CHAPTER XI

LIMITATION OF THE LINKAGE GROUPS

IT may be questioned whether we are at present justified in speaking of the limitation of the linkage groups to the number of chromosome pairs as one of the fundamental principles of heredity, since the only species in which a correspondence that is numerically significant between the two has been proved is *Drosophila melanogaster*. But despite the absence of other positive evidence, the fact that in no other animal or plant does the number of linkage groups exceed the number of the chromosome pairs, may be, I think, legitimately interpreted in favor of the view.

It may also be argued, that if the phenomena of linkage are assumed to be due to the genes being carried by the chromosomes, it follows that there could be no more groups of linked genes than there are chromosome pairs; hence one relation is the direct outcome of the other. But the proof of the linear order that has been developed here rests directly on the linkage data, and is independent of any assumption concerning the chromosomes. It has been shown, secondarily so to speak, that the chromosomes fulfill all the requirements of the abstract reasoning from the data, and therefore give a mechanism capable of performing all that the theory demands. The demonstration, then, that in *Drosophila* the linkage groups correspond in number to the chromosome pairs may be taken as a conclusion or a discovery independent of the other relations furnished by linkage. If then, as I anticipate will be the case, further work in other groups should show that the same relation holds everywhere, we should be fully warranted in stating the result as one of the general principles of heredity.

In *Drosophila melanogaster* the evidence is now very strong in favor of the identity in number of linkage groups and chromosome-pairs. As the new characters coming up, one after the other, have continued to fall into the four known groups, and as something like 200 characters have been so placed, and as none of them has failed to show linkage with one of the four established series, the probability is enormously in favor of a causal relation between the two events, especially in the light of the evidence from other sources that the chromosomes are the bearers of the hereditary factors—evidence from the sex-chromosomes, for example.

The only other species in which the heredity of known mutant characters approaches that of the chromosome group is the garden pea in which about 35 mutant factors have been studied. From the summary of what has been so far recorded, as well as from the results of his own work, White has recently given an account of what is fairly well established. Of the 35 mutant factors in this pea, seven independently inherited groups have been recorded, *i.e.*, each one of seven factors has been tested out and found to assort independently of the other six. There are seven pairs of chromosomes in the edible pea (Fig. 53, *a*). The agreement between the two is to date perfect. It is, of course, possible that the linkage between some of the factors tested was so loose that they appeared to give free assortment, and that until more factors have been studied the evidence is not above suspicion. Nevertheless, it is important to find that the number of independent mutant factors in *Pisum sativum* does not exceed the number of chromosome pairs.

White's study of the linkage of factors in the edible peas shows further that there are four linkage groups—three of them include factors that are also included in those that freely assort. It is fair, perhaps, to conclude that four of the possible seven-linked groups have been found. There are no other forms known in which the

number of linkage groups approaches so near the number of the chromosome pairs. In the snapdragon, Baur has described two linked groups. He states that there are 16 pairs of chromosomes. In wheat one linked group has been described. There are 8 pairs of chromosomes (Fig. 53, *b*). In Indian corn there appear to be a few linkage groups, and probably 10 pairs of chromosomes. In oats, Surface finds two linked genes. In *Primula* there is one group composed of several linked genes, and 12 pairs of chromosomes (Fig. 53, *c*).

In the silkworm moth one linked group of genes has been found by Tanaka, and Yatsu records (Fig. 55) 20 pairs of chromosomes. In *Drosophila virilis* three linked groups of genes have been found by Metz, who has also

FIG. 53.—Haploid chromosome group of pea, *a*, wheat, *b*, and primula, *c*.

described six pairs of chromosomes for this fly. In *Drosophila busckii* there is one group of linked genes and four pairs of chromosomes. In *D. repleta* one group, and six pairs of chromosomes. The groups of chromosomes in some of the different species of *Drosophila,* as described by Metz, are shown in Fig. 54. As indicated by the arrangement of the figures (that correspond fairly closely with the actual arrangement of the chromosome in the cells themselves) it appears that one pair of chromosomes in one species is at times represented by two pairs in related species, and this view is borne out by the attachment of the spindle fibre to the middle of the chromosomes in the bent pairs, but to the inner ends of the two that supposedly correspond to its halves in other species.

In the mouse one group of linked genes has been reported. There are 20 pairs of chromosomes (Fig. 55, *b*). In man no linked genes are known, if we do not count sex-

lined genes, which must, however, if carried by the sex-chromosomes, be linked to each other. The number of chromosome pairs in man is, according to Guyer, 12 (Fig. 55, *c*), but Winewarter describes 24 pairs (Fig. 55, *d*). The difference would seem to be due to technic, rather than to differences in different races of men.
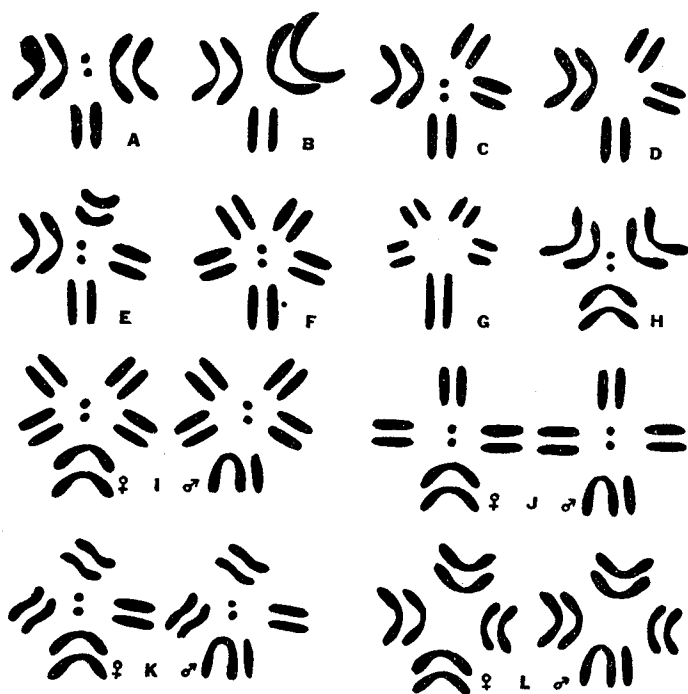

Fig. 54.—Types of chromosome groups found in *Drosophila*. A-H female groups; I-L female and male groups. In A, C, F, I, J, K, and L, the X-chromosome can be identified, because, in the male (After Metz), the Y-chromosome has a different shape from the X.

It should be emphasized that it is to be expected for new types that the number of characters that may seem to give independent assortment will be found at first greater than the number of chromosomes, because wherever two genes in the same chromosome are far apart they will appear to assort independently until the discovery

of intermediate genes shows their true relation. This will be especially the case when crossing over occurs in both sexes; when it occurs only in one sex, the linkage relations are more quickly determined. Moreover, in some cases where several genes are known the mutant characters have not yet been tested out against each other but against different ones. Such information does not furnish the data that are needed.
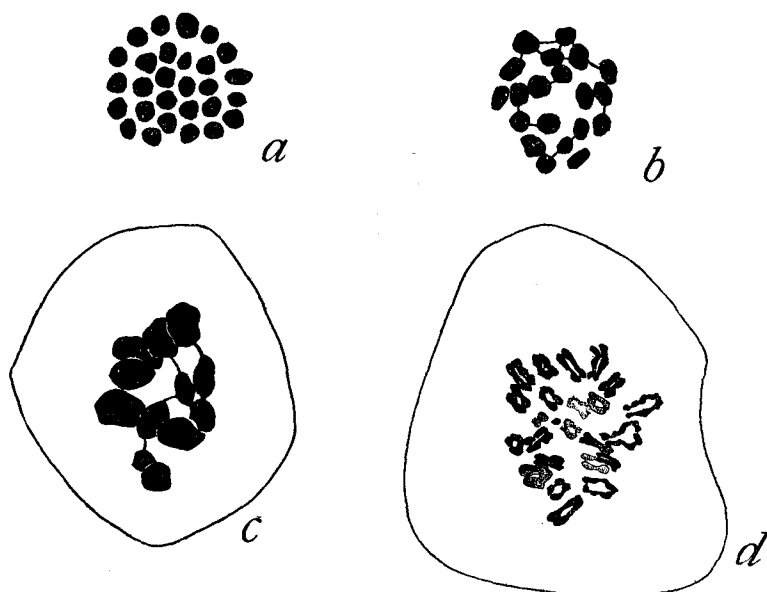

Fig. 55.—Haploid group of chromosomes of the silkworm moth (Yatsu) *a*. Haploid group of chromosomes of mouse (Yocom) *b*. Haploid group of chromosomes of man (Guyer), *c* and (von Winniwarter) *d*.

There are several forms in which there are two or more chromosomes that come together in a group at the time of segregation and move collectively to one pole. Such groups should be expected to count as a single chromosome so far as segregation is concerned, although the crossing over relations may turn out to be something different from anything as yet known.

An extension of the principle of agreement of linkage groups and chromosomes (if they are thought of only as a linear order of genes) is found in the case of "duplication" described by Bridges, where a short series of linked genes appears to lie at one end of the regular series, duplicating their number for this region of the chromosome. Obviously this is not to be looked upon so much as an exception to the principle but rather as a special case due to an accidental change in the mechanism. The number of linkage groups is not changed, but one of them has its genes duplicated for a short part of its length.