CROSSING OVER WITHOUT CHIASMATYPE?[1]

A. H. STURTEVANT
Columbia University, New York City

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In a recent number of this journal Professor RICHARD GOLDSCHMIDT has a paper (1917), *"Crossing over ohne Chiasmatypie?"*, in which he develops a hypothesis to account for crossing over without recourse to the chiasmatype theory of JANSSENS (which, according to GOLDSCHMIDT, "ziemlich in der Luft schwebt"), or to any similar process.

The argument is based on the "von jedermann anerkannten Voraussetzungen der Chromosomenlehre." Among these Voraussetzungen GOLDSCHMIDT includes the idea that the chromosomes lose their structure during the resting stages, so that it is necessary that the particles be reassembled later to form the chromosomes seen at mitosis. It need hardly be pointed out that this view is not entirely established. Among others, the studies of JÖRGENSEN (1913), BOVERI (1909), BONNEVIE, VEJDOVSKY, and of the students of the "pro-chromosomes," make it at least open to serious doubt. Yet this idea forms the basis of GOLDSCHMIDT'S whole argument, for it is assumed that the same mysterious "Kraft" is responsible for the rebuilding of the chromosomes and for crossing over.

However this may be, there are certain points in the further development of GOLDSCHMIDT'S hypothesis that seem to me to call for even more critical examination than do his cytological considerations.

On p. 83 he says: "Es ist aber doch klar, dass man jede Proportion geometrisch als Entfernungen auf einer Geraden darstellen kann," and if this representation agrees with the facts, it shows only "dass irgendwelche Kräfte im Spiel sind, deren relativer Effekt als Entfernungen auf einer Geraden dargestellt werden können." Of course any series of proportions can be represented geometrically as sections of a single straight line; but only in certain special cases will such a representation show the relation of the parts to each other. In GOLDSCHMIDT'S own imaginary case (pp. 90-91) the relations are not fully represented by placing the

[1] Contribution from the Zoölogical Laboratory of Columbia University and the Carnegie Institution of Washington.

factors in a straight line. The factors *I* and *F*, for example, might be interchanged without appreciably affecting the degree to which the ratios fit. It may perhaps be surmised that the same sort of juggling can be done just as easily with the actual data on which the chiasmatype hypothesis of crossing over is based. This is not the case. In the first place, GOLDSCHMIDT has used for comparison only the data from the first paper developing the linear arrangement idea in detail (STURTEVANT 1913), although these data were at the time stated to be inadequate for certain loci, and have been supplemented by two more recent and extensive tabulations (STURTEVANT 1915, MORGAN and BRIDGES 1916).[2] Many of the inconsistencies pointed out by GOLDSCHMIDT and by the writer (STURTEVANT 1913), disappear when these later figures are used.

In the second place, the evidence which really puts the linear arrangement and chiasmatype theories on a sound basis is that obtained from experiments involving three or more loci at the same time. This phase of the matter is dismissed by GOLDSCHMIDT with two short paragraphs and a passing reference to the important work of MULLER (1916). These two paragraphs contain calculations for an imaginary experiment involving three loci, *B*, *D*, and *C*. The table on p. 91 gives the observed single crossover values for these three loci as follows:

$BD = 22.9 \quad DC = 13.0 \quad BC = 25.5$

GOLDSCHMIDT states, without giving the derivation of the result, that if the three loci are followed in one experiment the result will be:

Non-crossovers	67%
BD singles	20%
DC singles	10%
BDC doubles	3%

If we ignore for the moment the information gained by including *D* in the experiment, the observed crossovers between *B* and *C* will be $20 + 10 = 30$. But *BC* has just been stated to give 25.5. If it is intended to imply that heterozygosis for *D* affects the result, the only comment necessary is that the facts show no such relation to exist. As a matter of fact the values for the *BDC* experiment should read:

(I)	Non-crossovers	69.3%
(II)	*BD* singles	17.7%
(III)	*DC* singles	7.8%
(IV)	*BDC* doubles	5.2%

[2] One of these appeared over a year before GOLDSCHMIDT's manuscript was received, the other a few months before.

These figures and only these, will satisfy the conditions that

(a) I + II + III + IV = 100.0
(b) II + IV = 22.9 (*BD* crossovers)
(c) III + IV = 13.0 (*DC* crossovers)
(d) II + III = 25.5 (*BC* crossovers)

GOLDSCHMIDT declines to discuss the double crossover data further "weil wir glauben dass die STURTEVANT'schen Vergleichszahlen auf Grund einer falschen Formel berechnet sind, und sodann weil es . . . gar nicht unsere Absicht ist, das hier benutzte Schema an Stelle des MORGANschen setzen zu wollen."

I am unable to understand the bearing of the last part of this statement. It hardly seems necessary to point out that there is *a priori* no reason why a chiasmatype hypothesis should be the only possible explanation of the facts; and there would seem to be no point in developing any particular explanation, unless for the purpose of seeing if that explanation fits the known facts. GOLDSCHMIDT develops his speculation in great detail, until he comes to the really crucial evidence in favor of a chiasmatype view, and then the discussion is dropped. The statement that my formula (for expected number of double crossovers) (STURTEVANT 1915, p. 242) is incorrect seems a scarcely sufficient justification for ignoring that evidence, unless we are told how and why the formula is incorrect. The "formula" in question, when put in terms of symbols, states simply that if a crossover in region *AB* occurs in *p* (a fraction) of the cases, and a crossover in region BC occurs in *q* of them, then if the two crossovers are independent they will occur simultaneously (double crossover *ABC*) in p × q of the cases. This seemed to me to be a perfectly obvious application of an elementary principle of probability, and still seems so in spite of GOLDSCHMIDT'S statement that he believes it to be incorrect.

By the use of this simple "formula" it has been found that the crossovers are in fact *not* independent, but that one crossover tends to prevent the occurrence of another one near it. By the same method it has been shown (see especially MULLER 1916) that large pieces of the chromosomes stick together, and *larger* pieces than would be expected as mathematical consequences of the single crossover values. These facts have been emphasized as forming perhaps the strongest evidence in favor of a chiasmatype hypothesis; in fact, they have been used to disprove the supposition "that at a resting stage the chromosomes go to pieces, and the fragments come together again before the next division period.

Linkage might then [be supposed to] mean the likelihood of fragments remaining intact, etc." (MORGAN, STURTEVANT, MULLER and BRIDGES 1915, p. 134). GOLDSCHMIDT, in effect, denies these facts *in toto*. Under the circumstances it seems natural to expect some cogent reason to be given for this denial. No explanation of linkage can have any claim to serious consideration unless it accounts for these facts.

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