

The Phenomenon of Secondary Association.

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THE discontinuity of chromosome associations observed at diakinesis and I metaphase in *Prunus* by Darlington (1928) led to the discovery of the phenomenon of secondary associations or secondary pairing. He suggested that the chromosomes showing this kind of affinity are related. This theory of secondary associations was further developed by Lawrence (1931 c) who adduced cytological and genetical evidence in favour of this theory and cited evidence of its occurrence from literature. Polyploidy occurs very frequently in the plant kingdom (at least fifty per cent. and probably more of the Angiosperm species, cf. Müntzing, 1936), hence this phenomenon is to be expected in all such forms. This has been now studied and described in detail by several workers in different materials: Lawrence (1929-31 a and b); Darlington and Moffett (1930); Moffett (1931); Meurman (1933); Wanscher (1934); Gustafsson (1935 a); Matsuura (1935); Heilborn (1935-36); Catcheside (1934); Gates (1935); Sakai (1935); Alam (1936). Recently Heilborn (1936) points out that he had already observed such associations in his studies on *Carex* (Heilborn, 1924) where he had also suggested that "this should probably be regarded as an expression of affinity between homologous gemini which arrange themselves in short rows of generally 3-5." He now thinks that "secondary association of chromosomes results from the action of the forces of nuclear division upon chromosomes of different size and mass," and he thus generalises, on insufficient grounds, that the chromosomes of equal size are associated irrespective of homology. Moreover, the presence of secondary pairing among chromosomes of unequal size observed (Richharia, 1936 a and b) is probably in direct contradiction to Heilborn's hypothesis, while the theory of secondary pairing allows such associations.

So far this phenomenon has been used only to determine the primary basic chromosome number, and has been shown to occur among bivalents which are morphologically the same. In our investigation (Richharia, 1936 a and b) on four *Brassica* species, viz., *B. oleracea* ($n = 9$), *B. chinensis* ($n = 10$), *B. pekinensis* ($n = 10$), *B. Rapa* ($n = 10$) and *Raphanus sativus* ($n = 9$) associations among

morphologically dissimilar types are observed. It has been suggested that such a condition may be due to certain structural rearrangements of chromosome parts, such as segmental interchange, fragmentation, translocation, etc., besides reduplication. Under these circumstances it will not be possible to disclose correctly the primary basic number in such forms. If such a hypothesis of "structural rearrangements" in explaining the secondary associations in these forms is correct it should be possible to detect such phenomena genetically. For example, Muller (1930) has shown in *Drosophila* that the translocations do to some extent influence the segregation of chromosomes, etc. It is quite probable that as a result of some sort of genetic balance or mutation primary pairing forming ring or chain does not occur in these forms and this relationship is shown only in the form of secondary associations. It is interesting to point out that Afify (1933) observed secondary pairing in *Lycopersicum esculentum* \times *L. racemigerum* but not in the parents. He gives the following explanation for such a behaviour (p. 236). "It may be suggested that this secondary association in the hybrid is the result of the lack of sufficient homology between the chromosomes of the two parents. In other words, the homology between the corresponding 12 chromosomes contributed from each parent is not as strong as in the pure species. Consequently there is not a satisfactory primary association at the prophase of meiosis, and to fulfil their capacity for further pairing, they pair at metaphase through secondary association." He also points out some objections to the soundness of this explanation. The same behaviour may be explained on the following assumption: "Let us represent two chromosomes from each gametic set by **AaB**, **CcD** and **AaD**, **CcB** respectively. It is evident that under these circumstances no secondary association will occur in the parents but in the hybrid the two bivalents with the constitution **AaB** and **CcD** and **AaD** and **CcB** would form secondary pairing because of the presence of common B D." Heilborn (1936), however, suspects that the secondary association observed in this case may be due to bad fixation, which is hardly true.

This phenomenon is not confined to bivalents only. Whenever univalents fail to pair at prophase, possibly due to weak homology, they form secondary associations at I metaphase. This has been observed in swede \times turnip cross by Catcheside (1934), Triploid *Pyrus minima* ($2n = 51$) by Moffett (1931), *Taraxacum* by Gustafsson (1934 *a* and *b*) and in *Raphanus* \times *Brassica* hybrids by Richharia (1936 *a*).

It is held that secondary associations possibly do not affect segregation. But it is worth noting what happens in male *Drosophila* where crossing-over does not occur (especially see Darlington, 1934). Here chiasmata are not formed and the chromosomes are seen secondarily associated followed by regular segregation. It may thus be suggested that it is quite possible to expect similar behaviour with some secondarily associated univalent pairs as well.

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