1. An unstable compound locus, $a_1{}^{p}{}_{m}$.

Rhoades reported the origin of a mutable locus at A, in the 1950 News Letter. Aged seed carrying a^{p}l/A^{p}l Dt/Dt was crossed by an a/a strain. Three separate mutations arose involving one or more kernels. Two of these mutants resembled the a_1 allele and were relatively stable. The third was a highly mutable form of the a^{p} allele, $A^{p}{}_{m}$.

Stocks carrying $A^{p}{}_{m}$ (A_2C R B_z) exhibit a pale aleurone which is mosaic with deep and colorless sectors. The plant color produced by this allele (B Pl B_z) is reddish-brown with stripes of deep purple and brown tissue. The pericerp is dominant brown in $A^{p}{}_{m}$ (P) stocks with occasional red sectors. Germinal and somatic mutations from pale to deeper and to lighter levels of anthocyanin intensity occur at high frequencies. Changes in mutability often occur jointly with changes in level. The mutation rate may vary for different forms or states of the $a^{p}{}_{m}$ allele; however, some representative mutation rates follow:

$a_1{}^{p}{}_{m}$ (Pale mosaic) - to germinal, stable, deep alleles - 1 in approximately 20,000 gametes

- to germinal, stable, light pale alleles - 1 in approximately 10,000 gametes

- to germinal, stable, colorless alleles - 1 in approximately 4,000 gametes

- to germinal, stable, colorless plus dot alleles - 1 in approximately 100 gametes

- to germinal, stable, medium pale alleles - 1 in approximately 30 gametes.

These germinal mutation rates in contrast to what is observed somatically indicate infrequent mutations to the deep level. Somatic deep sectors are abundant but generally they are very small. If these represent mutations, it is likely that their late occurrence is responsible for the low number of germinal changes.

The stable mutants from $a^{p}{}_{m}$ may be grouped into four general classes: I - deep aleurone, red pericarp; II - pale aleurone, dominant brown pericarp; III - colorless aleurone, recessive brown pericarp; and IV - colorless aleurone, dominant brown pericarp. Of 66 analyzed mutants, 8 were of class 1, 23 - class II, 31 - class III, and 4 - class IV. Since the parent allele was mutable and exhibited pale aleurone and dominant brown pericarp, Class I alleles were derived by an event affecting the mutability, aleurone, and pericarp portions of the A_1 locus. Class II alleles, however, arose from events affecting only the mutability component of $a_1{}^{p}{}_{m}$. Alleles of Class III again involve changes at the mutability, aleurone, and pericarp components. Changes at the mutability and aleurone components but not the pericarp component are involved when Class IV mutants arise.

One interpretation of this mutation pattern is that separable genic units at A_1 control the mutability, aleurone, and pericarp characteristics. Evidence for the presence of a mutability factor at A_1 is ample. There is a genetic factor for variegation in characters controlled by A_1 which is not segregated from A_1; nor has this factor been separated from A_1 by crossing-over. The existence of a spreading effect phenomenon involving A_1 and a closely associated gene on chromosome 3 indicates the presence of a mutability factor in this region, as does the alteration of the a_1-sh_2 crossover rate by $a_1{}^{p}{}_{m}$ derived alleles.

Laughnan has shown that two components, _ and _, controlling aleurone color exist in the allele A^{b}. It is possible that similar components are present in $a^{p}{}_{m}$. An _-like component is suggested by the similarity in phenotypes produced by $a^{p}{}_{m}$ and the A^{d} ( ) alleles described by Laughnan. Moreover, a large number of the pale self mutants derived from $a^{p}{}_{m}$ are phenotypically identical to the A^{d} alleles arising from A^{b}: Peru. A deep _-like component is thought to be present because if the large number of deep sectors which occur on plants carrying $a^{p}{}_{m}$. The germinal mutations to the deep

level indicate that these events actually are mutations at A. The large number of somatic alterations renders improbable the possibility that these are intragenic changes converting the pale component into a deep component. The possibility that _ is present in the $a_1{}^{p}{}_{m}$ allele but in inhibited in its expression by or the mutability factor or both is more likely. That $a_1{}^{p}{}_{m}$ contains P^{b} is suggested by the Class III and IV mutants, both of which exhibit colorless aleurone. Class III mutants produce recessive brown pericarp while dominant brown pericarp is characteristic of Class IV mutants. Thus, it is possible for mutational events to occur which affect both aleurone and pericarp properties and others which affect aleurone but not pericarp properties. The separate existence of a pericarp component in $a_1{}^{p}{}_{m}$ seems likely.

The linear arrangement of the four components at the A_1 locus may be computed by observing the mutational patterns of $a_1{}^{p}{}_{m}$. The evidence available indicates the sequence is β - M - α - P^{b} - sh_2.