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PNAS 1921;7;181-183
doi:10.1073/pnas.7.7.181

This information is current as of December 2006.

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PROCEEDINGS
OF THE
NATIONAL ACADEMY OF SCIENCES

Volume 7

JULY 15, 1921

Number 7

LINKAGE VARIATION AND CHROMOSOME MAPS

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Communicated by T. H. Morgan, March 10, 1921

A recent paper in this journal by Detlefsen¹ is introduced as follows:

"There is a well entrenched concept of recent genetics that hereditary factors or genes may be given fairly definite loci on chromosome maps and that these maps correspond to or represent, roughly perhaps, the actual conditions in the chromosome. The basis for this attractive and suggestive view is the premise that the distance between two genes is necessarily proportional to the percentage of crossing over which these two genes show, other things being equal. If the distance which gives one per cent of crossovers is used as an arbitrary unit of measurement, then it follows that distances on the chromosome may be calculated in terms of this unit. It has seemed to me for some time that the antecedent in this hypothetical proposition contains a more or less gratuitous assumption. We do not know that the distance which gives 1% (or $n\%$) of crossovers is a fixed unit. Stated differently, we do not know how constant the percentage of crossing over may be between two genes to which we give a fixed distance, i.e., our arbitrary unit of measurement may itself prove to be a variable. It may be possible for the distance which gives 1% of crossing over to differ in different females of the same population, or differ between stocks. In order to throw some light on these questions I began a set of experiments in 1916....."

Detlefsen then gives an account of an experiment in which crossover values for the white and miniature loci (in the *X*-chromosome of *Drosophila melanogaster*) ranging from 0% to about 33% have been obtained. Crosses between "high" and "low" lines are taken to indicate that a number of genetic factors influence the percentage of crossing over. The paper closes as follows:

"In view of these considerations it would perhaps be simpler to conclude that linkage is not a function of distance, i.e., crossing over is not necessarily proportional to distance. The distance between two genes may remain fairly constant, but the amount of crossing over depends upon numerous hereditary factors."

One unfamiliar with the literature of the subject would probably infer from Detlefsen's paper that the possibility of inherited linkage variations had not been taken into account by those concerned in constructing chromosome maps. In point of fact, the matter has not only been taken into account, but has been often discussed in the literature, as the following references will show.

In the first paper (1913) in which an attempt was made to construct a chromosome map,² the statement occurs (p. 49):

"Of course there is no knowing whether or not these distances as drawn represent the actual relative spatial distances apart of the factors.... we have no means of knowing that the chromosomes are of uniform strength, and if there are strong or weak places, then that will prevent our diagram from representing actual relative distances..."

Later than this³ definite evidence for the existence of genes modifying the amount of crossing over was reported, and in the "Mechanism of Mendelian Heredity"⁴ the situation was discussed as follows (pp. 67-68):

"It is not supposed, however, that the per cent of crossing over represents precisely the distance between the factors, for it may be that crossing over is more likely to take place in one region than in another. In that case the distances between factors in this region calculated from the amount of crossing over between them, would be relatively greater than the actual distance.... Sturtevant has found definite factors which alter the amount of crossing over in the chromosomes, and these factors actually do affect the amount of crossing over differently in the different regions.....however, ...the *order* of the factors remains unchanged."

The three papers mentioned above were all published before Detlefsen says he began his experiments, as was also Bridges,⁵ demonstration that frequency of crossing over in the second chromosome changes with the age of the female. Since that time the question has been discussed again and again, and several cases of inherited linkage variations have been thoroughly analyzed.⁶ The conclusions to be drawn from such evidence have been well stated by Morgan,⁷ in a chapter devoted entirely to variations in linkage (p. 125):

"It is to be understood, then, that when we substitute the idea of distance for crossing over values the term is not used in an absolute sense, but in a relative sense, and that it depends always on the conditions of the experiment. That the genes do stand at definite levels in the chromosome, and that in this sense they are definitely spaced, seems reasonable in the light of all the evidence bearing on this point; but even if they are so spaced that crossing over is a function of their distance from each other in the series, any influence that determines how often interchange between homologous pairs will take place would give the appearance that the actual distances themselves have changed."

As will be evident from the quotations given, the chromosome maps are intended to show the actual sequence of the loci, and the relative amounts of crossing over between them. The intervals between adjacent loci are not to be taken as necessarily proportional to the actual spatial distances between them—though that distance is evidently one of the elements concerned. When the amount of crossing over changes from any cause it is evident that we are dealing with a new system, and the intervals of the "normal" map will no longer be applicable (though in all cases so far investigated the *sequence* of loci shown in the "normal" map is unchanged). The "normal" map itself is based on the average results obtained under conditions in which no recognized disturbing factors (genetic or environmental) were known to be present. This map represents the results to be

expected from untried crosses, and has shown itself to be invaluable in everyday work. Detlefsen's own account is in agreement with this, for he says that his stock of white miniature has been used in class work and has always given the value to be expected from the published maps. When values that do not agree with the "normal" map are found, analysis has always shown some disturbing factor to be present; and in all cases where the point has been investigated it has been found that maps based on data uniform with respect to this disturbing factor are entirely self-consistent.

In view of these considerations it is clear that Detlefsen has misunderstood the significance of the published maps. The conception that he has attacked is one that has not been held or urged by those who have constructed chromosome maps.

¹ Detlefsen, J. A., These PROCEEDINGS, 6, 1920 (663-670).

² Sturtevant, A. H., *J. Exper. Zool.*, 14, 1913 (43-59).

³ Sturtevant, A. H., *Zs. ind. Abst. Vererb. Lehre*, 13, 1015 (234-287).

⁴ Morgan, T. H., A. H. Sturtevant, H. J. Muller, and C. B. Bridges, New York, 1915, 262 pp.

⁵ Bridges, C. B., *J. Exper. Zool.*, 19, 1915 (1-21).

⁶ Sturtevant, A. H., These PROCEEDINGS, 3, 1917 (555-558), and *Carnegie Inst. Washington Publ.*, No. 278, 1919 (305-341); Muller, H. J., These PROCEEDINGS, 3, 1917 (619-626), and *Genetics*, 3, 1918 (422-499); etc.

⁷ Morgan, T. H., *The physical basis of heredity*, Philadelphia, 1919, 305 pp.

ORIGIN AND HISTORY OF THE BEAR FAMILY IN THE WESTERN HEMISPHERE, WITH PARTICULAR REFERENCE TO THE RELATION OF THIS QUESTION TO PROBLEMS OF GEOGRAPHICAL HISTORY

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Read before the Academy, April 26, 1921

Although bears of many varieties are widely distributed in America and have been present in large numbers for a very long period measured in terms of years, the history of this group shows that as we go back in the geological record no evidence of representatives of the bear type are present in formations of the third geological period preceding the present in America, while they are known in considerable numbers in the rocks of this age found in the Old World. There is, therefore, good reason to believe that the bear group is derived from the other side of the earth and that the ancestors of the present American bears migrated to this continent at a time geologically not far removed from the present.

The bears of the world may be divided into two large groups, one some-