Table 2 lists the phenotypic classes arising from the backcross of a homozygous medium variegated parent. It can be seen that red and light variegated types are in equal frequency. In comparison, in a similar mating, with a heterozygous variegated parent, the red class is repeatedly found in a significantly higher frequency than the light variegated. This difference in relative frequency of mutant class is due to the recombination of the Modulator elements which have transposed from the P locus. In the case of heterozygous medium variegated, potential light variegated individuals among the progeny are converted to medium variegated due to recombination of tr-Mp with the $P^{rr}Mp$, (tr-Mp segregates with the colorless allele, P^{ww}), and thus are not recorded as mutants. Whereas, in the progeny of a homozygous medium variegated, the recombining tr-Mp will segregate with another $P^{rr}Mp$ complex and thus the tr-Mp will not be lost to the total count of mutants. Thus, recombination in homozygous medium parents does not alter the expected mutant ratio while in heterozygous medium parents the ratio is expected to be altered by the loss of light variegated types.

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2. Proximal-distal polarity of Modulator transpositions upon leaving the P locus.

Modulator has been previously shown to transpose from the P locus on chromosome 1 to receptor sites throughout the genome in a nonrandom pattern. The major prior findings were that the nonrandom movement resulted in a disproportionately large number of transpositions to chromosome 1 locations and that the number of receptor sites increased as the distance from the P locus decreased. Findings reported here for the first time show that this high frequency of transposition to chromosome 1 locations occurs more often to distal locations than proximal ones relative to P. As striking as this left/right total difference is the additional finding that a region proximal to P and extending approximately three recombinational units from P is totally refractory to Modulator, while the distal equivalent length of chromosome contains the highest frequency of receptor sites.

Studies of Modulator locations after transposition from the P locus were conducted employing the P locus, transposed Modulator, and the

breakpoint of the reciprocal translocation T1-2b as a three marker system in a backcross mating. The location of the receptor site was estimated in 105 independent cases in which (1) a twin spot of multiple kernels was found in the pericarp, (2) the red sector was analyzed for the presence or absence of Modulator, and (3) semisterile light variegated offspring resulted from the backcross seed within the light variegated sector of the twin mutation.

Of these 105 cases, 41 showed transposed Modulator recombining at random with P, 39 were linked and distal to P, while only 18 were linked and proximal to P. The remaining 7 cases all showed Modulator linked to P but a proximal/distal relationship was not obtained. Thus, there are twice as many recovered transpositions to distal sites as to proximal sites on chromosome 1. Any sites on chromosome 1 which result in high recombination frequencies (42% or more) are tallied with the random group; thus the sites listed here as distal or proximal represent only those within a detectable linkage arc with the P locus. In addition, the proximal portion of the chromosome, three map units from P in length, was void of any receptor sites. This contrasts with the equivalent distal portion of the chromosome, which produced seventeen events. This difference in receptor site positioning adjacent to the P locus is the most striking aspect of this three-point linkage study. When transpositions occur, the condition of the immediate proximal length of chromosome is obviously in a very different state than the equivalent length of chromosome distal to the P locus.

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3. Modulator: A modifier of crossing over.

During the analysis of recombination data using P, transposed Mp and the breakpoint of T1-2b, an unexpected find was uncovered; Modulator increases the frequency of crossing over in chromosome segments adjacent to its position! Specifically, the interval T to P was found to produce recombination rates which increase when Mp is located adjacent to, but not within, the interval (see Table 3).