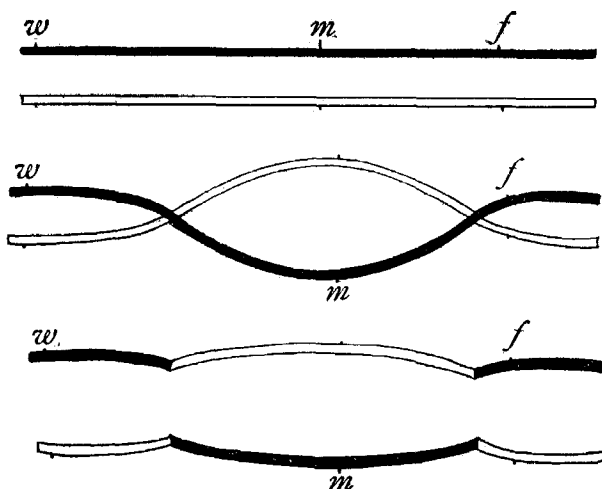

FIG. 38.—Scheme to illustrate double crossing over between white and forked. The gene for miniature standing between furnishes the evidence.

the linear order of the genes has been discussed, I shall not press further the discussion here. It should be pointed out, however, that the question of crossing over involves more than the independent action of the pairs in the cases so far considered; for, as will be shown later, when crossing over takes place not single genes but great groups of genes are involved. This block effect, as it may be called,

is not in evidence unless a larger number of genes than two is studied in the same experiment. These questions will be discussed in Chapter IX.

For the purpose of clearer exposition I spoke of linkage, in the preceding chapter, as though the term should be limited to cases where all the genes of a group hold together, and have used the term crossing over to mean the breaking of the group in one or more pairs. As a matter of fact, it is not desirable to emphasize this sharp distinction. There is, however, a real distinction that lies behind the phenomena. In the male of *Drosophila* there is no crossing over at all between homologous chromosome groups, while in the female there is crossing over between the pairs of chromosomes. The cases of the male and female are, therefore, on a different footing here.

We speak of pairs of characters as being loosely linked, meaning that crossing over of genes frequently takes place, and as strongly linked when crossing over is very infrequent. We have seen that yellow and white break apart only once in 100 times. If characters (or the genes) were still more closely linked, they might break only once in a thousand times, and if closer still once in many thousand times, in which case they would appear to be completely linked for all practical purposes. Such a gradation, however, does not appear to be the case, but the lower limit of crossing over seems to be well within the range of human capacity to detect. This means probably that there is a limiting value for crossing over, and if this can be established it may give us the lower limit of size of the gene (in terms of chromosome length), or at least it may allow us to form some idea as to how many genes are present in the hereditary material.

In this same connection it has been suggested that when more than two allelomorphs occur, we may be dealing only with close or even absolute linkage. For instance, suppose in a white-eyed race of flies a mutation should take place in a gene so closely tied up in some way to the

gene for white that the two never separated, and suppose
the new mutation affected the eye so that its effect could
be observed (for if not the change would not concern us).
The new mutation would behave towards white in the
same way as do all pairs of allelomorphs and yet in a
strict sense is not allelomorphic.   It is not necessary to
elaborate here this idea, because fortunately in the case
of *Drosophila* there is strong evidence to show that multi-
ple allelomorphs do not arise in this way.   The evidence
for this statement will be given in Chapter XVII.