a major fraction of an artificial quota, scaled up or down from the true quota to meet the requirements of the computation.)

The *d'Hondt method*, originated in Belgium and now widely used in European elections, employs "multipliers" 1, 1/2, 1/3, 1/4... and can be shown to favor the larger states to the extent of violating all four of the conditions expressed in our Fundamental Principle.

[2] If one should try to minimize the *sum of the squares* (or the sum of the absolute values) *of the deviations of the a's themselves* from their true values (with or without "weighting" by the population of the state), the resulting methods would all lead to an Alabama paradox. The same is true of the weighted sum of the absolute values of the deviations of a/A (or of A/a). The same is also true of the absolute values of the logarithms of the ratios between the a'S and their true values.

[3] This Postulate III was added on April 23, after Professor F. W. Owens had shown (at the meeting of the American Mathematical Society on February 26) that the method of minimizing the sum of terms like $A[(a/A) - (\alpha/A)]^2$ leads to th same result as the Willcox method of major fractions. It may be noted that the method of minimizing the sum of terms like $a[(A/a) - (A/\alpha)]^2$ leads, not as one might expect, to the method of the harmonic mean, but to the method of the geometric mean.

CURRENT MAPS OF THE LOCATION OF THE MUTANT GENES OF DROSOPHILA MELANOGASTER[1]

BY CALVIN B. BRIDGES

COLUMBIA UNIVERSITY, N. Y.

Communicated by T. H. Morgan, December 5, 1920

The maps that have been published[2] showing the distribution of the mutant genes of D. melanogaster can now be much improved because of the discovery of new mutants and the accumulation of crossover data. Figure 1 gives in simplified form the maps that are in use in our laboratory.

The distances on the maps are based on the total amount of crossing over between the loci, one unit of distance representing one per cent of crossing over. The map-distances are the same as the observed crossover values or "percentages of exchange" whenever the two loci considered are so close together that no, or only a negligible amount of, double crossing over occurs between them. In the first (X-) chromosome this practical equivalence of map-distance and exchange-value holds for loci not farther apart than about 15 units. In the middle of the second chromosome and of the third chromosome the equivalence holds for only about 10 units. In the end-regions of the second and third chromosomes it holds up to nearly 20 units. For distances somewhat greater than these the map-distances exceed the observed percentages of exchange by an amount equal to twice the percentage of double crossing over between the given loci. For still greater distances the difference includes also three times the percentage of triples. The number of quadruple crossovers is negligible except perhaps when the whole length of the second chromosome is to

be considered. For each chromosome and for each region within a chromosome the amount of this multiple crossing over is characteristic, and may not be the same in amount for different sections of equal map-distance. Because of this variation, the accurate expression of the relation between map-distance and exchange-values for the more distant loci, requires a table of conversion corrections for each pair of loci considered. Such tables will be published with the more detailed maps of the chromosomes. In general, the correction is relatively slight with distances that are under 20–40, but for longer intervals the correction increases at an accelerated rate. We have not met with percentages of exchange that exceed 50.0, though two of the maps are about a hundred units long.

The map of the third chromosome is the most accurate, since the calculation of the distances between the principal loci is made on the basis of all data up to 1920, and an improved method of weighting and interrelating the data has been followed. Relatively little change in these primary distances—the "triangulation" of the map—is expected with the further accumulation of data. There is still some uncertainty with regard to the region to the left of spineless, for the different sets of data upon that region may not be comparable because of the possible presence of crossover variations. The data used in the calculations for the primary distances in the first and second chromosomes are homogeneous, and although not including the last four years' work, are still fairly ample in amount. Changes are to be expected when these two maps are recalculated with the improved method and complete data.

The most useful mutants are those that are separable from the wild-type with completeness and ease, that are not inferior to the wild-type in viability and productivity, and that do not interfere with the use in the same experiment of any large class of the other mutant characters. Dominants are more valuable than recessives. Mutants accurately located in the chromosome are more valuable than those whose positions are less well established, though if the other desirable features mentioned above are present in a given new mutant the position will be found rather quickly. A very large factor in the value of the mutant is its position in the chromosome. The end positions are most valuable. Throughout the remainder of the chromosome the most favorable positions are those evenly spaced and just close enough together so that no double crossing over occurs between them. If the interval is too small there is trouble in getting double recessives, and the crossover classes are so small that large totals are required to make differences significant.

The mutants that fulfill all the above requirements most nearly are followed by an asterisk (*) in the maps. Their loci are the primary bases with relation to which the other mutants are located. There are several cases in which two or more excellent mutants affecting quite different

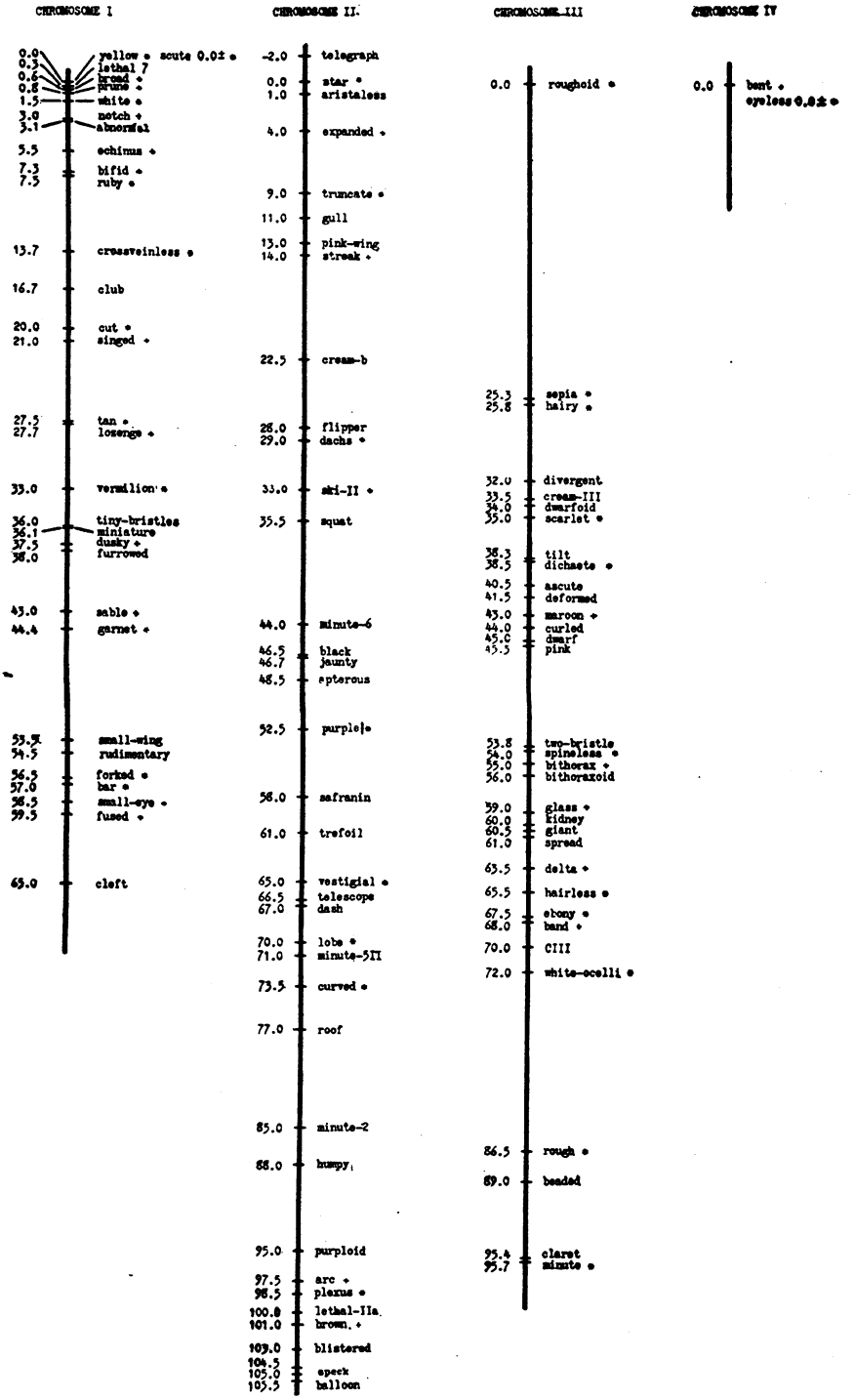

FIG. 1. Maps showing the distribution of mutant loci in the four chromosomes of *Drosophila melanogaster* (Oct. 15, 1920).

[A † sign should be added to miniature (I,36.1) and gull (II,11.0), and a * sign to black (II,46.5), speck (II,105.0), pink (III,45.5), and claret (III,95.4).]

regions of the body are located very close to one another (e. g., yellow and scute, sable and garnet, forked and bar, sepia and hairy, hairless and ebony, claret and minute). Of these neighboring mutants that one is used which interferes least with the other characters in the particular experiment, and the results of all such experiments are correlated by a simple correction made possible by knowledge of the distance between the loci. Such groups of loci, the members of which can be used as alternates, are treated as one base in the construction of maps and in linkage work.

The mutants followed by a plus sign (+) are somewhat less valuable in one or another respect, perhaps only in that of position.

Of the remaining mutants, not marked, some are exceedingly valuable in special work. As an example of these may be mentioned CIII, which prevents practically all crossing over within the right half of the third chromosome and thus is much used in holding other mutants in their proper relations in balanced stocks and while making up multiple stocks. But most of the unmarked mutants are those more difficult to separate, of poor viability, or less accurately located. Thus the mutant bithorax, which is located very close to spineless, has second rank and would be used as an alternate to spineless if the relation between the loci were accurately known. But the loci of these two mutants are so close together that as yet no double recessive has been obtained, and hence no back-cross test of the order and distance between these two loci has been made. Dominants, and recessives close to dominants, are easily and accurately placed, but there may be an error of five or even more units in the indicated positions of certain (unmarked or omitted) second-chromosome recessives whose positions are as yet known only through reference to a distant base. These are relatively unimportant mutants, and since they are not very useful, there is little incentive to determine their locations more accurately. The serial order of the loci marked with an asterisk is certain, and in only a few cases are the positions of the second-rank mutants likely to be shifted with the accumulation of data. Most of the unmarked mutants have their proper position with respect to the first and even second rank mutants, but their order with respect to each other is often uncertain in the absence of direct tests.

About 25 of the mapped loci represent more than one mutant allelomorph; thus, there are twelve allelomorphs at the white locus, and three to six allelomorphs at each of several other loci. Many of the mutants are recurrent; e. g., vermilion, notch, and rudimentary have each arisen independently on more than ten occasions.

It will be noticed that the mutant loci are not distributed at random along the chromosome maps, but are more closely spaced at the left end of the first, at both ends of the second, and throughout the mid-region of the third. This massing may correspond to a like massing of the genetic

materials. When orthopteran chromosomes are in the extended phase preceding their condensation as tetrads they may be seen to consist of granules of unequal size distributed at unequal distances along the linin thread, both granule size and spacing being characteristic and relatively constant for a given chromosome. Another explanation of the uneven spacing seems more probable: The amount of crossing over between given loci, e. g., black and purple in the second chromosome, is known to vary in a definite manner with the age of the mother, with temperature, and with genetic modifiers of crossing over. Since a unit of map-distance is thus known to represent different lengths of chromosome thread, the regions in which loci appear relatively closely spaced may be regions in which one unit of map distance represents a longer section of chromosome than in those regions that appear relatively unoccupied. It may be supposed that each region of chromosome has its characteristic relation between unit of map-distance and corresponding length of chromosome. It is probably significant that in the second and third chromosomes the distribution of mutant loci is approximately symmetrical about their midpoints, for these chromosomes are V-shaped with median attachment of the spindle fibre, while the first chromosome, which has the massing at one end, has terminal attachment. The variations, from region to region, in the proportion of double crossing over, referred to above, show a distribution that is symmetrical in the second and third chromosomes. From this and other evidence it is probable that there is a definite relation between the region of chromosome, considered morphologically, and the variations in the ratio of map-unit to length of chromosome thread. When the different chromosomes are compared the average ratios are found to be practically the same for all. Thus, the lengths of chromosomes as measured directly in metaphase plates are in the ratio of 100 : 159 : 159: 12, while the known lengths of the chromosomes as mapped are in the ratio of 100 : 165 : 155 : 2.[3] This is a surprisingly close agreement between the observed lengths of the condensed chromosomes and their lengths in terms of map-units.

[1] Contribution from the Carnegie Institution of Washington.

[2] The maps in the frontispiece of the Mechanism of Mendelian Heredity were made in 1914, and are both incomplete and out of proportion. A new frontispiece, practically the same as the figure accompanying this paper, has been supplied for a revision of the Mechanism and for a French edition. A similar figure is to appear in a book by Dr. Sharp of Cornell. The best of the earlier maps of the first chromosome is that given in *Carnegie Institution Publication* No. **237**, p. 22. Partial maps of the first chromosome that are more modern have been given in connection with special papers (*Genetics*, **1**, 1916 (8); *Amer. Nat.*, **1916** (421); *J. Gen. Physiol.*, **1919** (646). A map of the second chromosome, complete to 1916, is given in *Carnegie Institution Publication* No. **278**, p. 303. No satisfactory map of the third chromosome has previously been published, though partial maps based on special work have been given (*Amer. Nat.*, **1916** (217); *Genetics*, **1919** (208).

[3] Since figure 1 was drawn (Oct. 15, 1920) a mutant (M-23) has been located at 101 in chromosome III, and there has been found to be about 1% of crossing over between bent and eyeless in the fourth chromosome. (Scarlet is at 41.5, Chromosome III.)