A CORRELATION OF CYTOLOGICAL AND GENETICAL CROSSING-OVER IN ZEA MAYS

BY HARRIET B. CREIGHTON AND BARBARA MCCLINTOCK

BOTANY DEPARTMENT, CORNELL UNIVERSITY

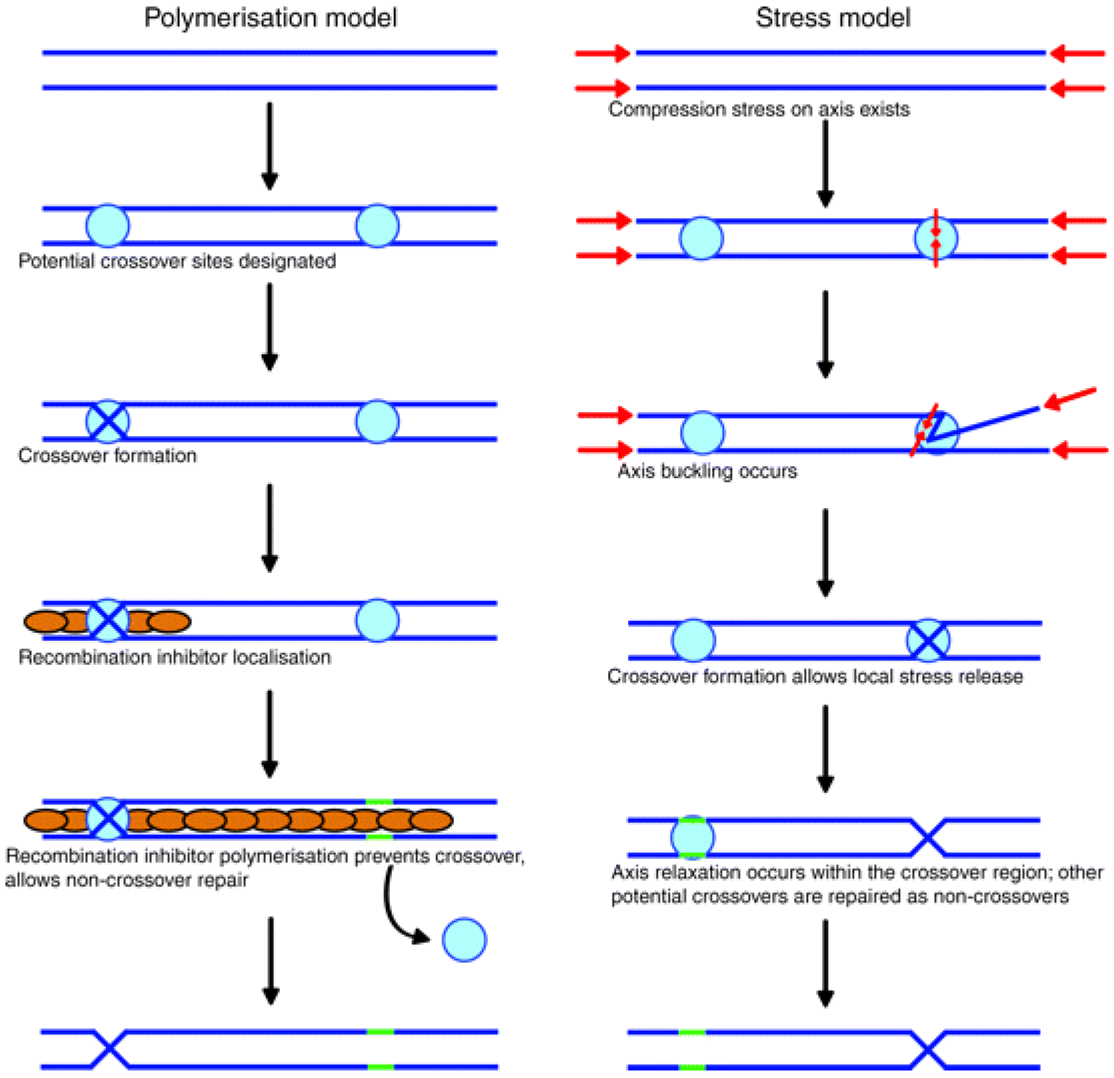
Communicated July 7, 1931

Methods & Logic

4.2.15

Interference

- Double strand breaks occur frequently and regularly, only a few repair by crossing-over
- Cross-over assurance- at least one cross-over event/chromosome
- Cross-over events regulated by # of DSB and mechanism of non-cross-over repair



Barbara McClinock (1902-1992)

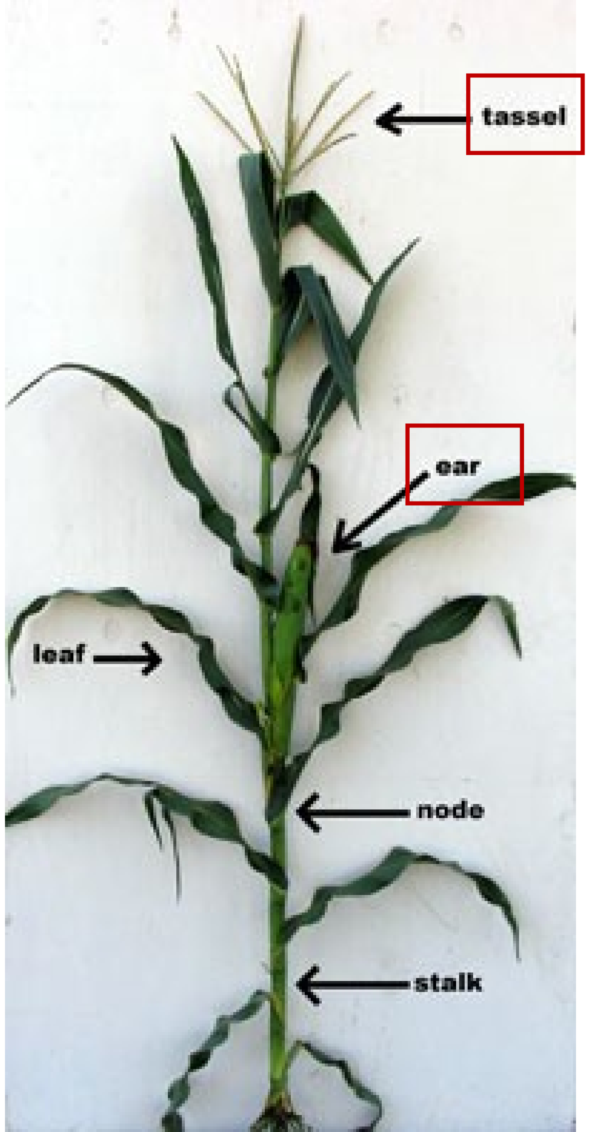
- 1923: Undergraduate at Cornell University
- 1927: PhD in Botany at Cornell University (Rollins Emerson)
- 1927-1931: Cornell University
- 1931-1933: National Research Counsel Fellowship at CalTech
- 1933-1934: received Guggenheim Fellowship to study in Germany
- 1934-1936: Cornell University
- 1936-1941: University of Missouri
- 1941-1967: Cold Spring Harbor
- 1957-1981: Traveled South America tracing the origin of races of maize

Barbara McClintock as a graduate student at Cornell, 1929. (L-R standing) Charles Burnham, Marcus Rhoades, Rollins Emerson, and Barbara McClintock. George Beadle is kneeling by the dog

Harriet B. Creighton (1909-2004)

- 1929 Undergraduate at Wellesley College
- 1933 PhD at Cornell University
- 1934-1940 Ass. Prof. at Connecticut College
- 1940-1974 Wellesley College

Maize-*Zea Mays*-Corn



Male: releases pollen

Female:
Each kernel contains one egg

One silk grows from each kernel

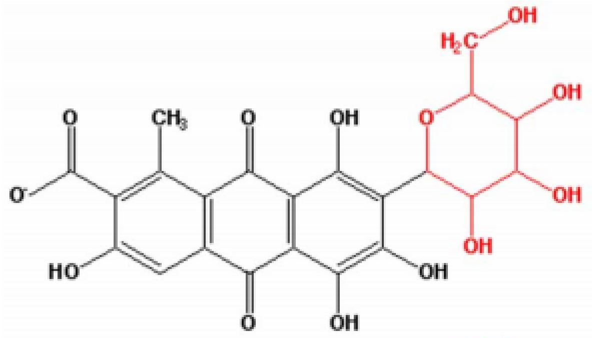
One pollen will bind one silk and grow to the kernel and fertilize the egg

McClintock’s Career Goal

- Create a map for the entire Maize genome

Identification of Maize Chromosomes

- McClintock took an assistant position under her advisor, a cytogenticist, where she learned many staining techniques
- Partnered with Dr. Randolph (cytogenetics and botanist) to investigate Maize chromosomes
  - Carmine Staining



- 1927: Randolph identified Maize has 10 chromosomes, but could not differentiate between the chromosomes
- 1929: McClintock published the ideogram of all 10 chromosomes

Maize cytogenetics

- 10 chromosomes
- Contain B chromosomes
  - Supernumerary or accessory chromosomes
  - Usually contain heterochromatin and are not essential for life
  - Required for Maize

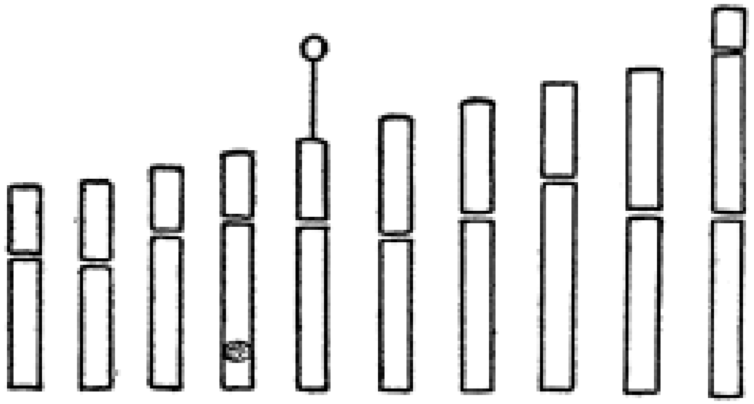
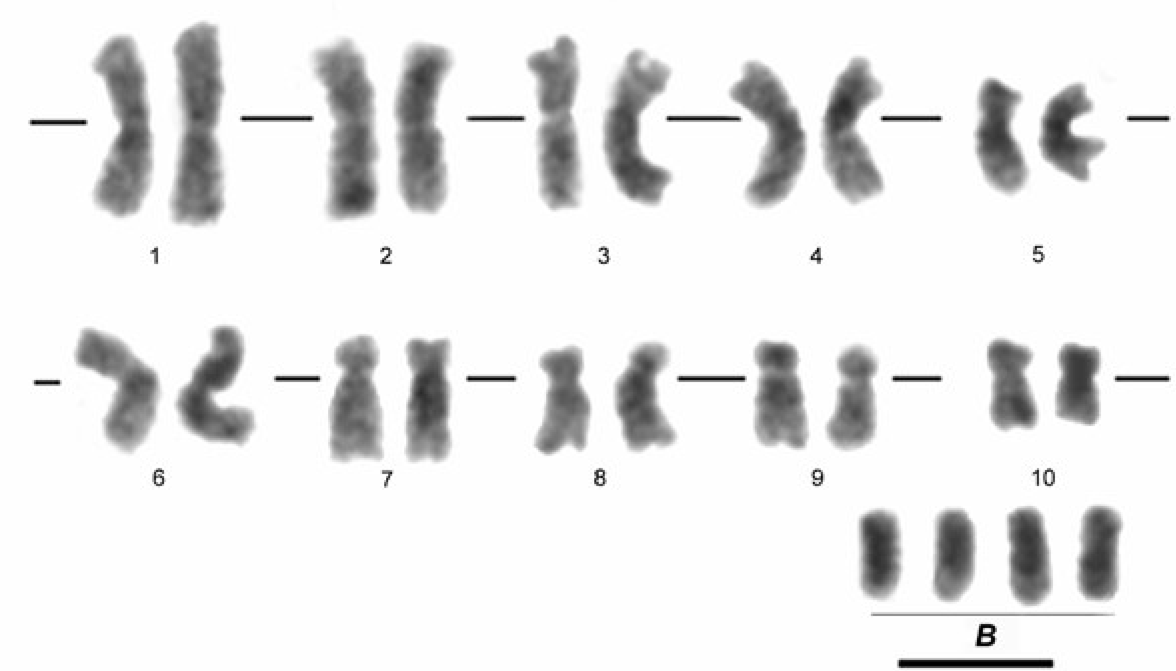


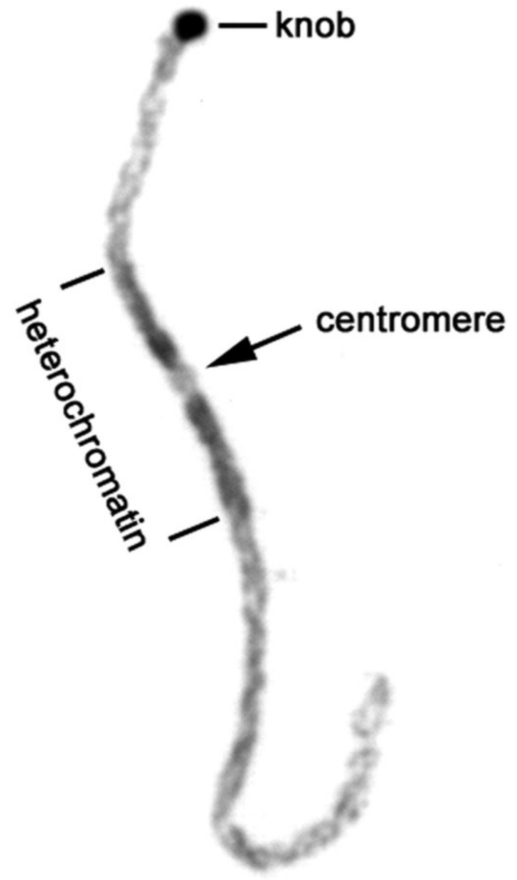
FIG. 1

McClintock. Science. 1929



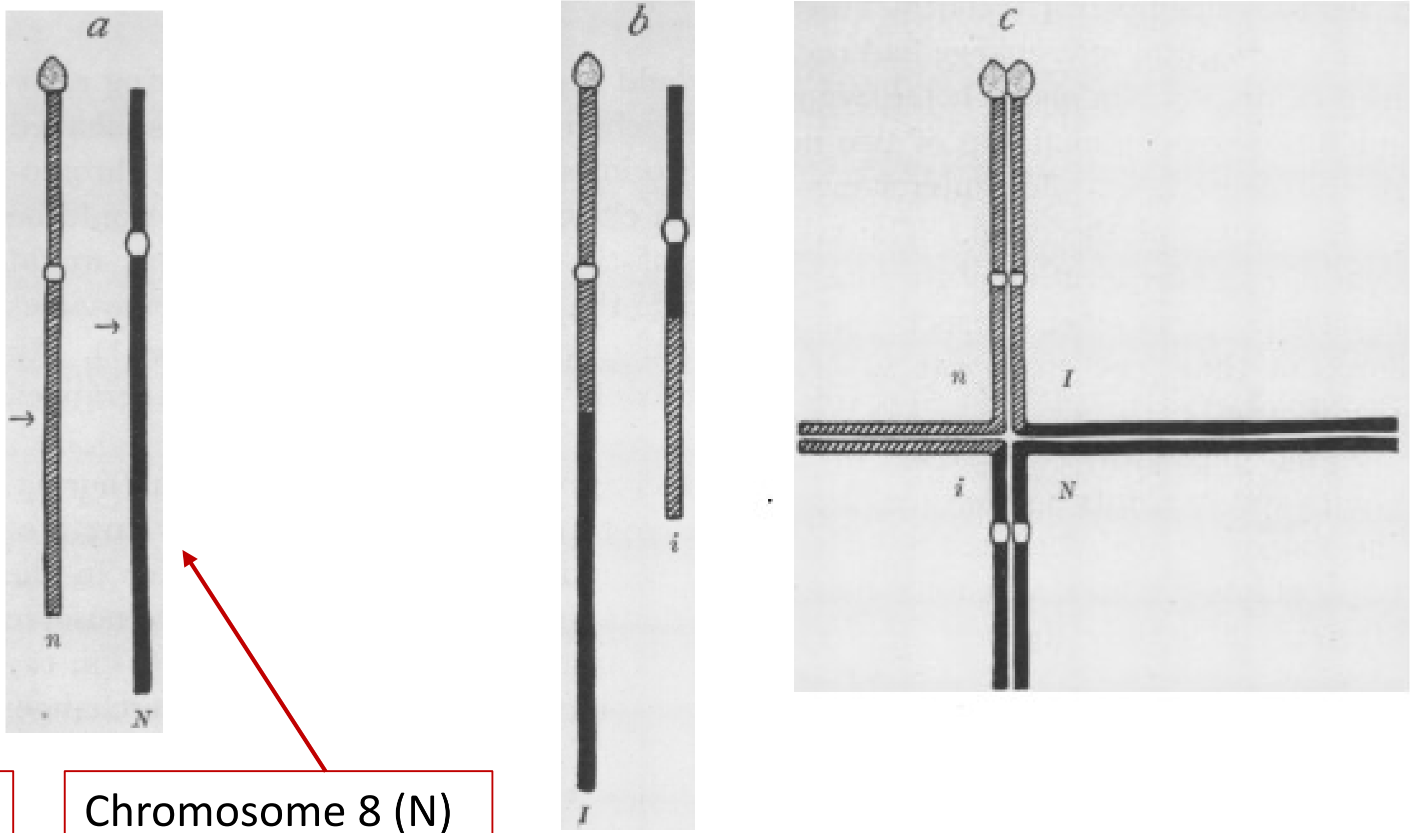
Chromosome 9

- Second smallest chromosome
- Some strains of Maize contain a knob at the end of the short arm
- Used as an identification marker
- Passed on as if it were a gene
  - First physical evidence of chromosomes passing their material to their offspring



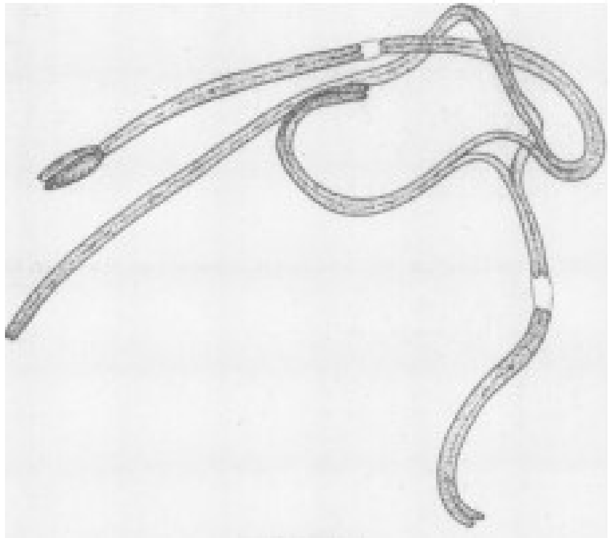
Anderson, et al. Genome Research. 2006

Interchange between two non-homologous chromosomes of *Zea Mays*



Chromosome 9 (n)

Chromosome 8 (N)



McClintock, PNAS 1930

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Figure 1: Diagram of chromosome 9 types

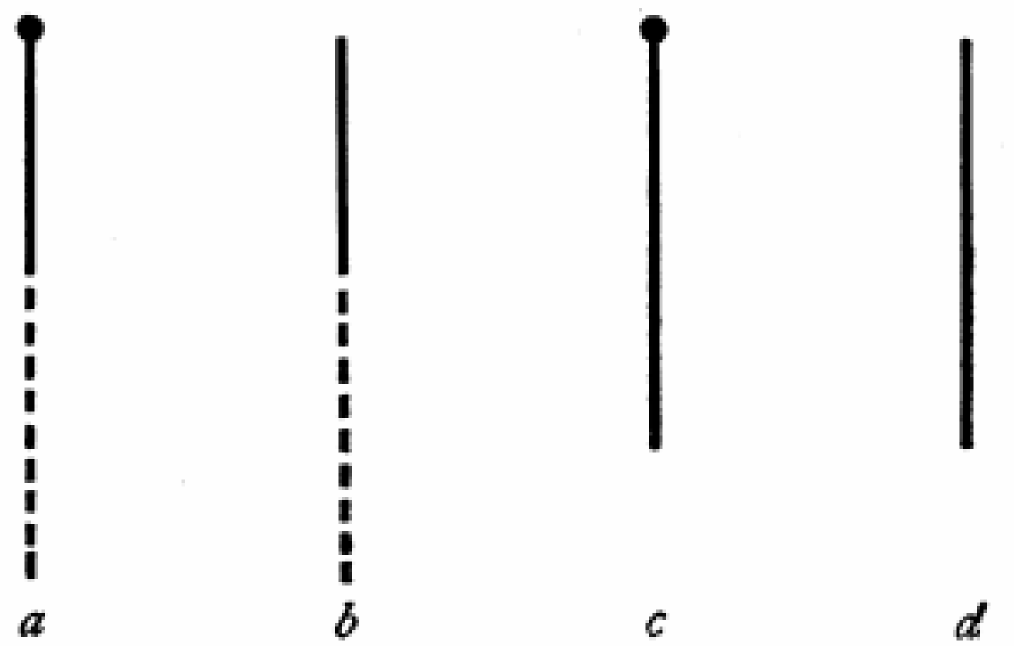
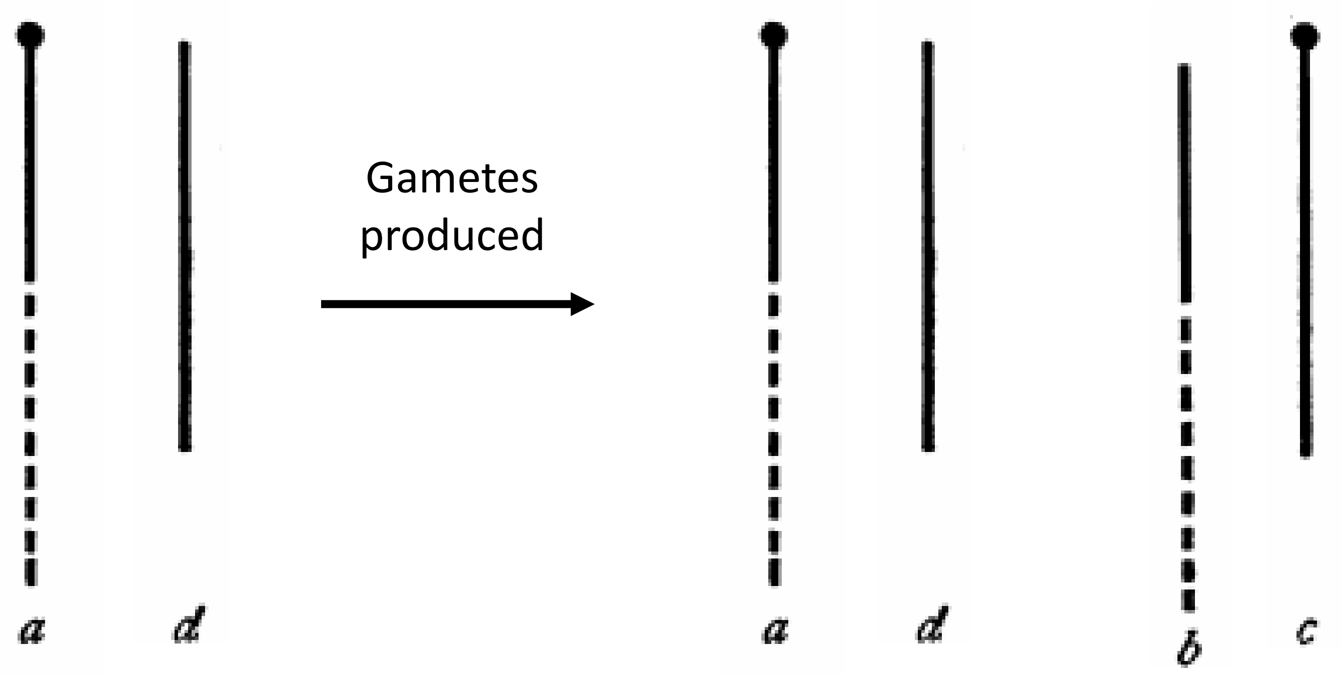


FIGURE 1

a—Knobbed, interchanged chromosome.
b—Knobless, interchanged chromosome.
c—Knobbed, normal chromosome.
d—Knobless, normal chromosome.

Heterzygote will produce different gametes if a cross-over even occurs

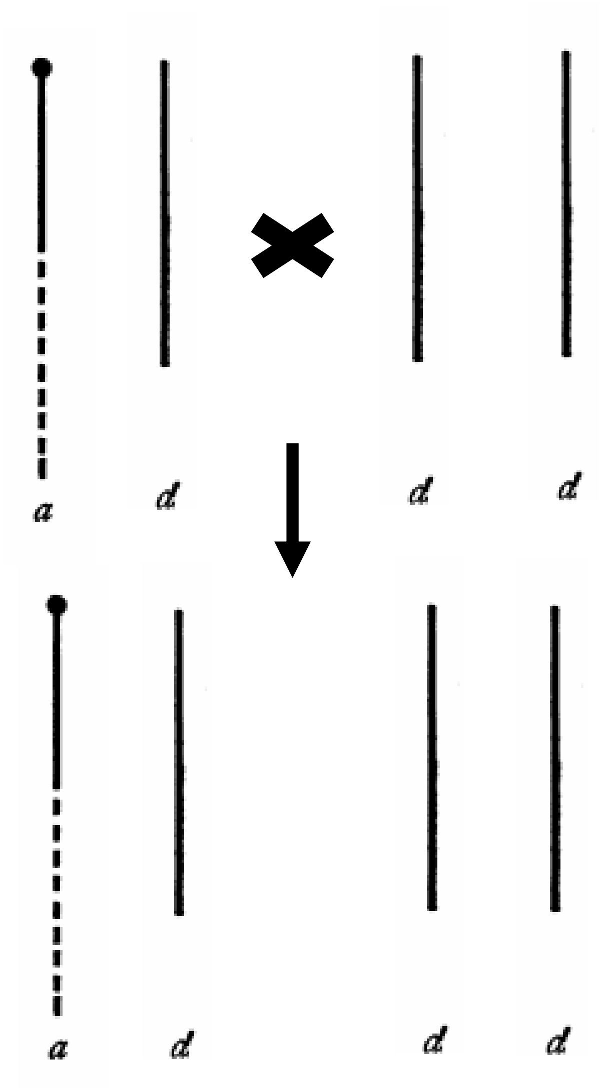


No crossing-over

Crossing-over event between the interchange and the knob

Culture 337

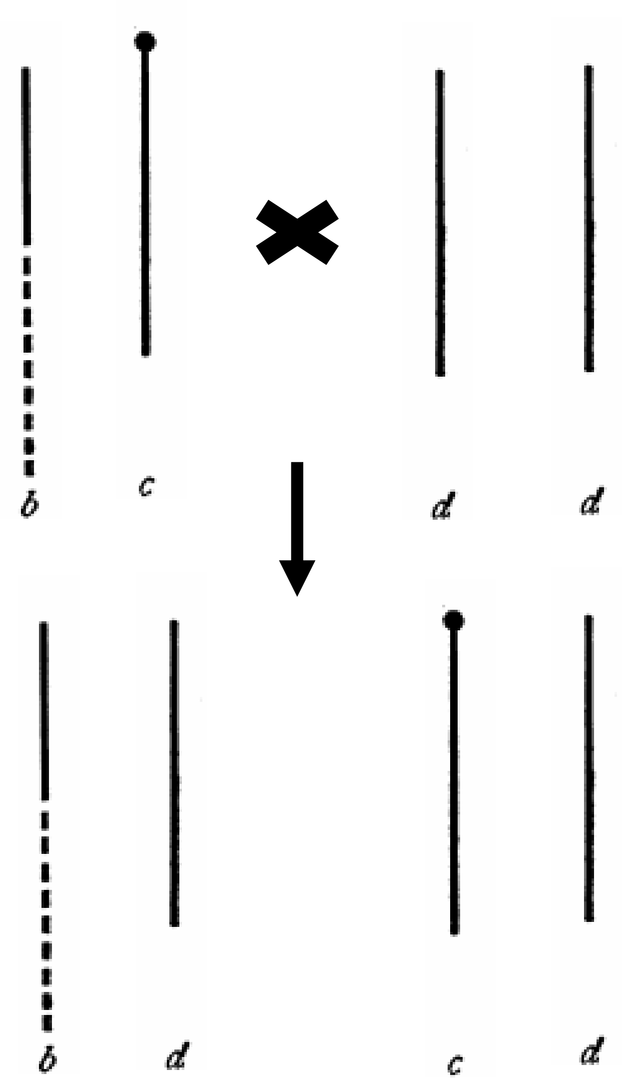
No crossing-over



6

8

crossing-over event

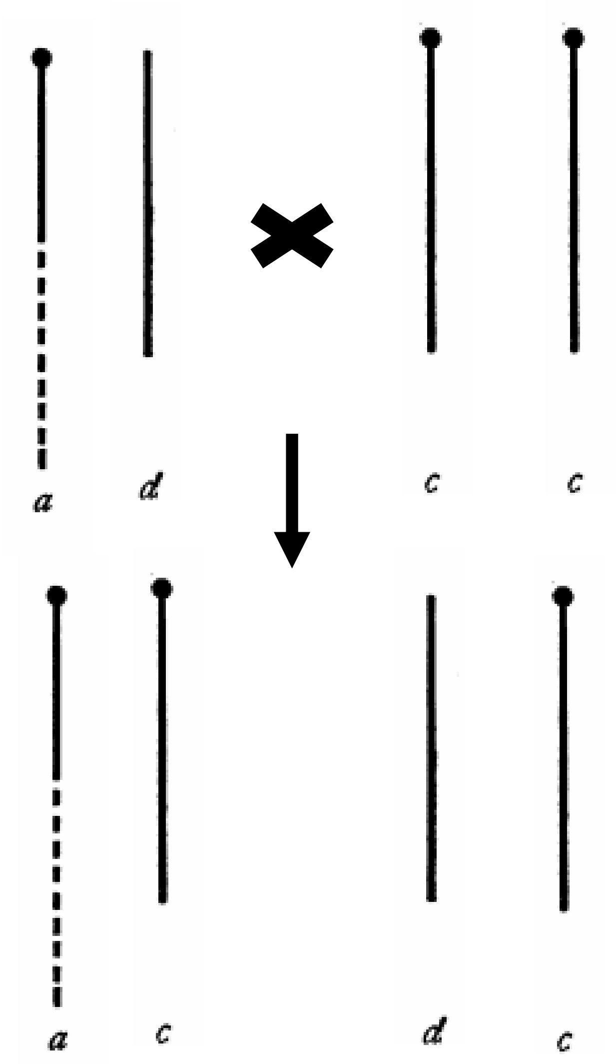


2

3

Cultures A125 & 340

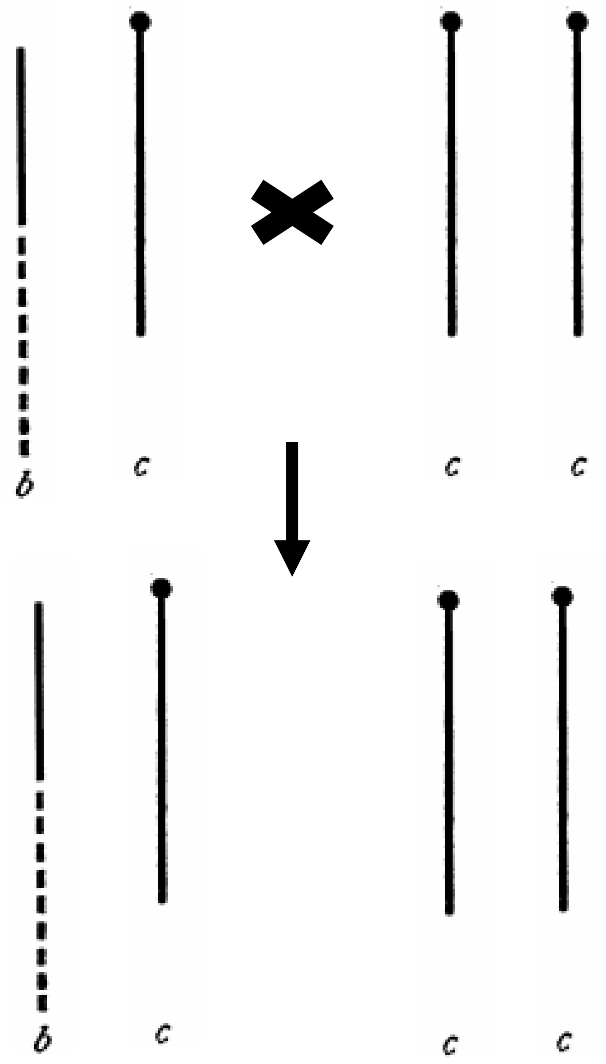
No crossing-over



36
5

39
5

crossing-over event



23
3

31
3

Percentage of Cross-overs

TABLE 1

$\frac{\text{KNOB-INTERCHANGED}}{\text{KNOBLESS-NORMAL}}$ × KNOBLESS-NORMAL, CULTURE 337 AND KNOBBED-NORMAL CULTURES A125 AND 340

CULTURE	PLANTS POSSESSING 2 NORMAL CHROMOSOMES		PLANTS POSSESSING AN INTERCHANGED CHROMOSOMES	
	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

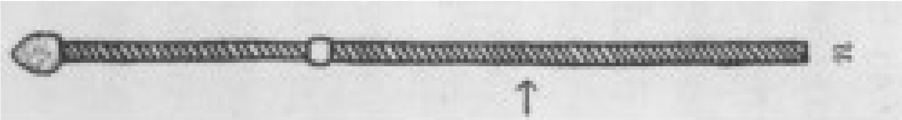
Cross-overs 37+28= 65
Total = 164

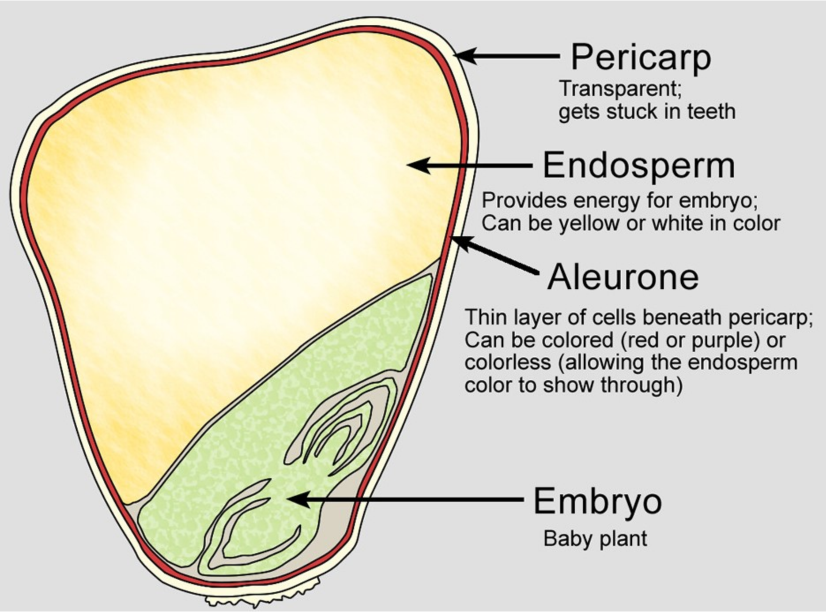
$$\frac{65}{164} \times 100 = 39\%$$

Traits on Chromosome 9

Letter	Dominant	Recessive
C,c	Colored aleurone	Colorless
Sh, sh	Wild type	Shrunken endosperm
Wx, wx	Wild type 75% amylopectin & 25% amylose	Waxy endosperm 100% amylopectin

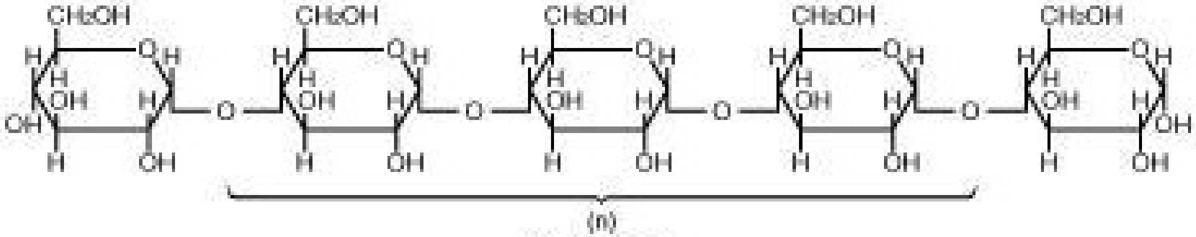
C Sh Wx





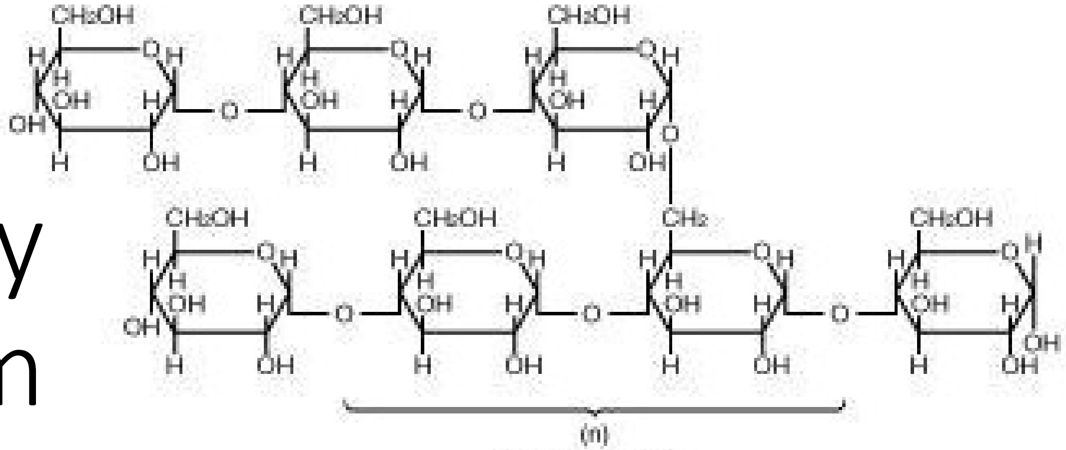
Colored Aleurone

Shrunken Endosperm



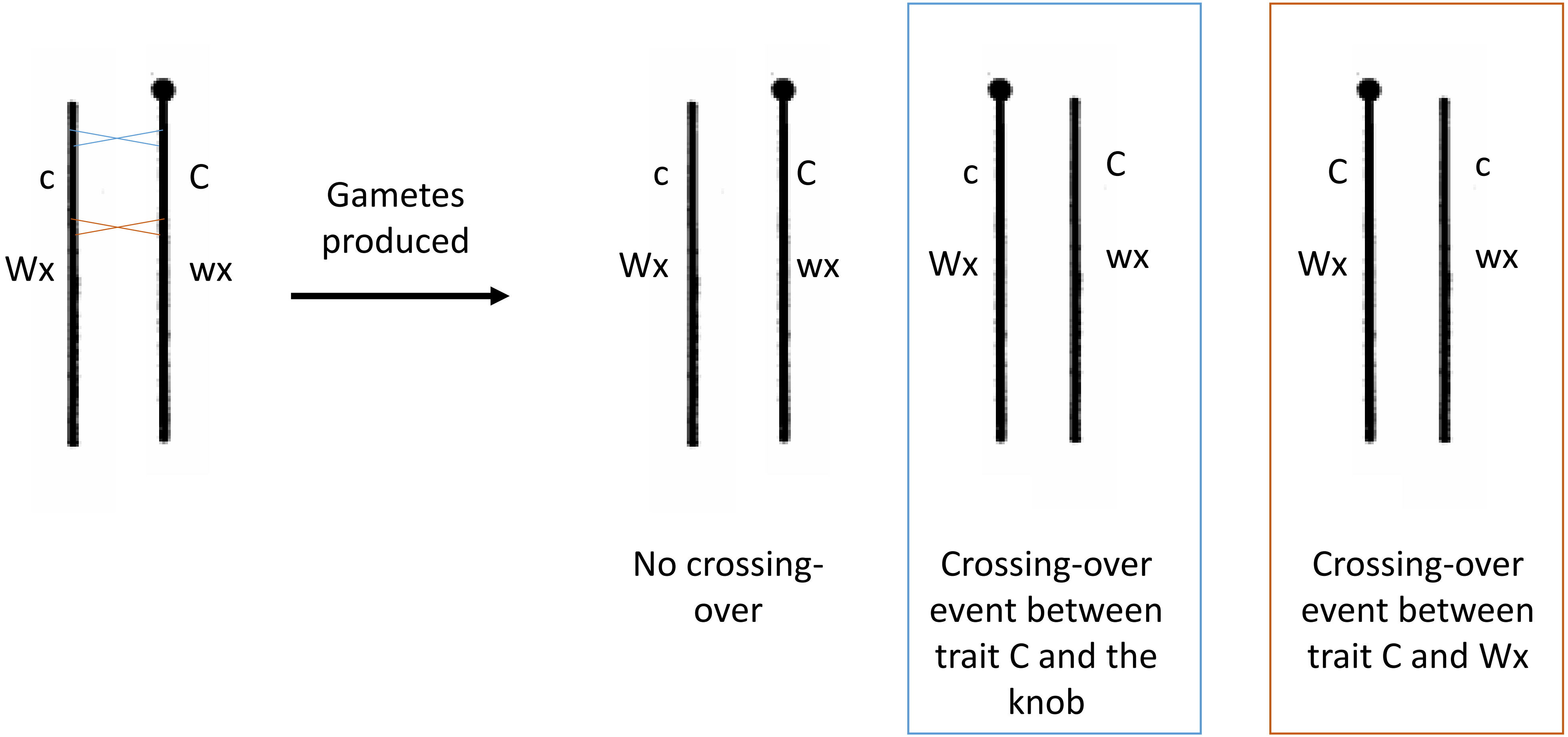
Amylose.

Waxy Endosperm



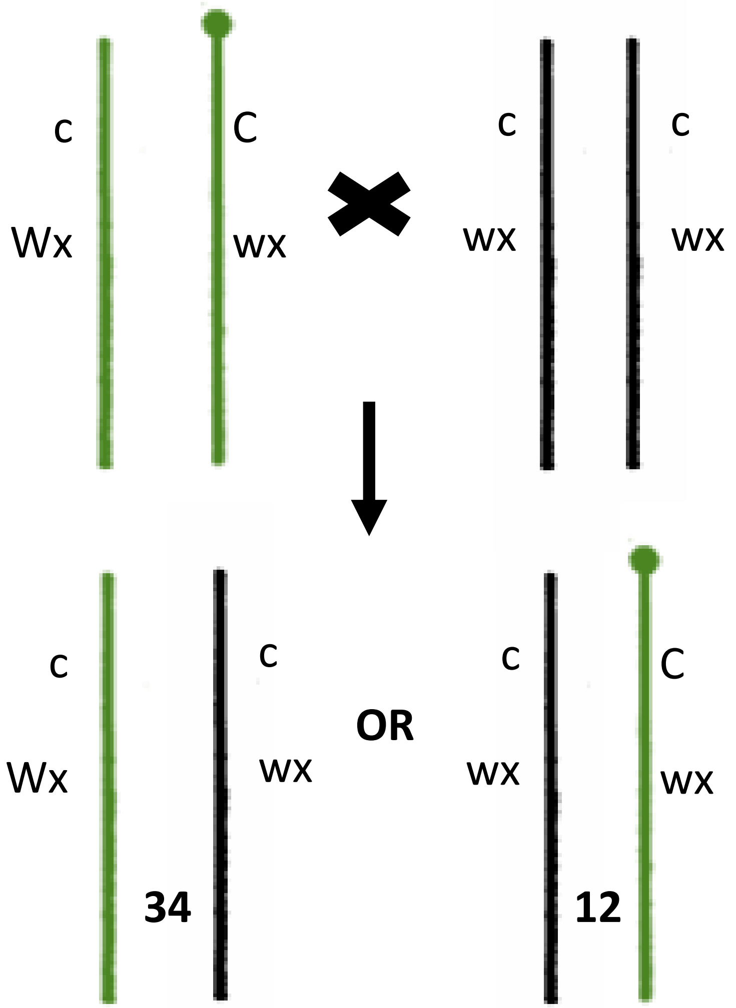
Amylopectin.

Table 2

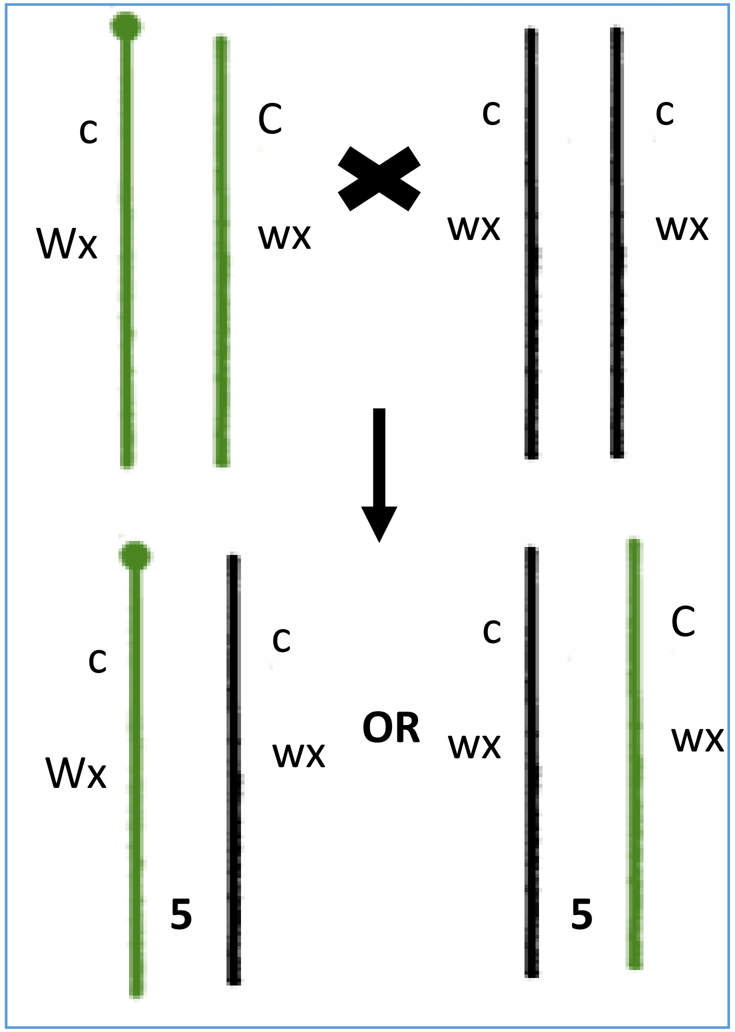

c
C
Wx
wx
Gametes produced
c
C
Wx
wx
c
C
Wx
wx
C
c
Wx
wx
No crossing-over
Crossing-over event between trait C and the knob
Crossing-over event between trait C and Wx

Close association between the knob, C and Wx

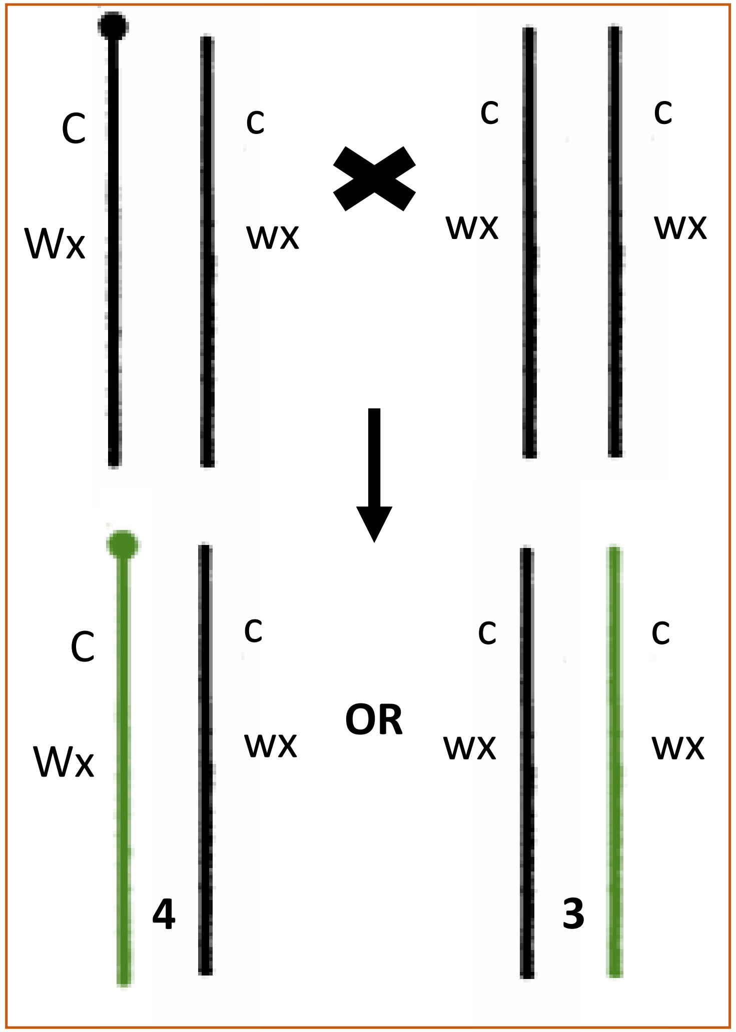
No crossing-over



crossing-over in Region 1

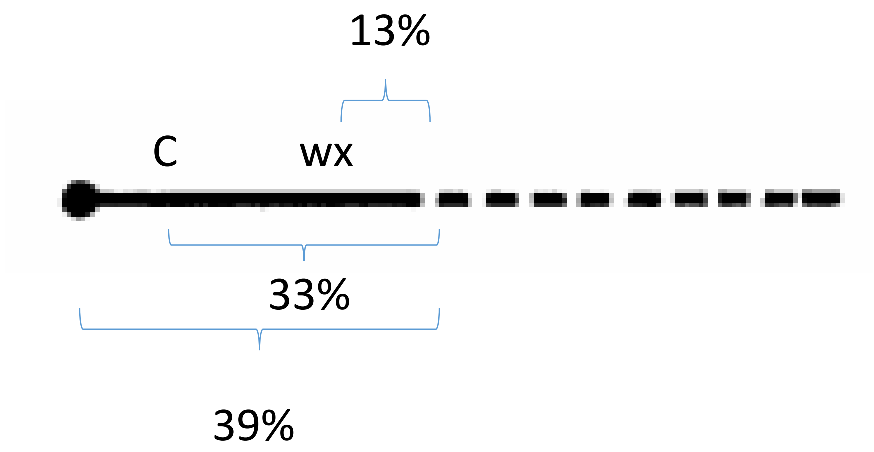


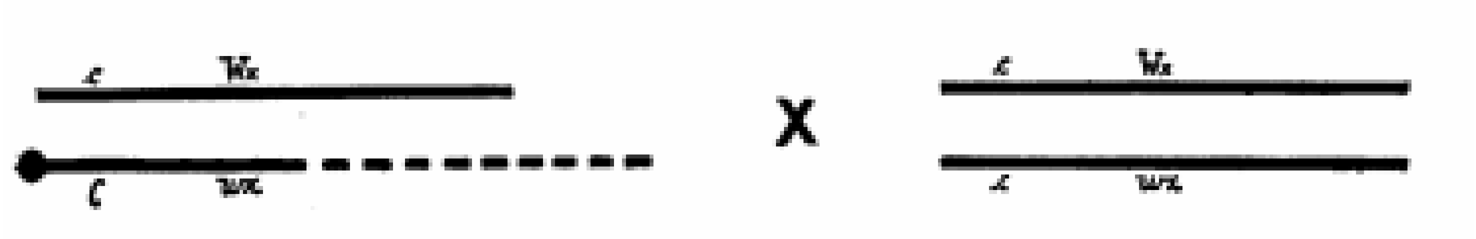
crossing-over in Region 2



Correlation between cytological and genetic crossing-over

- Requires a plant that:
  - Is hetermorphic for the knob
  - Contains genes *c* and *wx*
  - Contains chromosome 8/9 interchange





Cytological crossing-over occurs and is accompanied by the expected types of genetic crossing-over

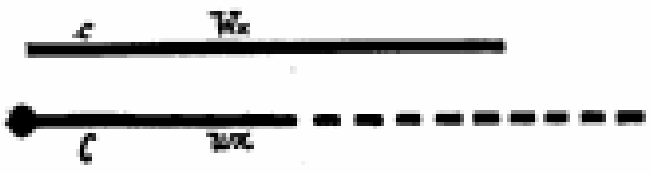


TABLE 3

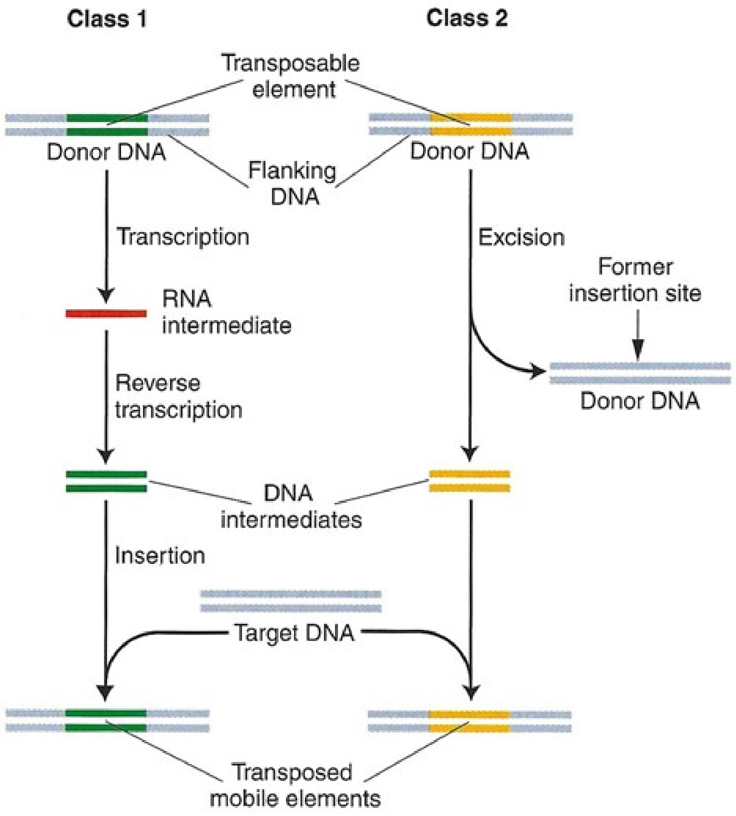
$\frac{\text{KNOB-}C\text{-}wx\text{-INTERCHANGED}}{\text{KNOBLESS-}c\text{-}Wx\text{-NORMAL}} \times \frac{\text{KNOBLESS-}c\text{-}Wx\text{-NORMAL}}{\text{KNOBLESS-}c\text{-}wx\text{-NORMAL}}$

PLANT NUMBER	KNOBBED OR KNOBLESS	INTERCHANGED OR NORMAL	
Class I, *C-wx* kernels			
1	Knob	Interchanged	
2	Knob	Interchanged	
3	Knob	Interchanged	
Class II, *c-wx* kernels			
1	Knobless	Interchanged	
2	Knobless	Interchanged	
Class III, *C-Wx* kernels			*Pollen*
1	Knob	Normal	*WxWx*
2	Knob	Normal	....
3	....	Normal	*WxWx*
5	Knob	Normal	....
6	Knob	......	....
7	Knob	Normal	....
8	Knob	Normal	....
Class IV, *c-Wx* kernels			
1	Knobless	Normal	*Wxwx*
2	Knobless	Normal	*Wxwx*
3	Knobless	Interchanged	*Wxwx*
4	Knobless	Normal	*Wxwx*
5	Knobless	Interchanged	*WxWx*
6	Knobless	Normal	*WxWx*
7	Knobless	Interchanged	*Wxwx*
8	Knobless	Interchanged	*WxWx*
9	Knobless	Normal	*WxWx*
10	Knobless	Normal	*WxWx*
11	Knobless	Normal	*Wxwx*
12	Knobless	Normal	*Wxwx*
13	Knobless	Normal	*WxWx*
14	Knobless	Normal	*WxWx*
15	Knobless	Normal	*Wx*—

But that’s not all….

Transposable Elements (TEs)

- McClintock discovered the transposons *Dissociator (Ds)* and *Activator(Ac)* in 1951
- Was not accepted by other scientists because it was not completely understood
- Others thought it was specific to corn
- In the late 1960's and early 1970's, TEs were discovered in bacteria, yeast and bacteriophages



Nobel Prize in Physiology or Medicine (1983)

- Discovery of mobile genetic elements
- First woman to win the prize unshared

- Understood epigenetics 40 years before it was described

"[T]he progeny of two (such) sister cells are not alike with respect to the types of gene alteration that will occur. Differential mitoses also produce the alterations that allow particular genes to be reactive. Other genes, although present, may remain inactive. **This inactivity or suppression is considered to occur because the genes are 'covered' by other nongenic chromatin materials. Gene activity may be possible only when a physical change in this covering material allows the reactive components of the gene to be 'exposed' and thus capable of functioning**."

-McClintock, 1951

Cytogenetics

- 1878-1882
  - Walther Flemming used a basophilic dye and found it stained ‘chromatin’ located in the nucleus
  - Studied ‘mitosis’ and the distribution of chromosomes to the daughter nuclei
  - To early to make the connection with Mendel’s work
- 1904
  - Gustav Giemsa developed the Giemsa Dye- Results in a dark and light patterning called G-banding
    - Euchromatin: less affinity→lighter stain
    - Heterchromatin: dense chromatin→darker stain