CHAPTER VI

LINKAGE

Mendel's *results involving two or more pairs of characters* led to the conclusion that distribution of the members of one pair of genes is independent of the distribution of the members of other pairs. This process may be called free or independent assortment, and is what is expected if each pair of genes is carried by a different pair of chromosomes. If this rule held for all pairs of characters then there could be no more pairs that assorted independently than there were pairs of homologous chromosomes. On the other hand, if the chromosomes carry the genes we should anticipate from what we have found out concerning the individuality of the chromosome, and from what we know concerning the large number of inherited characters, that many of these factors must be carried in the same chromosome. If this is true, then Mendel's second law can have only a very limited application.

As our information about the mode of inheritance of characters has widened, the number of cases in which free assortment does not occur has steadily increased. Many characters have been found to keep together in successive generations. This tendency to keep together rather than to assort freely is called linkage. The most extreme cases are those where characters hold together completely; at the other extreme are those that show only a slightly greater probability of holding together than of assorting freely. Between these extremes all intermediate degrees of linkage are found. For the sake of simplicity, cases of complete linkage will be dealt with in this chapter; the others will be taken up in the next chapter.

If a fly (*Drosophila*) with two recessive mutant characters, black body color and vestigial wings (Fig. 33), is mated to a fly with wild-type body color and long wings, the offspring (F_1) are wild type. If one of the F_1 *sons* is back-crossed to a black vestigial female from stock,

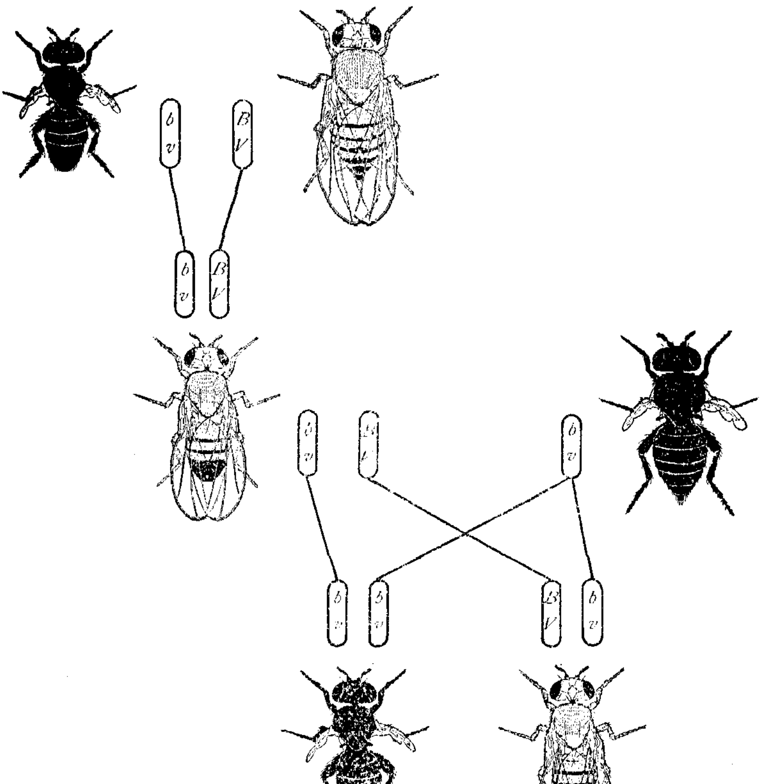

FIG. 33.—Back-cross of F_1 male (out of black vestigial by wild), to black vestigial.

the offspring (F_2) are of two kinds only, half are black vestigial, and the other half are wild type. In other words, the two mutant characters that went in together, black and vestigial, have come out together; and their two normal allelomorphic characters, wild-type body color and long wings, have also come out together. There are no F_2 flies that are black and long, and none that are vestigial and gray, as would be the case if independent assortment took place.

In the diagram (Fig. 33) the results are worked out on the chromosome theory. The genes for black (*b*) and for vestigial (*v*) are represented as carried by the same chromosome (*bv*); the homologous chromosome of the wild-type fly carries the normal allelomorphic genes (*BV*). In F_1, one of each of these two chromosomes is present, and the fly is normal because the two normal allelomorphs are dominant. In the F_1 male these two chromosomes (*bv* and *BV*) separate at the reduction division of the germ-cells, one going to each gamete. If this F_1 male is mated to a black vestigial female, all of whose eggs carry genes for black and for vestigial, the offspring should reveal the composition of the gametes of the F_1 male, since the eggs of the black vestigial fly, containing only two recessive factors, will not cover up the effects of the factors contained in the gametes of the F_1 male.

Unless we knew that the two characters black and vestigial are distinct mutant characters, the preceding experiment would not necessarily show that the characters are linked, because the same result would have followed if black and vestigial were both due to the effect of a single gene. Other experiments, however, show that they are independent characters.

It is interesting to compare the preceding cross with another in which black comes in from one parent, and vestigial from the other. For instance, if a black fly with long wings is crossed to a wild-type fly with vestigial wings (Fig. 34), the F_1 offspring will be wild type both in their color and in their wings, because the black fly brings in the normal allelomorph of vestigial, and the vestigial fly brings in the normal allelomorph of black. If the F_1 sons are back-crossed to black vestigial females, the offspring are of two kinds only, namely, black long, and wild-type color vestigial. The combinations that went into the cross together have come out together. The diagram,

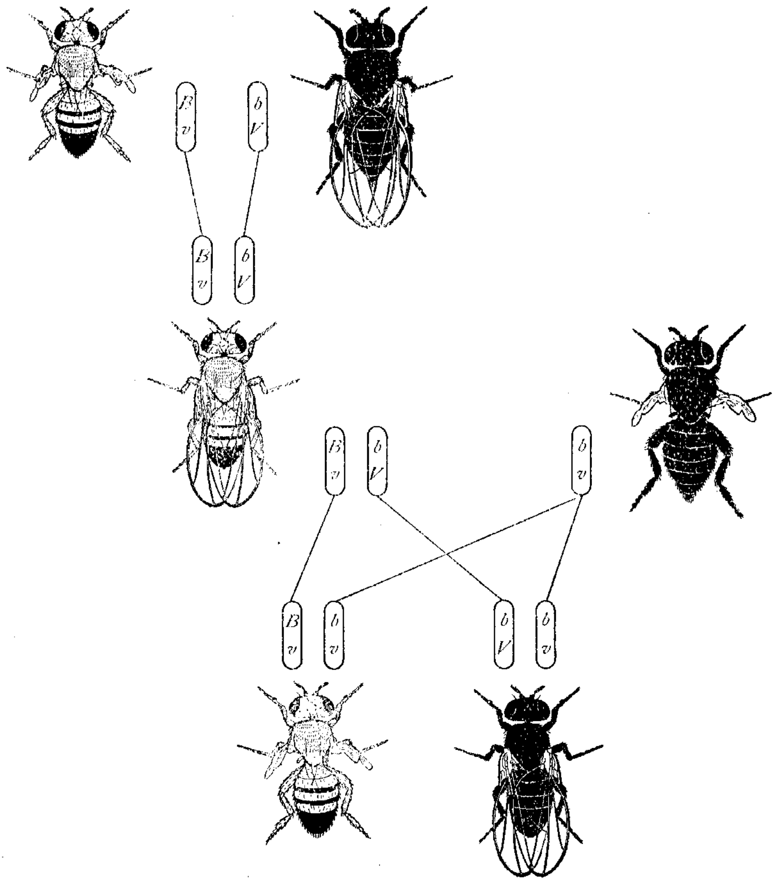

FIG. 34.—Back-cross of F_1 male (out of gray vestigial by black) to black vestigial.

based on the chromosomes, shows that the genetic results, as before, follow the chromosome behavior, provided there has been no interchange of genes in the male.

For the sake of simplicity only two linked factors were utilized in the preceding cases. Three, four, five, or, theoretically, any number of characters may show this relation to each other. Thus there is a stock of *Drosophila* with five linked mutant characters, namely, black, purple, curved, plexus, speck. In a back-cross, like the one above, all the mutant characters, if they went in together, will come out together in half of the second generation (back-cross) flies, and their wild type allelomorphic characters in the other half.

There is another way in which linkage may be very simply illustrated. There are certain characters, called

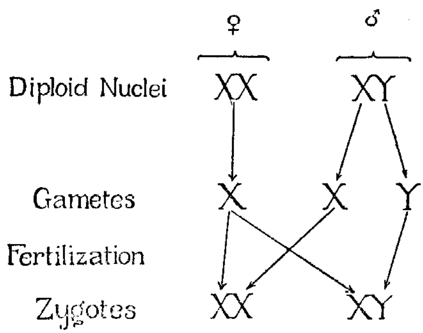

FIG. 35.—Scheme showing the inheritance of the sex-chromosome in *Drosophila*.

sex-linked characters, because their factors follow the sex-chromosomes, or may be said to be carried by them or to be in them. Now in *Drosophila*, the female has two *X*-chromosomes (Fig. 35), the male one *X* (and a *Y*). After reduction the eggs have each one *X* chromosome. Any such egg fertilized by a *Y*-bearing sperm will produce a male (*XY*), as shown in the scheme above. The single X-chromosome that this male gets is therefore from his mother. If her *X*-chromosome carried sex-linked factors, these should be present in the son. Such, in fact, is the case. For example, a female *Drosophila* with yellow wings and white eyes mated to a wild-type male will produce wild-type females, and yellow white-eyed sons (like the mother). Here the son gets his sex-linked characters from his mother, since his only *X* is derived from her. Experiments have shown that this holds for any number of sex-linked characters that are present in the mother.*

Linkage has been demonstrated in a number of animals and plants. The first case discovered was in sweet peas. Bateson and Punnett (1905) found that when purple flowers and long pollen grains went in from one parent, and red flowers and round pollen went in from the other parent, they tended to come out together more frequently than would be expected on the two-factor ratio, 9 : 3 : 3 : 1. In the case of these sweet peas the linkage is not complete, apparently not in either sex. At present two different linkage groups are known in sweet peas, one made up of three linked characters, and the other of three, possibly four. In the edible or garden pea there are two linked characters, and two that are doubtful (Bateson and Vilmorin, White). Mendel did not happen to make any combinations of linked characters in this form, hence he got free assortment. In the primrose (*P. sinensis*) there is a group of five linked characters (Gregory, Altenburg); in the snapdragon a group of five (Baur); in stocks a group of three or four (Saunders). In the groundsel (*Senecio vulgaris*) there are two linked characters known; other cases occur in corn (Lindstrom), tomatoes (Jones), wheat (Engledow), oats (Surface), œnothera (DeVries, Muller). In animals the largest number of linked characters is found in the vinegar fly, *Drosophila melanogaster,* in which there are four groups—a sex-linked group containing about 100 characters, a second group containing 75 characters, and a third group containing about 60 characters, and a fourth group of two characters. In other species of *Drosophila,* linked characters (other than sex-linked) are beginning to be reported as more characters are studied (Metz in *D. virilis,* Warren

* A reservation for crossing over in a heterozygous mother must be added to this statement.

in *D. busckii*, Sturtevant in *D. repleta*). Nabours has found a case in one of the grouse locusts, and Castle and Wright in rats. In the silk-worm moth, Tanaka has found one group of linked characters. In poultry Goodale has found one case. In the moths and poultry it appears that linkage is complete in the female, incomplete in the male. In this respect the situation is the reverse of that in *Drosophila*. There are some other cases where linkage is suspected but uncertain.

The fact that relatively so few cases of linkage have been as yet reported is due in part to the fact that in most species the heredity of only a very few characters is generally known. Where more are known each has as a rule not been examined in relation to all the others, so that even if some of the factors were linked it would not have been found out. Furthermore, in Mendelian crosses, the practice of mating F_1*'s* instead of back-crossing, tends to conceal the linkage phenomena if present. The fact of greatest significance, however, is that the number of cases of linkage is steadily increasing as the inheritance of more characters in each species is becoming known.