

A CORRELATION OF CYTOLOGICAL AND GENETICAL CROSS-
ING-OVER IN ZEA MAYS

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A requirement for the genetical study of crossing-over is the heterozygous condition of two allelomorphous factors in the same linkage group. The analysis of the behavior of homologous or partially homologous chromosomes, which are morphologically distinguishable at two points, should show evidence of cytological crossing-over. It is the aim of the present paper to show that cytological crossing-over occurs and that it is accompanied by genetical crossing-over.

In a certain strain of maize the second-smallest chromosome (chromosome 9) possesses a conspicuous knob at the end of the short arm. Its distribution through successive generations is similar to that of a gene. If a plant possessing knobs at the ends of both of its 2nd-smallest chromosomes is crossed to a plant with no knobs, cytological observations show that in the resulting F_1 individuals only one member of the homologous pair possesses a knob. When such an individual is back-crossed to one having no knob on either chromosome, half of the offspring are heterozygous for the knob and half possess no knob at all. The knob, therefore, is a constant feature of the chromosome possessing it. When present on one chromosome and not on its homologue, the knob renders the chromosome pair visibly heteromorphic.

In a previous report¹ it was shown that in a certain strain of maize an interchange had taken place between chromosome 8 and 9. The interchanged pieces were unequal in size; the long arm of chromosome 9 was increased in relative length, whereas the long arm of chromosome 8 was correspondingly shortened. When a gamete possessing these two interchanged chromosomes meets a gamete containing a normal chromosome set, meiosis in the resulting individual is characterized by a side-by-side synapsis of homologous parts (see diagram, figure 1 of preceding paper). Therefore, it should be possible to have crossing-over between the knob and the interchange point.

In the previous report it was also shown that in such an individual the only functioning gametes are those which possess either the two normal chromosomes (N, n) or the two interchanged chromosome (I, i), i.e., the full genom in one or the other arrangement. The functional gametes therefore possess either the shorter, normal, knobbed chromosome (n) or the longer, interchanged, knobbed chromosome (I). Hence, when such a plant is crossed to a plant possessing the normal chromosome complement,

the presence of the normal chromosome in functioning gametes of the former will be indicated by the appearance of ten bivalents in the prophase of meiosis of the resulting individuals. The presence of the interchanged

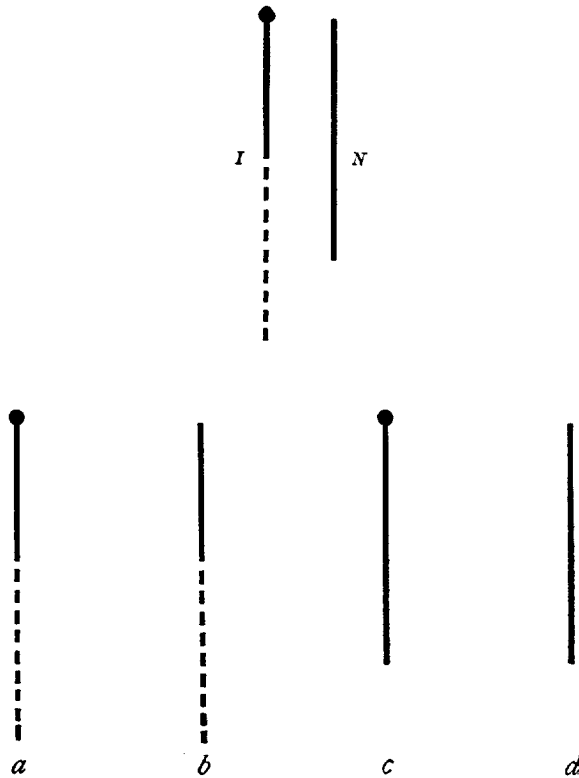


FIGURE 1

Above—Diagram of the chromosomes in which crossing-over was studied. (Labeled as in figure 1, preceding paper.)

Below—Diagram of chromosome types found in gametes of a plant with the constitution shown above.

- a*—Knobbed, interchanged chromosome.
 - b*—Knobless, interchanged chromosome.
 - c*—Knobbed, normal chromosome.
 - d*—Knobless, normal chromosome.
- a* and *d* are non-crossover types.
b and *c* are crossover types.

chromosome in other gametes will be indicated in other F_1 individuals by the appearance of eight bivalents plus a ring of four chromosomes in the late prophase of meiosis.

If a gamete possessing a normal chromosome number 9 with no knob,

meets a gamete possessing an interchanged chromosome with a knob, it is clear that these two chromosomes which synapse along their homologous parts during prophase of meiosis in the resulting individual are visibly different at each of their two ends. If no crossing-over occurs, the gametes formed by such an individual will contain either the knobbed, interchanged chromosome (*a*, Fig. 1) or the normal chromosome without a knob (*d*, Fig. 1). Gametes containing either a knobbed, normal chromosome (*c*,

TABLE 1

CULTURE	KNOB-INTERCHANGED KNOBLESS-NORMAL × KNOBLESS-NORMAL, CULTURE 337 AND KNOBBED-NORMAL CULTURES A125 AND 340			
	PLANTS POSSESSING 2 NORMAL CHROMOSOMES		PLANTS POSSESSING AN INTERCHANGED CHROMOSOME	
	NON-CROSSOVERS	CROSSOVERS	NON-CROSSOVERS	CROSSOVERS
337	8	3	6	2
A125	39	31	36	23
340	5	3	5	3
Totals	52	37	47	28

Fig. 1) or a knobless, interchanged chromosome (*b*, Fig. 1) will be formed as a result of crossing-over. If such an individual is crossed to a plant possessing two normal knobless chromosomes, the resulting individuals will be of four kinds. The non-crossover gametes would give rise to individuals which show either (1) ten bivalents at prophase of meiosis and no knob on chromosome 9, indicating that a gamete with a chromosome of type *d* has functioned or (2) a ring of four chromosomes with a single conspicuous knob, indicating that a gamete of type *a* has functioned. The crossover types will be recognizable as individuals which possess either (1) ten bivalents and a single knob associated with bivalent chromosome 9 or

TABLE 2

<i>C-wx</i>		$\frac{\text{KNOB-}C\text{-}wx}{\text{KNOBLESS-}c\text{-}Wx} \times \text{KNOBLESS-}c\text{-}wx$		<i>C-Wx</i>		<i>c-wx</i>	
Knob	Knobless	Knob	Knobless	Knob	Knobless	Knob	Knobless
12	5	5	34	4	0	0	3

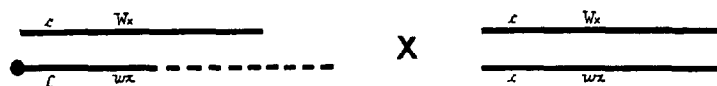
(2) a ring of four chromosomes with no knob, indicating that crossover gametes of types *c* and *b*, respectively, have functioned. The results of such a cross are given in culture 337, table 1. Similarly, if such a plant is crossed to a normal plant possessing knobs at the ends of both number 9 chromosomes and if crossing-over occurs, the resulting individuals should be of four kinds. The non-crossover types would be represented by (1) plants homozygous for the knob and possessing the interchanged chromosome and (2) plants heterozygous for the knob and possessing two normal chromosomes. The functioning of gametes which had been produced as the result of crossing-over between the knob and the interchange would give rise to (1) individuals heterozygous for the knob and possessing the

interchanged chromosome and (2) those homozygous for the knob and possessing two normal chromosomes. The results of such crosses are given in cultures A125 and 340, table 1. Although the data are few, they are consistent. The amount of crossing-over between the knob and the interchange, as measured from these data, is approximately 39%.

In the preceding paper it was shown that the knobbed chromosome carries the genes for colored aleurone (*C*), shrunken endosperm (*sh*) and waxy endosperm (*wx*). Furthermore, it was shown that the order of these genes, beginning at the interchange point is *wx-sh-c*. It is possible, also, that these genes all lie in the short arm of the knobbed chromosome. Therefore, a linkage between the knob and these genes is to be expected.

One chromosome number 9 in a plant possessing the normal complement had a knob and carried the genes *C* and *wx*. Its homologue was knobless and carried the genes *c* and *Wx*. The non-crossover gametes should contain a knobbed-*C-wx* or a knobless-*c-Wx* chromosome. Crossing-over in region 1 (between the knob and *C*) would give rise to knobless *C-wx* and knobbed-*c-Wx* chromosomes. Crossing-over in region 2 (between *C* and *wx*) would give rise to knobbed-*C-Wx* and knobless-*c-wx* chromosomes. The results of crossing such a plant to a knobless-*c-wx* type are given in table 2. It would be expected on the basis of interference that the knob and *C* would remain together when a crossover occurred between *C* and *wx*; hence, the individuals arising from colored starchy (*C-Wx*) kernels should possess a knob, whereas those coming from colorless, waxy (*c-wx*) kernels should be knobless. Although the data are few they are convincing. It is obvious that there is a fairly close association between the knob and *C*.

To obtain a correlation between cytological and genetic crossing-over it is necessary to have a plant heteromorphic for the knob, the genes *c* and *wx* and the interchange. Plant 338 (17) possessed in one chromosome the knob, the genes *C* and *wx* and the interchanged piece of chromosome 8. The other chromosome was normal, knobless and contained the genes *c* and *Wx*. This plant was crossed to an individual possessing two normal, knobless chromosomes with the genes *c-Wx* and *c-wx*, respectively. This cross is diagrammed as follows:



The results of the cross are given in table 3. In this case all the colored kernels gave rise to individuals possessing a knob, whereas all the colorless kernels gave rise to individuals showing no knob.

The amount of crossing-over between the knob and the interchange

point is approximately 39% (Table 1), between *c* and the interchange approximately 33%, between *wx* and the interchange, 13% (preceding paper). With this information in mind it is possible to analyze the data given in table 3. The data are necessarily few since the ear contained but few kernels. The three individuals in class I are clearly non-crossover types. In class II the individuals have resulted from a crossover in region 2,

TABLE 3

PLANT NUMBER	$\frac{\text{KNOB-C-}wx\text{-INTERCHANGED}}{\text{KNOBLESS-c-Wx-NORMAL}}$	\times	$\frac{\text{KNOBLESS-c-Wx-NORMAL}}{\text{KNOBLESS-c-wx-NORMAL}}$	INTERCHANGED OR NORMAL	
Class I, <i>C-wx</i> kernels					
1			Knob	Interchanged	
2			Knob	Interchanged	
3			Knob	Interchanged	
Class II, <i>c-wx</i> kernels					
1			Knobless	Interchanged	
2			Knobless	Interchanged	
Class III, <i>C-Wx</i> kernels					
1			Knob	Normal	<i>Pollen</i> <i>WxWx</i>
2			Knob	Normal
3			Normal	<i>WxWx</i>
5			Knob	Normal
6			Knob
7			Knob	Normal
8			Knob	Normal
Class IV, <i>c-Wx</i> kernels					
1			Knobless	Normal	<i>Wxwx</i>
2			Knobless	Normal	<i>Wxwx</i>
3			Knobless	Interchanged	<i>Wxwx</i>
4			Knobless	Normal	<i>Wxwx</i>
5			Knobless	Interchanged	<i>WxWx</i>
6			Knobless	Normal	<i>WxWx</i>
7			Knobless	Interchanged	<i>Wxwx</i>
8			Knobless	Interchanged	<i>WxWx</i>
9			Knobless	Normal	<i>WxWx</i>
10			Knobless	Normal	<i>WxWx</i>
11			Knobless	Normal	<i>Wxwx</i>
12			Knobless	Normal	<i>Wxwx</i>
13			Knobless	Normal	<i>WxWx</i>
14			Knobless	Normal	<i>WxWx</i>
15			Knobless	Normal	<i>Wx—</i>

i.e., between *c* and *wx*. In this case a crossover in region 2 has not been accompanied by a crossover in region 1 (between the knob and *C*) or region 3 (between *wx* and the interchange). All the individuals in class III had normal chromosomes. Unfortunately, pollen was obtained from only 1 of the 6 individuals examined for the presence of the knob. This one individual was clearly of the type expected to come from a gamete produced through crossing-over in region 2. Class IV is more difficult to analyze.

Plants 6, 9, 10, 13, and 14 are normal and $WxWx$; they therefore represent non-crossover types. An equal number of non-crossover types are expected among the normal $Wxwx$ class. Plants 1, 2, 4, 11 and 12 may be of this type. It is possible but improbable that they have arisen through the union of a $c-Wx$ gamete with a gamete resulting from a double crossover in region 2 and 3. Plants 5 and 8 are single crossovers in region 3, whereas plants 3 and 7 probably represent single crossovers in region 2 or 3.

The foregoing evidence points to the fact that cytological crossing-over occurs and is accompanied by the expected types of genetic crossing-over.

Conclusions.—Pairing chromosomes, heteromorphic in two regions, have been shown to exchange parts at the same time they exchange genes assigned to these regions.

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¹ McClintock, B., *Proc. Nat. Acad. Sci.*, 16, 791-796 (1930).
