forms in diploid tissue. It is unlikely that the
enzymes formed by the same allele in different tissues
have different specific activities, but not impossible.
We propose that in the seedling both alleles are equally
active but in the endosperm the mutant allele is
partially repressed. A similar situation was found for
the pH 7.5 esterase when the relative activity of two
alleles in different tissues was compared.

<div align="right">Drew Schwartz
Toru Endo</div>

2. Further studies on preferential segregation.

In the 1958 Maize News Letter data were presented
showing that the preferential segregation produced in
non-homologous chromosomes by abnormal 10 occurred only
when there was crossing over between the knob and the
centromere to produce heteromorphic dyads consisting of
one knobbed and one knobless chromatid. The test
referred to above came from plants with a normal
chromosome 9 and one in which a piece of 3L had been
inserted into 9S between the Sh and Wx loci. The
latter chromosome was designated Dp9. Crossing over in
the entire length of 9S was found to be greatly reduced
when the Dp9 chromosome was heterozygous. When plants
heterozygous for Dp9 and abnormal 10 and also heterozygous
for the terminal knob in 9S were testcrossed as the
female parent, there was a striking reduction in the
degree of preferential segregation for the distal Yg2
marker in 9S compared to that found in sib plants
homozygous for normal chromosomes 9. The conclusion was
drawn that the formation of heteromorphic dyads via
crossing over is an essential antecedent to preferential
segregation. That this conclusion is indeed valid is
shown by the following experiments involving chromosomes
3 and 9.

The rearranged chromosome 9, (R)9, studied by McClintock
(1944) is known to drastically reduce the amount of
crossing over in the short arm of 9. The (R)9
chromosome possesses a terminal knob of medium size on
its short arm. Plants heterozygous for the (R)9
chromosome and for the wd and wx markers were test-
crossed as the female parent. Sib plants with and
without abnormal 10 were available. As expected there
was an extremely low amount of crossing over between
wd-wx in the homozygous k10 plants and the contrasting
alleles for the two segregating loci were each recovered
in 50% of the progeny. Although plants heterozygous
for a knobbed 9 and a knobless 9 (wd) undergo preferential

segregation if K10 is present, no marked deviations from a 1:1 ratio for $\underline{Wd}:\underline{wd}$ would be expected in K10 plants if crossing over was a requisite for preferential segregation. On the other hand, the usual percentage of preferential segregation found in K9 k9 heterozygotes should occur if preferential segregation of K9 chromatids to the basal megaspore is unrelated to recombination and is due to some intrinsic property of the knobs. The data obtained from both K10 k10 and k10 k10 backcrossed individuals show a very close fit to a 1:1 ratio for both the $\underline{wd}$ and $\underline{wx}$ loci. This experiment, like the Dp9 tests, indicates that preferential segregation is dependent on crossing over.

Substantiating data were also obtained from studies of plants heterozygous for three paracentric inversions involving the long arm of chromosome 3. The breakpoints of In 3a are 3L .4 and .95, the breakpoints of In 3b are 3L .25 and .75, while In 3c involves nearly the whole long arm with the proximal break near the centromere and the distal one near the tip. The knob at .6 is included in the inverted segment of all three inversions. $\underline{Gl}_6$ is in the proximal uninverted segment of In 3a while $\underline{Lg}_2$ and $\underline{A}_1$ are included in the inversion. $\underline{Lg}$ is in the inverted region of In 3b, $\underline{Gl}$ is in the proximal segment, and $\underline{A}$ is in the distal non-inverted segment. All three loci are in the inverted portion of In 3c with one breakpoint close to $\underline{Gl}$ and the $\underline{A}$ locus approximately 5 crossover units from the distal break.

The testcrosses of K10 k10 plants singly heterozygous for the three inversions, for the large knob in 3L, and for the $\underline{Gl}$ $\underline{Lg}$ $\underline{A}$ loci gave the following percentages of recovery of the alleles carried by the knobbed chromosome 3.

	% Gl	% Lg	% A
In 3a/N	52.7	60.4	60.1
In 3b/N	50.3	51.6	49.7
In 3c/N	50.0	56.1	49.9

The complete backcross data from the In 3b heterozygotes were presented in the 1964 News Letter. The In 3a/N and the In 3c/N data are presented in Table 1. No data are presently available for comparison of sib k10 k10 and K10 k10 plants heteroyzgous for In 3c.

Table 1
Testcross Data from Plants Heterozygous for In 3a or In 3c Showing Preferential Segregation of
the Knobbed Chromosome 3

Female Parent	(1) Gl Lg A	(2-3) Gl lg A	(0) gl Lg A	(3-4) gl lg A	(3-4) Gl Lg a	(0) Gl lg a	(2-3) gl Lg a	(1) gl lg a	Σ	% gl	% Lg	% A	Recombination % Gl-Lg	Lg-A
25971														
$\dfrac{Gl\ a\ k\ lg\ In3a}{gl\ A\ K\ Lg\ N}\ \dfrac{k10}{k10}$	138	2	1020	0	5	1035	10	140	2350	49.8	49.9	49.4	12.0	0.7
$\dfrac{Gl\ a\ k\ lg\ In3a}{gl\ A\ K\ Lg\ N}\ \dfrac{K10}{k10}$	279	13	736	17	24	507	11	152	1739	52.7	60.4	60.1	27.1	3.7

Female Parent	(0)	(2-3)	(1-3)(3-4)	(1-2)(2-4)	(1-2)(2-4)	(1-3)(3-4)	(2-3)	(0)	Σ	% Gl	% Lg	% A	Recombination % Gl-Lg	Lg-A
Fla. 64-212														
$\dfrac{a\ k\ lg\ gl\ In3c}{A\ K\ Lg\ Gl\ N}\ \dfrac{K10}{k10}$	603	126	45	28	46	29	208	523	1608	50.0	56.1	49.9	25.4	25.4

The varying percentages of recovered alleles in the three inversions are intelligible on the assumption that heteromorphic dyads are required for preferential segregation to occur. With In 3a, crossing over is frequent in the proximal segment between Gl and the first breakpoint. This leads to preferential segregation for alleles distal to the crossover. Lg and A are recovered with the same frequency since they are separated only by rare double crossovers in the loop. In In 3b heterozygotes, heteromorphic dyads are produced following the single crossovers in the proximal region and with certain of the double crossovers. The genetic data show that these crossovers were infrequent although when they did occur the reciprocal classes were not equal (see MNL 38: 75). In 3c is a long inversion and double crossovers within the loop are frequent. When one crossover occurs to the right and one to the left of Lg, heteromorphic dyads result and preferential segregation for Lg is found. Since one of the two crossovers usually separates Lg and A, the A locus shows random segregation.

The question next considered was whether or not preferential segregation invariably occurred in all heteromorphic dyads and to the same degree. The answer to this was obtained from the testcrosses of K10 k10 N3 N3 Gl Lg K A/ gl lg k a plants which gave the following data (previously reported data from similar crosses were not used because of the disturbing effect of the segregating et allele):

26549 and 25938	(0) Gl Lg A	(0) gl lg a	(1) Gl lg a	(1) gl Lg A	(2) Gl Lg a	(2) gl lg A	(1-2) Gl lg A	(1-2) gl Lg a
	777	359	272	661	343	197	108	250
	26.2%	12.1%	9.2%	22.3%	11.6%	6.6%	3.6%	8.4%

$\Sigma = 2967$

The double crossover chromatids arise from heteromorphic dyads. Therefore, the percentage of double crossover strands with a knobbed chromatid gives a direct measure of the frequency of preferential segregation in bivalents having double chiasmata. Since Lg is close to the knob, this locus can be used in following transmission of the knob. Three hundred and fifty-eight double crossover strands were found, of which 250 or 70% had the Lg

allele. Double crossover bivalents contribute single crossover strands to the region (1) and region (2) classes and noncrossover strands to the (0) class and it was assumed the complementary strands would occur in the same proportion of 70% Lg and 30% lg. Bivalents with single chiasmata in region (1) also give rise to heteromorphic dyads and again the assumption of 70% preferential segregation was made. Noncrossover bivalents and bivalents having a single chiasma in region 2, according to the crossover hypothesis, result in homomorphic dyads and random segregation. If there is no chromatid interference, the percentage of megasporocytes with double chiasmata, with a single chiasma in region 2 (Lg-A), with a single chiasma in region 1 (Gl-Lg), and with no chiasma in the long arm of chromosome 3 can be calculated. The chiasma values can then be converted back to strand frequencies. The calculated frequencies of the different kinds of chromatids are given below with the actual numbers obtained.

	(0) Gl Lg A	(0) gl lg a	(1) gl Lg A	(1) Gl lg a	(2) Gl Lg a	(2) gl lg A	(1-2) gl Lg a	(1-2) Gl lg A
obs.%	26.2	12.1	22.3	9.2	11.6	6.6	8.4	3.6
calc.%	25.5	12.8	22.1	9.4	11.5	6.7	8.4*	3.6*

*Observed values used as basis for calculation.

The close agreement between the calculated and observed values suggests that the same amount of preferential segregation takes place in all heteromorphic dyads and is further indication of the validity of the crossover hypothesis.

M. M. Rhoades

3. <u>A test of preferential segregation in microsporo- genesis</u>.

Preferential segregation through the female of heterozygous abnormal chromosome 10 and other chromosomes heterozygous for knobs in the presence of