homomorphs. The "zig-zag" type of effect on recombination by the supernumeraries has been observed in rye by Jones and Rees, and in <u>Listera</u> <u>ovata</u> by Vosa and Barlow. Our work on the B:Knob interaction is in need of further experimentation. It would be interesting to know whether the "zig-zag" effect observed in chromosome 9 is displayed in the other A-genome chromosomes.

It becomes increasingly clear that the effect of the B-chromosomes on recombination is not simply an additive one. It is also quite clear that the effect of the B-chromosomes on recombination is modifiable not only by the abnormal chromosome 10 but also by the knobs of chromosome 9.

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## 2. Probable weak fusion of chromatids broken during a breakage-fusion-bridge cycle.

McClintock (Genetics 26:234) first described the chromatid type of breakage-fusion-bridge cycle in which a dicentric chromatid introduced into the initial triploid nucleus of the maize endosperm will persist throughout both the gametophyte and endosperm divisions. Variegation patterns of endosperm markers in mature kernels provide evidence of the cycle.

In the present study plants heterozygous for a ring chromosome 10 carrying the dominant R color factor allele and the dominant allele for non-striate plant (Sr<sub>2</sub>) were crossed to chromosome 10 testers marked by the recessive alleles (figure 1). Three classes of progeny resulted. The largest class of kernels (84.4%) was colorless and yielded green, non-striate plants which were shown cytologically to contain normal chromosomes 10. These individuals arise from one of the noncrossover classes. The second class of kernels comprised 10.4% of the progeny. The kernels were variegated for R. The variegation of the endosperm tissue indicated that either the ring was present or a crossover between the ring and the rod had produced a dicentric chromosome that was undergoing the chromatid type breakage-fusion-bridge cycle. Of the 10 kernels in this class which germinated, 4 produced plants variegated for striate. These plants, designated class II-A in figure 1, represent the other non-crossover class. The presence of the ring was confirmed cytologically.

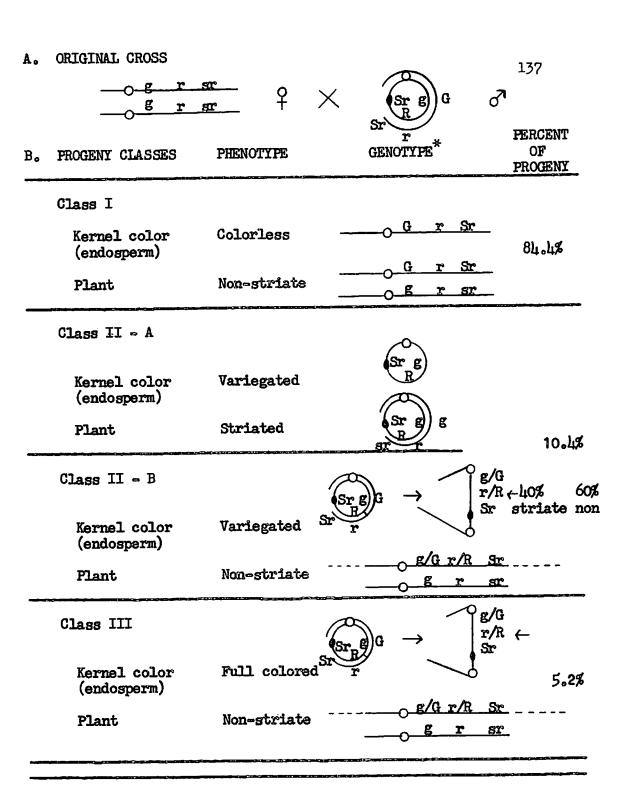


Figure 1. - Origin of progeny classes resulting from the cross k10k10 ? X ring-10/k10 d. The percent of progeny in each class is given for a total of 270 kernels from one cross. Of the 10 kernels in Class II which germinated, four were striated and six were not.

\*The endosperm genotype was deduced from evidence presented in the text; only the chromosome contributed from the male parent is shown. The plant genotype was determined after cytological examination; the chromosomes contributed by both parents are shown.

The remaining six plants were not striate and contained stable rod derivatives produced when the breakage-fusion-bridge cycle ceased in the sporophytic tissues.

The third progeny class was unexpected. The kernels were full colored and yielded non-striate plants. Pachytene squashes revealed each plant had received from the male parent, a stable rod chromosome. Of the six derivatives studied from this group, five possessed the heterochromatic knob from the ring plus the three prominent chromomeres; one contained only the three chromomeres. As each included at least the three chromomeres, and since crossing over between the R locus and the knob of KlO is very rare (Rhoades, Genetics 27:395), the derivatives could not have come from a double crossover on each side of the R locus. Rather, each derivative appears to have been the result of a single crossover between the ring and the rod chromosome which led to the formation of a dicentric bridge at anaphase I. According to McClintock, the breakage-fusion-bridge cycle should have continued in the endosperm giving an endosperm variegated for R. However, in this instance it appears that the chromosomes formed by the crossover between the ring and the rod did not undergo the typical breakage-fusion-bridge cycle as described by McClintock. Two explanations could account for the nonvariegated kernels. First, the broken end of the chromosome could have healed permanently in the endosperm. This contradicts all evidence accumulated by previous investigations on the healing of broken ends of chromosomes. A more plausible explanation is that the initial break of the dicentric occurred at a point in the chromosome where fusion of the sister chromatids was not complete. Because of the weak fusion, all successive breaks would occur at the same position and the original genetic constitution would be preserved. This explanation is supported by McClintock's original observation of a tendency for successive breaks to occur at positions of previous fusions, indicating that in many cases the fusion of sister chromatids is weak. In addition, Schwartz and Murray (Supplement volume of Cytologia, Proc. Intern. Gen. Symp. 1956: 277) examined cytologically the types of anaphase bridge configurations in developing endosperms containing a dicentric chromatid. Since the dicentric was introduced into the initial triploid nucleus from which

the endosperm develops, all anaphases in the young embryo should have shown single bridges as a consequence of a continuous breakage-fusion-bridge cycle. On the contrary, none of the kernels examined showed more than a scattering of single bridges. Schwartz and Murray suggested therefore, that the fusion of sister chromatids was not always complete at anaphase. An incomplete fusion would result in a weak bridge which would rupture early at the next anaphase and not be scored at middle or late anaphase.

Examination of the rod chromosomes derived from the full colored kernels provided support for the "weak fusion" hypothesis. Four of the derivatives came from breaks either through or very close to the heterochromatic KlO knob. A fifth derivative was produced after a break adjacent to one centromere, and the sixth came from a break adjacent to the other centromere. Each of the breaks was in or near heterochromatin of the knob or proximal heterochromatin surrounding the centromere. It is suggested fusion of sister chromatids may be less strong in heterochromatin.

It can be concluded that crossovers between the ring of abnormal chromosome 10 and its homologous rod produced dicentric bridges which yielded stable rods in the next sporophytic generation. Apparently, two types of chromosomes were formed. The first type (Class II-B) underwent a typical breakage-fusion-bridge cycle in the endosperm tissue as evidenced by the variegation for the  $\underline{R}$  allele. The second type (Class III) presumably underwent a cryptic breakage-fusion-bridge cycle where incomplete fusion always resulted in breakage of the chromatid bridge at the point of previous fusion. Continuous breakage at the same point did not alter the genic constitution of the daughter cells, the  $\underline{R}$  allele was not lost, and thus, the endosperm was not variegated.

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