parental plants classified as being heterozygous for a translocation were in fact aneuploid. The indicated recombination values in these cases are obviously subject to correction.

Recombination values for markers in only one of the two translocated chromosomes have been included where relevant. Fairly extensive data on lg_1-gl_2 recombination were obtained and are presented to indicate the variability encountered. These data should serve as a caution in comparing recombination values obtained in tests lacking adequate controls.

The last column of the table includes additional information provided by published or unpublished work of others, or derived from this or other phases of the present study.

E. B. Patterson

UNIVERSITY OF ILLINOIS
Urbana, Illinois
Department of Botany

1. A genetic analysis of a duplication and a deficiency involving chromosomes 9 and 3.

Some years ago I received an aberration identified by Frances Clark Beard as one in which a segment from the long arm of chromosome 3 had been inserted into the short arm of 9. Inasmuch as this constituted a type of aberration not previously subjected to genetic analysis, a number of tests have been performed. The chromosome 3 deficient for a segment in the long arm is designated as Df 3 and the chromosome 9 with this piece inserted into the short arm is called Dp 9. Heterozygous plants of Dp 9/ N 9 Df 3/ N 3 constitution produce the following four kinds of spores in equal numbers: Dp 9 Df 3, Dp 9 N 3, N 9 Df 3, N 9 N 3. The N 9 Df 3 class of megaspores and microspores aborts. Female transmission of the remaining three classes is normal. When heterozygous plants are used as the pollen parent, the Dp 9 N 3 class of pollen is handicapped and functions infrequently. From backcrosses of Dp 9 Wx/ N 9 wx; Df 3 A/ N 3 a plants used as the egg parent the following data were obtained:

A Wx	A wx	a Wx	a wx	
2618	431	2409	2262	$\Sigma = 7720$
33.9%	5.6%	31.2%	29.3%	

% A = 39.5   % a = 60.5
%Wx = 65.1   %wx = 34.9

Inasmuch as the A allele was in Df 3, a ratio of 1 A: 2 a would be expected if no crossing over occurred between A and the deficiency. The deviation from this ratio is due to crossing over between A and the deficiency. More specifically, the percentage of A wx kernels among the colored class is 1/2 the recombination value between A and the deficiency if the wx allele is invariably in N 9 and the Wx allele in Dp 9. Since there is a low percentage of crossing over between Wx and the Dp, the calculated recombination value of 11.2% between A and the Df is only a close approximation of the correct value.

A total of 142 plants from A Wx kernels was tested for the kind of chromosome 3 contributed by the heterozygous female parent. Of these, 127 had a Df 3 and 15, representing crossovers between A and the Df, possessed a N 3. This is a recombination value of 10.6 percent. Sixty a Wx kernels were similarly tested and only 6, or 10 percent, had a Df 3 arising from crossing over. The evidence is good, therefore, that in A Df 3/ a N 3 plants the A locus is 10-11 recombination units from the deficiency. That the A locus is not included in the piece of 3L inserted into 9S is evident from the approximate 1 A: 2 a backcross ratio. If it were so placed, the number of A kernels would be nearly twice as great as that of a kernels.

The location of the Df in 3L is revealed from the backcross of Dp 9/ N 9; + + Df +/ gl_6 lg_2 N a_1 plants. When these heterozygotes were used as the female parent, the data shown in item 1 of Table 1 were obtained. The marked reduction of crossing over in the Lg-A region strongly suggests that the Df includes a segment between these two loci. The recombination value for Gl-Lg is higher than normal and the 14 percent recombination found for the A-Et interval is also slightly higher than normal; the only reduction occurred in the Lg-A interval. When heterozygous plants of the same constitution were used as the pollen parent in backcross tests, the data shown in item 2, Table 1 were obtained. Again a reduction in crossing over is found in the Lg-A region, thus confirming the data from the female B.C. That the Df is nearer Lg than to A is evident from the analysis of the frequency of certain of the crossover classes.

If the Df is close to Lg, then the + + a crossover chromatids would possess the Df and the gl lg + chromatids would have a N chromosome 3. Since the Df 3 N 9 spores abort, a ratio of 1 + + a: 2 gl lg + would be expected. The observed ratio was 44: 83. Among the double crossover strands a ratio of 2 + lg + : 1 gl + a would be expected and the observed numbers were 32: 19. The above calculations are based on the assumption that all crossing over between Lg and A occurs to the right of the deficiency. If the Df were very close to A, then the ratios of the single and double crossover classes would be the reverse of those given above. Equal amounts of crossing over between Lg-Df and Df-A would produce 1:1 ratios of the crossover classes. The unequal frequencies of the crossover classes indicate that the Df is much closer to Lg than to A. This conclusion is supported by the male B.C. data in

Table 1.

		(0) + + +	(0) gl lg a	(1) + lg a	(1) gl + +	(2) + + a	(2) gl lg +	(1-2) + lg +	(1-2) gl + a
1. $\frac{\text{Dp 9}}{\text{N 9}}$ $\frac{+\ \ +\ \ \text{Df}\ \ +}{\text{gl lg N a}}$	♀ B.C.	275	504	292	147	44	83	32	19
	Σ = 1396	Gl-Lg = 35.1%				Lg-A = 12.8%			
2. $\frac{\text{Dp 9}}{\text{N 9}}$ $\frac{+\ \ +\ \ \text{Df}\ \ +}{\text{gl lg N a}}$	♂ B.C.	176	368	151	83	51	112	27	13
	Σ = 981	Gl-Lg = 27.9%				Lg-A = 20.7%			
3. $\frac{\text{Dp 9}}{\text{N 9}}$ $\frac{+\ \ +\ \ \text{N}\ \ +}{\text{gl lg N a}}$	♀ B.C.	347	338	154	168	155	156	32	53
	Σ = 1403	Gl-Lg = 29.0%				Lg-A = 28.2%			
4. $\frac{\text{Dp 9}}{\text{N 9}}$ $\frac{+\ \ +\ \ \text{N}\ \ +}{\text{gl lg N a}}$	♂ B.C.	466	339	119	128	150	178	49	38
	Σ = 1467	Gl-Lg = 22.7%				Lg-A = 28.3%			
5. $\frac{\text{N 9}}{\text{N 9}}$ $\frac{+\ \ +\ \ \text{N}\ \ +}{\text{gl lg N a}}$	♀ B.C.	381	370	168	180	188	200	41	55
	Σ = 1583	Gl-Lg = 28.0%				Lg-A = 30.6%			
6. $\frac{\text{N 9}}{\text{N 9}}$ $\frac{+\ \ +\ \ \text{N}\ \ +}{\text{gl lg N a}}$	♂ B.C.	64	42	17	38	28	14	9	8
	Σ = 220	Gl-Lg = 32.7%				Lg-A = 26.8%			

which there were 51 + + a : 112 gl lg + single crossovers and 27 + lg +: 13 gl + a double crossovers. The data are consistent and place the Df between the Lg and A loci but much closer to Lg than to A.

Extensive data from Drosophila has demonstrated that a duplicated segment markedly reduces crossing over in the homologous segments of two structurally normal chromosomes. Since a comparable experiment has never been made with plants, it seemed desirable to test the effect of the piece of 3L inserted into 9S on crossing over in two normal chromosomes 3. The data listed in items 3, 4, 5, and 6 of Table 1, which are from full sibs of the Dp 9/ N 9 Df 3/ N 3 plants described above,

Table 2.

			(0) + + +	(0) sh bz wx	(1) + bz wx	(1) sh + +	(2) + + wx	(2) sh bz +	(1-2) + bz +	(1-2) sh + wx	Crossover percentages Sh-Bz	 Bz-Wx	
1.	$\frac{+\ \ +\ \ Dp\ \ +}{sh\ bz\ N\ \ wx}\ \frac{N\ 3}{N\ 3}$	♀ B.C.	5371	5391	8	6	103	95	1	0	0.14	1.8	$\Sigma = 10975$
2.	$\frac{+\ \ +\ \ Dp\ \ +}{sh\ bz\ N\ \ wx}\ \frac{N\ 3}{N\ 3}$	♂ B.C.	687	2956	34 (26?)	5	5	68	2	0	0.39?	2.0	$\Sigma = 3757$
3.	$\frac{+\ \ +\ \ Dp\ \ +}{sh\ bz\ N\ \ wx}\ \frac{Df\ 3}{N\ \ 3}$	♂ B.C.	2267	1817	7	15	34	18	0	0	0.5	1.3	$\Sigma = 4158$
4.	$\frac{+\ \ +\ \ Dp\ \ +}{sh\ bz\ N\ \ wx}\ \frac{Df\ 3}{N\ \ 3}$	♀ B.C.	1808	921	3	5	60	27	0	0	0.3	3.1	$\Sigma = 2824$

Table 3.

			(0) + + +	(0) yg sh wx	(1) + sh wx	(1) yg + +	(2) + + wx	(2) yg sh +	(1-2) yg + wx	(1-2) + sh +	Crossover percentages Yg-Sh	 Sh-Wx	
1.	$\frac{+\ \ +\ \ Dp\ \ +}{yg\ sh\ N\ \ wx}\ \frac{N\ 3}{N\ 3}$	♀ B.C.	1174	1033	22	21	18	10	2	0	1.96	1.32	$\Sigma = 2280$

show that the presence of the duplicated piece of 3L in 9S caused no significant reduction in crossing over in either the Gl-Lg or Lg-A regions when the two chromosomes 3 are structurally normal.

Having located in 3L the original site of the transposed segment, we next turned our attention to the effect of the inserted piece on crossing over in 9S and to the determination of the place of insertion. Plants of Dp 9/ N 9 N 3/ N 3 constitution, with the Dp 9 carrying normal alleles of chromosome 9 markers and the N 9 possessing the recessive sh bz wx alleles, were used in backcrosses both as the female and male parent. The female B.C. data are given in line 1, Table 2. It is evident that crossing over in the two marked regions of 9S is greatly reduced. A similar reduction was found in female backcrosses of + + Dp +/ sh bz N wx/ Df 3/ N 3 plants as is shown in line 4 of Table 2.

When + + Dp +/ sh bz N wx Df 3/ N 3 plants were used as the male parents the data shown in line 3 were obtained. The data from backcrosses of + + Dp +/ sh bz N wx N 3/ N 3 plants as the pollen parents are given in line 2. There is some uncertainty about the recombination values of the Sh-Bz region in the latter cross because, in a number of kernels, classification for sh was difficult. Of the 34 + bz wx kernels, only 8 were proven to be + bz wx and the remainder could not be tested. A number of others that had been included in this class, later were shown to be sh bz wx. Therefore, the recombination percentage is uncertain from this cross.

In order to test the effect of the Dp on crossing over in the distal portion of 9S, backcrosses using + + Dp +/ yg sh N wx N 3/ N 3 plants as the female parents were made and the data in Table 3 were obtained.

The great reduction in crossing over throughout the length of 9S was wholly unexpected and is in contrast to the much smaller effect on crossing over found in chromosome 3 with the heterozygous Df. In both Dp 9/N 9 and Df 3/N 3 bivalents the size of the unpaired segment is precisely the same, yet a much greater reduction in crossing over took place in chromosome 9 than in chromosome 3. This may well be related to the more frequent occurrence of non-homologous pairing in Dp 9/N 9 bivalents than in Df 3/ N 3 bivalents.

The place of insertion of the 3L segment into 9S was determined to be between Bz and Wx. Among 85 crossovers between Bz and Wx which were analyzed for the presence or absence of the Dp, there occurred 3 to the left of the Dp and 82 to the right of the Dp. The Dp is therefore inserted between Bz and Wx but is much closer to Bz than to the Wx locus. Tests to determine which of the chromosome 3 loci are included in the transposed segment have been negative to date. The loci known not to be included are lg_2, pm, na, gl_6 and ts_4--all of which are proximal to A.

2. Relation of crossing over to preferential segregation.

Some years ago, I advanced the hypothesis that preferential segregation caused by abnormal 10 occurred only when a crossover (or crossovers) resulted in the formation of dyads composed of a knobbed and a knobless chromatid, and that the knobbed chromatid was preferentially segregated to the basal megaspore from which the embryo sac was derived. In the presence of abnormal 10, either heterozygous or homozygous, other chromosomes of the complement also undergo preferential segregation if one homologue is knobbed and the other knobless. The preferential segregation of heteromorphic homologues other than chromosome 10 was first demonstrated by Longley whose observations have been amply confirmed in this laboratory. According to the hypothesis that preferential segregation occurs only when heteromorphic dyads are produced, and it is the knobbed chromatid which segregates preferentially at anaphase II, those loci closer to the knob would undergo a higher degree of preferential segregation than would more distant loci. There is abundant evidence that this is so (for example, see Kikudome's report in this News Letter).

A test of the hypothesis that preferential segregation is dependent upon crossing over giving heteromorphic dyads was made possible by studying the ratios of genes in 9S from plants in which the amount of crossing over was greatly reduced compared to that in sibs in which recombination was normal. Such a test was made using the Dp9 chromosome described earlier in this report since it was demonstrated that the amount of crossing over in Dp9/N9 plants is greatly reduced in 9S. Sib plants of three classes, all heterozygous for abnormal 10, were obtained. One class was of Dp9/N9 constitution. The chromosome with the Dp had a small terminal knob (K^s) on 9S and carried the *yg* allele while the N9 had a much larger knob (K^m) and the *Yg* allele. The second class of plants was of N9/N9 constitution. One chromosome 9 had the prominent knob and the *Yg* allele; the other possessed the small knob and the *yg* allele. The third class had two N9's, one with the small knob and the *yg* allele, the other possessing the *wd* allele and wholly devoid of a knob. All three classes were heterozygous for abnormal 10 and had heteromorphic chromosomes 9. Preferential segregation takes place when the two chromosomes 9 differ in knob size (as convincingly demonstrated by Kikudome in this News Letter) so studies of preferential segregation were made. The first two classes were pollinated by *yg* plants and the ratio of *Yg*: *yg* plants obtained. The third class was pollinated by *wd* pollen and the *yg*: *wd* ratio determined. In back crosses of K^m *Yg* N/K^s *yg* Dp plants, in which crossing over is greatly reduced in 9S the *Yg* plants constituted 54.7% of the offspring. Plants of K^m *Yg* N/K^s *yg* N constitution with normal crossing over in 9S gave 65.2% of *Yg* plants. Individuals of K^s *yg* N/k *wd* N genotype, again with no reduction in crossing over, produced 60.4% *yg* seedlings. Data from K^s *yg* Dp/k *wd* N plants have not yet been obtained. Control data from closely related plants of K^s *yg* N/k *wd* N constitution and homozygous for N10 gave 50.2% *yg* plants. The data from the above crosses are