Letter to the editor

Crossover effects of B chromosomes may be 'selfish'

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The initial studies of Barker (1960) on grasshoppers showed that B chromosomes can raise chiasma frequencies in A chromosomes. Subsequent studies were made by different investigators on chiasma effects and/or crossover effects of B chromosomes in many species of plants and animals (reviewed by Jones & Rees, 1982, p. 85ff; Bell & Burt, 1990). In a number of cases, the B chromosome raises chiasma frequency. However, in some species, B chromosomes cause a significant reduction in chiasma frequency and, in other species, they have little or no effect on chiasmata. B chromosomes may also modify the distribution of chiasmata along the chromosomes or their variance in frequency between cells or between bivalents.

Several explanations for the effects of B chromosomes on chiasmata and crossing-over have been proposed. One widely discussed theory is based on an idea of Darlington (1956, p. 26). He proposed that B chromosomes increase the variability of a species. Increased variability could be achieved by increasing or modifying chiasma frequency (Hewitt & John, 1967; Jones & Rees, 1967). Bell and Burt (1990) criticized this idea. Instead, they suggested that B chromosomes act as parasites that evoke a response in the host organism. One response of the host is an increase in crossing-over, which may serve to produce a greater variety of offspring and a better chance of developing individuals that block accumulation of the parasitic Bs.

In addition to Darlington's theory and the proposal of Bell & Burt, is the simplest hypothesis: the crossover effects of B chromosomes do not have a specific function. This idea has been mentioned by some authors (Bell & Burt, 1990; Jayalakshmi & Pantulu, 1984). Such a crossover effect might occur if the addition of an extra chromosome(s) could evoke a general response in the crossover system of the organism.

Recently, a different theory was put forward (Carlson *et al.*, 1993). Studies with the maize B

chromosome, in the translocation TB-9Sb, showed the importance of controlling meiotic loss in the transmission of B-type chromosomes (Carlson and Roseman, 1992). One factor that reduces meiotic loss is crossing-over (Carlson, 1986). It was proposed that crossover effects of B chromosomes may have a 'selfish' function: they may reduce the rate of meiotic loss of Bs through increased bivalent formation. Crossover effects by B chromosomes on A chromosomes might be explained as side effects of systems that primarily act to increase pairing between Bs, thus reducing meiotic loss.

It is unlikely that this theory can explain all B chromosome effects on crossing-over. For example, some B chromosomes always remain univalent in meiosis, even when two or more chromosomes are present. In some cases, this property might be explained by the small size and/or heterochromatic nature of the Bs (Jones & Rees, 1982, p. 47). However, it is also possible that some B chromosomes carry genes that *inhibit* bivalent formation by Bs, rather than promote it. The blocking of bivalent formation, in certain circumstances, could represent another 'selfish' function for B chromosomes. Such a function can be postulated for those B chromosomes that have meiotic accumulation mechanisms which operate in the female meiosis. B chromosomes that accumulate in meiosis migrate as univalents to the 'egg' pole at anaphase I. It is advantageous for these chromosomes to remain unpaired so that they do not disjoin to opposite poles. Selection, therefore, should operate to prevent rather than encourage crossing-over between Bs. A possible case of selection for lack of pairing in the female was reported by Hewitt (1976). He found evidence that B chromosomes in *Myrmeleotettix maculatus* pair less often in the female meiosis than in the male. Such a difference between males and females seems unlikely to be coincidental, since a lack of pairing in the female

is advantageous to the accumulation mechanism, whereas a lack of pairing in the male is not.

A third 'selfish' function for crossover effects can be proposed. Assuming that B chromosomes evolve from A chromosomes (Jones & Rees, 1982, p. 137), the establishment of a new B chromosome as a separate entity requires repression of crossing-over between the B and its source chromosome. A-B crossing-over could be prevented if the new B is a shortened or rearranged version of an A chromosome, such that pairing with the source chromosome is difficult. However, inhibition of A-B crossing-over could also be genetically controlled. Either selection for a lack of pairing by the B chromosome or selection for preferential pairing between B chromosomes would help establish the B as a separate chromosome. A possible example of the latter type of selection is found in studies with *Lolium* hybrids. The B chromosome of *Lolium perenne* can act in a similar manner to the 5B chromosome of wheat in its ability to restrict homoeologous pairing (Evans & Macefield, 1972, 1973; Evans & Taylor, 1976; Macefield & Evans, 1976; Jenkins & Scanlon, 1987). This B chromosome property has a strong effect on A chromosome pairing in certain *Lolium* hybrids, but its actual function may be to prevent crossing-over between the B chromosome and its chromosome of origin, as proposed by Dover (1975) and Gupta (1981).

Considering the three selfish functions proposed for B crossover effects, one might ask what predictions can be made. If a crossover effect is intended to promote bivalent formation between Bs, it should raise chiasma frequency. If the function is to prevent bivalent formation, it should lower chiasma frequency. If the purpose is to restrict A-B pairing, the effect should be to reduce chiasmata, but mainly or exclusively in hybrids or allopolyploids. The effects described are not always found. For example, the B chromosome in *Myrmeleotettix maculatus*, discussed above, does not lower crossing-over in the female. Instead, it raises chiasma frequency in both males and females (Hewitt, 1976). However, the reason that predictions do not always match observations may be that measurements of crossover effects are usually made on A chromosomes, while the target is the B chromosome. On the 'selfish' hypothesis, A chromosomes are only affected secondarily by the B chromosomes. Therefore, measurement of crossover effects in the A chromosomes may be misleading.

Studies that measure chiasmata among B chromosomes as well as A chromosomes are few in number. The ones that have been made give varying results, probably because crossover rates can be modified in a number of different ways. Brown & Jones (1976) found with *Crepis capillaris* that increasing numbers of

B chromosomes raised the chiasma frequency for both A and B chromosomes. In this case, Bs seem to have a general effect on chiasmata, elevating their frequency in all chromosomes. Work in pearl millet gave different results. Pantulu & Manga (1975) and Subba Rao & Pantulu (1978) showed that the standard B chromosome in pearl millet produces a strong increase in chiasma frequency among Bs, but has little effect on the A chromosomes. Apparently, the B has an effect on crossing-over that is specific for B chromosomes. An interchromosomal effect between B and A chromosomes has also been reported. Henriques-Gil *et al.* (1982) found, in the grasshopper *Eyprepocnemis plorans*, that increased chiasma frequency in the B chromosomes was associated with lower chiasma frequency in the A chromosomes and vice versa. The role of the B chromosome in this interchromosomal effect is not clear, but the finding makes it obvious that interpretation of chiasma data based solely on A chromosome effects is risky.

Another problem in data interpretation is present when B chromosomes redistribute chiasmata from distal to proximal sites (Barlow & Vosa, 1970; Ward, 1976; Remis & Vilardi, 1986) or proximal to distal (Parker *et al.*, 1990). Since B chromosomes often have difficulty in forming chiasmata, such a redistribution effect could be critical in determining whether or not Bs are univalent or paired at meiosis, while having no such effect on A chromosomes.

In summary, at least three 'selfish' functions can be proposed to explain B chromosome crossover effects. These functions are targeted on the B chromosome, and only modify crossing-over in A chromosomes incidentally. The 'selfish' hypothesis may not explain all crossover effects of B chromosomes, but it can be used in comparison to other hypotheses when attempting to interpret chiasma and crossover data.

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