

SPECIAL ARTICLES

RANDOM SEGREGATION VERSUS COUPLING IN
MENDELIAN INHERITANCE

MENDEL'S law of inheritance rests on the assumption of random segregation of the factors for unit characters. The typical proportions for two or more characters, such as 9:3:3:1, etc., that characterize Mendelian inheritance, depend on an assumption of this kind. In recent years a number of cases have come to light in which when two or more characters are involved the proportions do not accord with Mendel's assumption of random segregation. The most notable cases of this sort are found in sex-limited inheritance in *Abraxas* and *Drosophila*, and in several breeds of poultry, in which a coupling between the factors for femaleness and one other factor must be assumed to take place, and in the case of peas where color and shape of pollen are involved. In addition to these cases Bateson and his collaborators (Punnett, DeVilmorin and Gregory) have recently published¹ a number of new ones.

In order to account for the results Bateson assumes not only coupling, but also repulsions in the germ cells. The facts appear to be exactly comparable to those that I have discovered in *Drosophila*, and since these results have led me to a very simple interpretation, I venture to contrast Bateson's hypothesis with the one that I have to offer.

The facts on which Bateson bases his interpretation may be briefly stated in his own words, namely: "that if *A*, *a* and *B*, *b* are two allelomorphic pairs subject to coupling and repulsion, the factors *A* and *B* will repel each other in the gametogenesis of the double heterozygote resulting from the union $Ab \times aB$, but will be coupled in the gametogenesis of the double heterozygote resulting from the union $AB \times ab$," and further, "We have as yet no probable surmise to offer as to the essential nature of this distinction, and all that can yet be said is that in these special cases the distribution of the characters in the heterozygote is affected by the distribution in the original pure parents." Bateson further points out that since "sex in the fowls acts as

a repeller of at least three other factors, . . . some of them may be found able to take precedence of the others in such a way as to annul the present repulsion with subsequent coupling as a consequence."

In place of attractions, repulsions and orders of precedence, and the elaborate systems of coupling, I venture to suggest a comparatively simple explanation based on results of inheritance of eye color, body color, wing mutations and the sex factor for femaleness in *Drosophila*. If the materials that represent these factors are contained in the chromosomes, and if those factors that "couple" be near together in a linear series, then when the parental pairs (in the heterozygote) conjugate like regions will stand opposed. There is good evidence to support the view that during the strepsinema stage homologous chromosomes twist around each other, but when the chromosomes separate (split) the split is in a single plane, as maintained by Janssens. In consequence, the original materials will, for short distances, be more likely to fall on the same side of the split, while remoter regions will be as likely to fall on the same side as the last, as on the opposite side. In consequence, we find coupling in certain characters, and little or no evidence at all of coupling in other characters; the difference depending on the linear distance apart of the chromosomal materials that represent the factors. Such an explanation will account for all of the many phenomena that I have observed and will explain equally, I think, the other cases so far described. The results are a simple mechanical result of the location of the materials in the chromosomes, and of the method of union of homologous chromosomes, and the proportions that result are not so much the expression of a numerical system as of the relative location of the factors in the chromosomes. *Instead of random segregation in Mendel's sense we find "associations of factors" that are located near together in the chromosomes. Cytology furnishes the mechanism that the experimental evidence demands.*

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¹ *Proc. Royal Soc.*, Vol. 84, 1911