

## SHORT NOTES

### The relation of reduplication, recombination, synapsis and chromosome coiling

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It has long been believed that partially paired chromosomes observed at early meiotic prophase represent synapsis caught in the act and that crossing over must follow or accompany this stage. In contradiction to this it has often been suggested that certain observations (e.g. the occurrence of 3 : 1 ratios from individual tetrads of yeast, *Neurospora* and *Aspergillus*) are most easily explained if it is assumed that crossing over occurs at the time of reduplication which in turn is now thought to occur during the premeiotic interphase (Taylor, 1957). Another phenomenon, which has been reported in *Neurospora*, *Drosophila* and bacteriophage, and apparently must be fitted into any successful model of recombination, is localized negative interference.

To reconcile the seemingly contradictory observations Pritchard (1960) has ingeniously proposed that localized negative interference is a consequence of limitation of pairing which is effective for crossing over to short segments distributed throughout the complement, so that at any point on the chromosome such effective pairing would occur in only a small fraction of cells. This pairing of short segments presumably occurs during interphase when homologous parts may occasionally meet. As Pritchard pointed out, the increased chiasma frequency found in triploids and trisomics by Darlington (1934, 1941) and others would be consistent with the increased probability of contact in such organisms, although, as he also indicated, other similar observations of increased chiasma frequency or recombination cannot be accounted for in this way. Sturtevant (1951) reported increased coincidence in chromosome IV of diplo-IV triploid *Drosophila* females. Spurway & Philip (1952) reported negative interference across an inverted segment, and Maguire (1957) found about 90% chiasma frequency in a region including about thirty crossover units in a maize structural hybrid although no homologous segments were represented more than twice. There are a number of cases where increases in chiasma frequency per chromosome in polyploids or polysomics are not in proportion to the increased probability of contact. Furthermore, the work of Dobzhansky (1934) seems to indicate a strong correlation between reduced chiasma frequency and regions of probable synaptic failure in completed translocation, inversion and duplication configurations. It is not immediately obvious to the writer why such regions should tend to escape segmental pairing of the sort postulated by Pritchard.

The purpose of this note is to suggest an alternative hypothesis for the limitation of pairing effective for crossing over to short segments to account for localized negative interference. It has already been suggested (Maguire, 1960) that synapsis usually may be completed during interphase and that partially paired chromosomes at the stage traditionally called zygotene may represent premature dissociation in slightly unbalanced cells. It seems probable that, at whatever stage crossing over occurs (and certainly in *Neurospora*), the chromosomes are somewhat coiled. In such a state consecutive homologous points could establish intimate contact only for short segments along their length although on a grosser level homologous chromosomes might be completely paired. Although at first glance it appears that matching points could pair at every turn of the coil,

slight differences between homologues in pitch and diameter of internal coiling, or minute differences in position of matching points and various modes of the twisting of chromosomes about each other, might drastically reduce the frequency of effective pairing and result in a more or less random distribution of these pairing regions throughout the complement in different cells.

Partially homologous chromosomes from divergent species thus might appear to pair normally while intimate meeting of their comparatively few exactly matching points would occur so infrequently as to make genetic recombination rare.

It is pointless to speculate further how partner exchange in multivalents or inversion or translocation configurations might affect coiling or intertwining of chromosomes and thus chiasma frequency, or how coiling interrelationships among apparently non-homologous members of the complement might exist, but it is evident that if crossover frequency depends on the precise manner of internal coiling and intertwining of chromosomes, there may be a basis for variation from one region to another and for the mutual dependence of all regions upon external factors. To the extent that coiling changes during the time interval when synapsis is in progress, gradients in crossover frequency along chromosomes might exist in relation to order of pairing. Also the average time of pairing (within the synaptic span) of a chromosome region is probably influenced by the number of homologues present and possibly by its position in the genome.

It should be mentioned that if at least some of the chromomeres in maize are a consequence of knots of coiling, gross coiling differences may exist between homologues at pachytene. The writer has noticed that pachytene chromomere patterns frequently do not match in synapsed homologues, and further that they sometimes clearly do not match in sister chromatids of univalent chromosomes.

A study of probable modes of internal coiling and intertwining of chromosomes at the probable time of crossing over might indicate whether the hypothesis proposed above is a reasonable one.

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