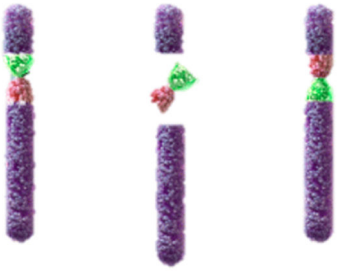
# Inversions

Muller, 1916, working with Drosophila, found C (for crossover reducers) factors reduced or suppressed

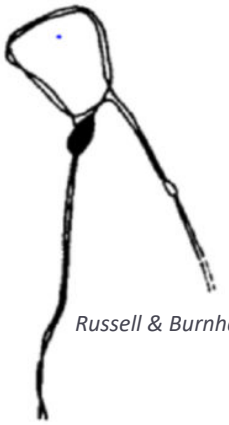
A paracentric inversion

*From US National Library of Medicine*

A pericentric inversion



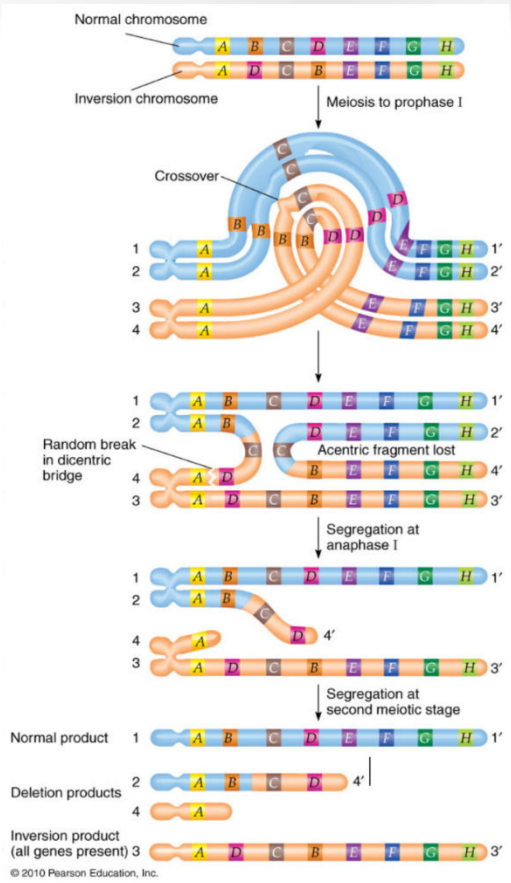
## Paracentric inversions



*Russell & Burnham 1950*

## Crossover suppression

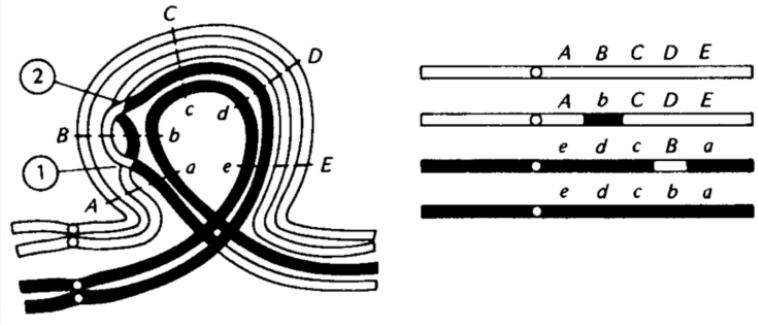
**McClintock, 1931; 1933**



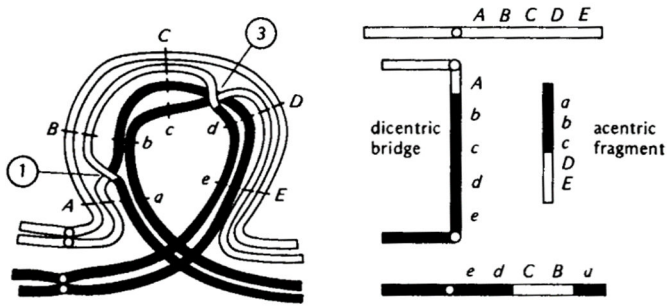

## Double Crossovers in the Inversion Loops

graphics from **Strickberger, 1976**

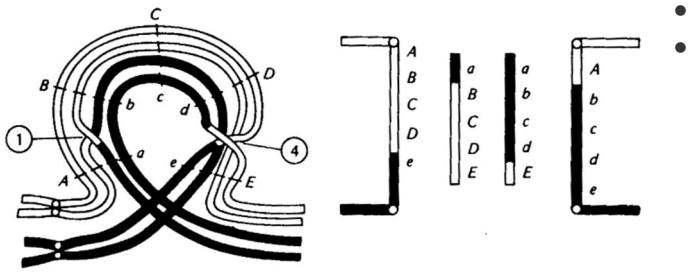
### 1) 2-strand double crossover



### 2) 3-strand double crossover




### 3) 4-strand double crossover




## If one of the double crossovers occurs outside of the loop

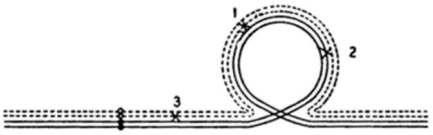
Modified from **McClintock, 1938**

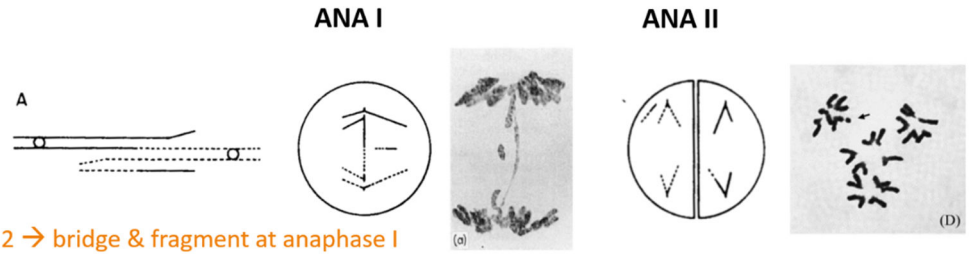
A. Get same configuration for a 1 or 3 strand double crossover
   - Not affected by CO outside of inversion area

From **Burnham, 1962**, after **McClintock, 1938**

Ana I from Stevens & Bougourd. 1991. Heredity 66: 391-401

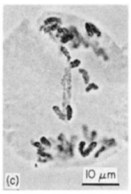
Ana II from Wang & Zhang. 2007. Plant Sci 172: 380-392



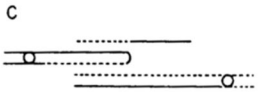

Single Crossover @ 1 or 2 → bridge & fragment at anaphase I

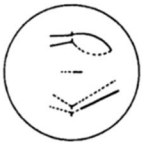
B. Configuration of 4-strand double crossover

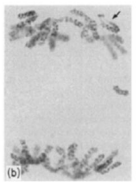




CO @ 1 & 2 → 4 strand double crossover → 2 bridges and two fragments

C.





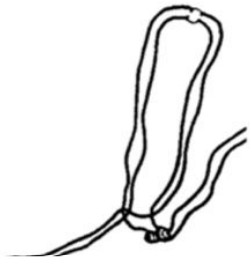


3-strand DCO @ 1 or 2 & 3 → linear & U-shaped fragments @ anaphase I + a bridge @ anaphase II

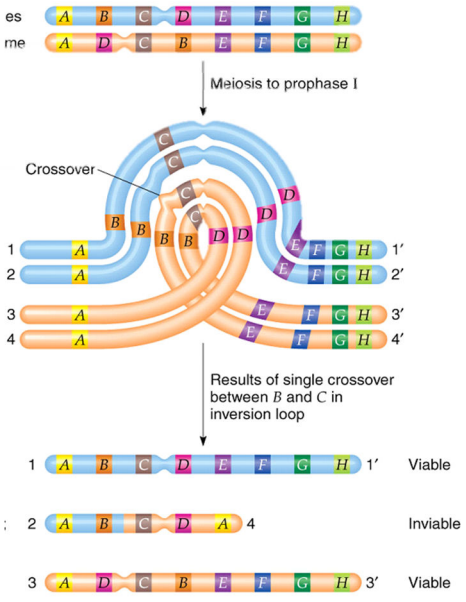
D.


4-strand TCO @ 1 & 2 & 3 → 2 linear fragments + 2 U-shaped fragments at anaphase I and 2 bridges at anaphase II

## Pericentric inversions

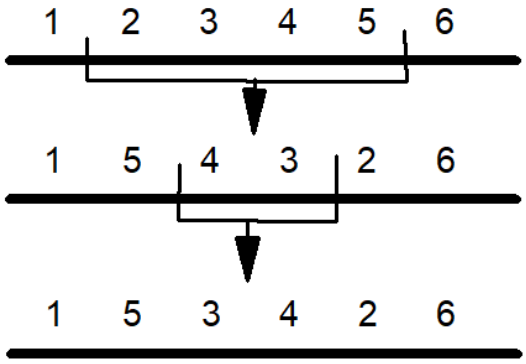


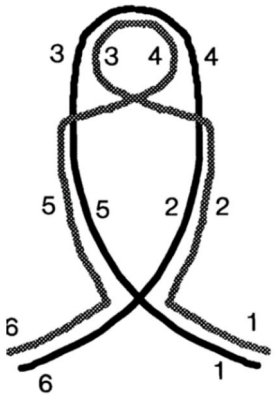
*McClintock, 1931*



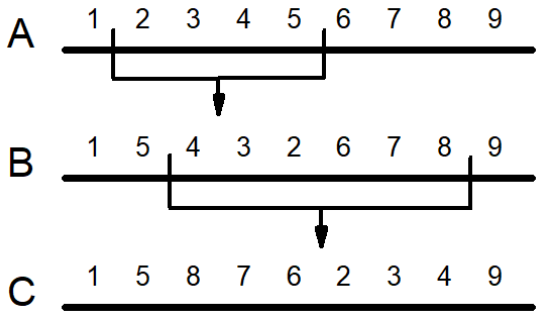
## Multiple inversions

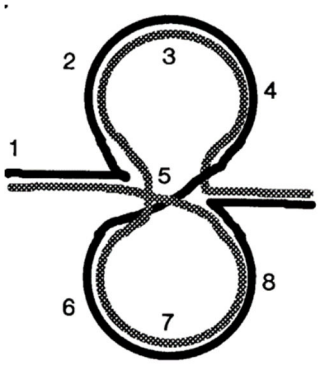
### Case 1: Nested inversions




### Case 2: Overlapping inversions



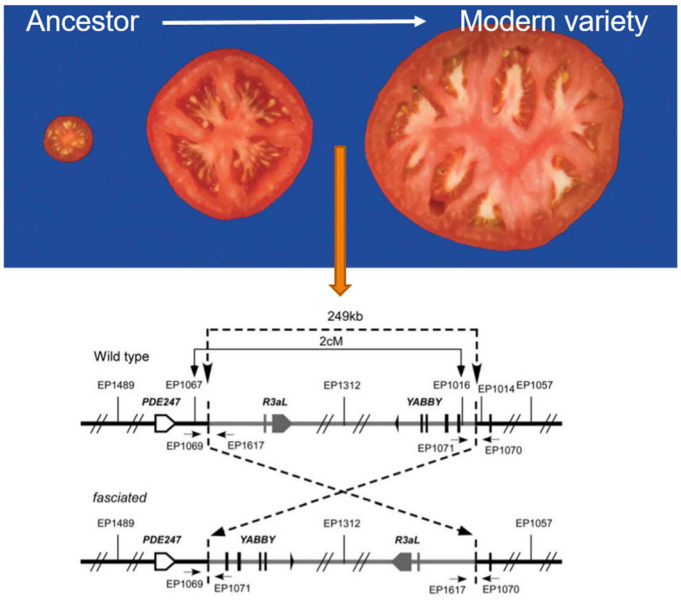



## Role of inversions

**Dobzhanski, with Drosophila:**

## Structural variants - inversions

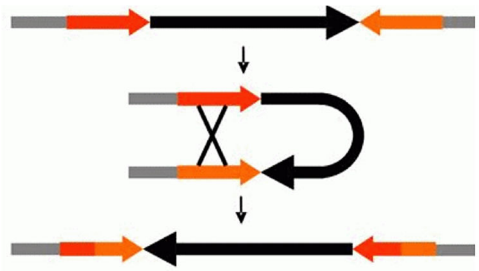
**Huang & van der Knaap, 2011**



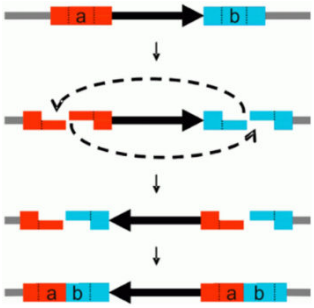
## Origin of inversions

**Casals & Navarro, 2007**

### Model 1: Duplications lead to inversions



### Model 2: Staggered breaks




## Reversing inversions

**Schmidt et al, 2020**

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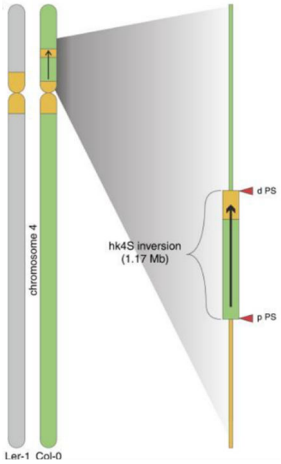
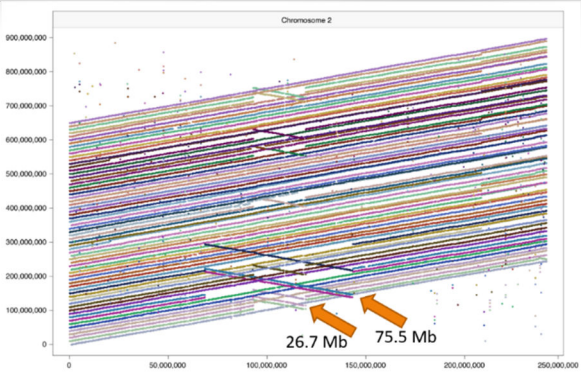
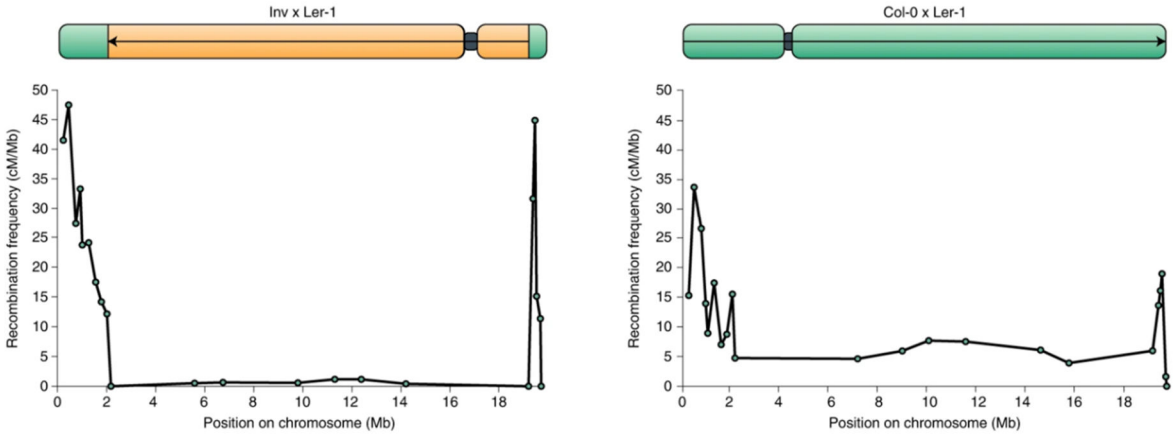


**Schwartz et al, 2020**




## Creating inversions to preserve linkage blocks

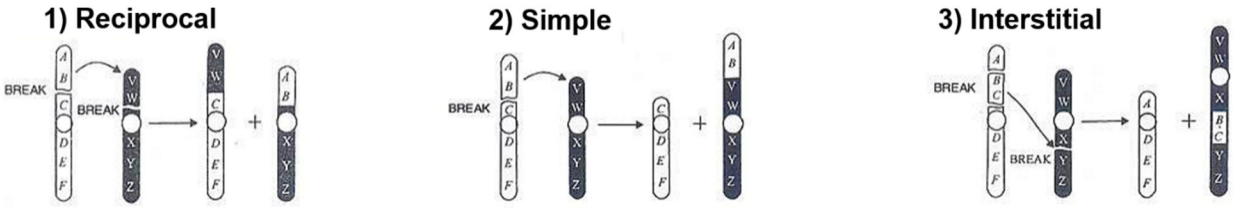
**Rönspies et al, 2022**



# TRANSLOCATIONS or INTERCHANGES

Exchanges between non-homologous chromosomes

- Three types



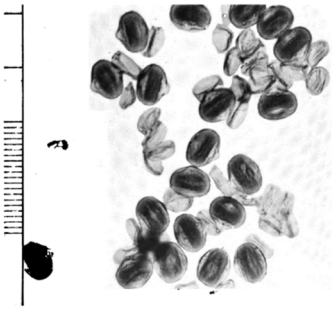

- Simple translocations are rare
  - Normally need broken ends to bind with a fragment

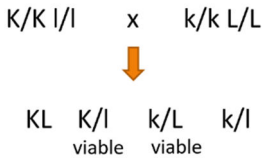
## Semisterility in Florida velvet bean

**Belling 1914/1915**

Working with the Florida velvet bean, *Stizolobium deeringianum* = *Mucuna pruriens*

*https://www.etsy.com/listing/635026498/mucuna-pruriens-velvet-bean-cowitch-raw*






Postulated 2 genes, K and L, such that

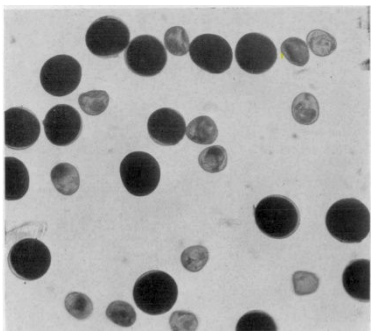
- Presence of K or L gave fertility

**Belling & Blakeslee 1924; 1925**


**Blakeslee 1928**

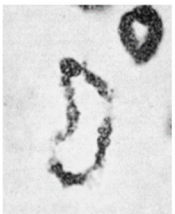
## Semisterility in corn

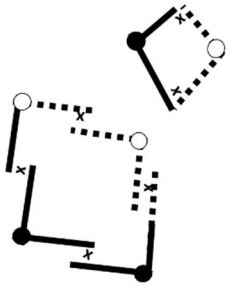
**Brink, 1927; Brink & Burnham, 1929**



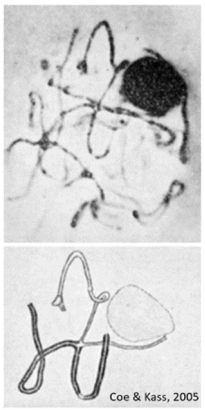
**Burnham, 1930**

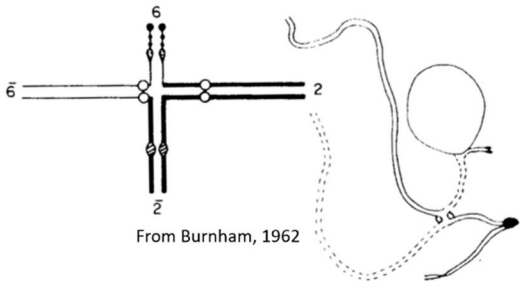
A ring of 4 in maize.
Coe & Cass, 2005





**McClintock, 1930**



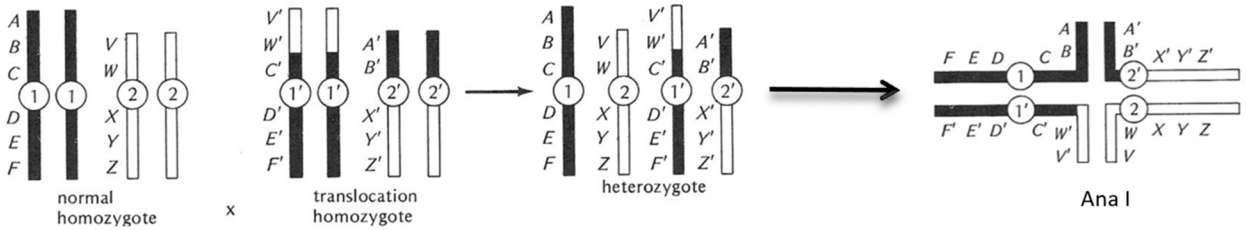



From Burnham, 1962

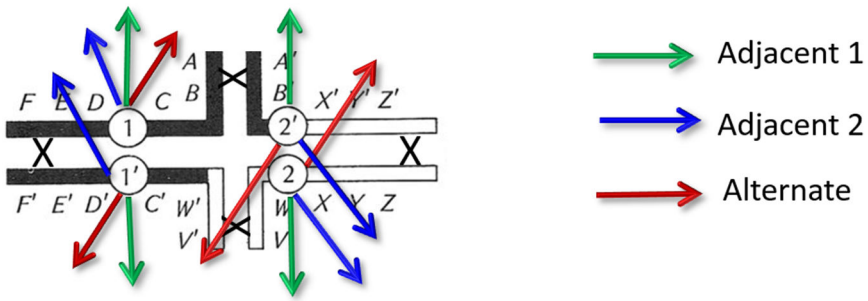
## Meiosis in translocation heterozygotes

graphics from **Strickberger, 1976**

Normal × translocation homozygote to give a translocation heterozygote. Forms cross @ pachytene.




3 possible disjunctions




## Case 1 – Crossovers in the Arms

## Adjacent 1 separation

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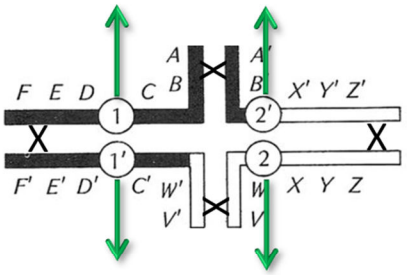


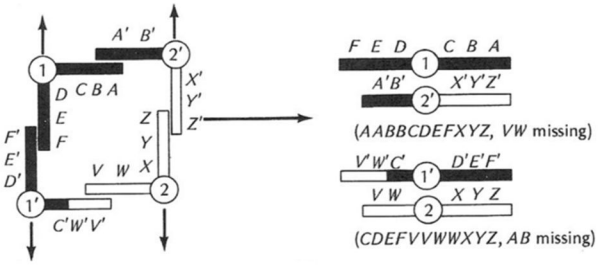


All gametes abort

## Adjacent 2 separation

- 
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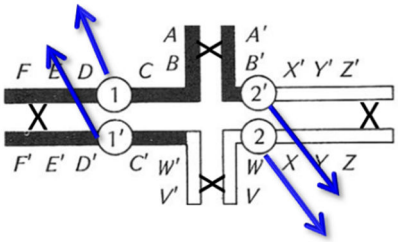
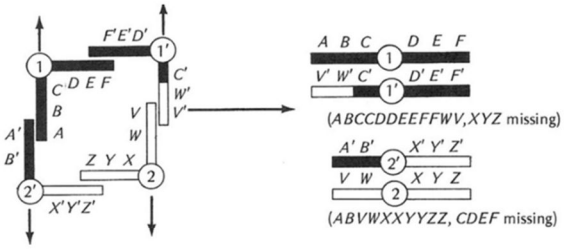
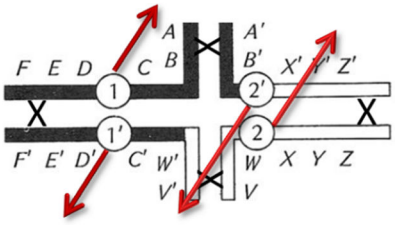
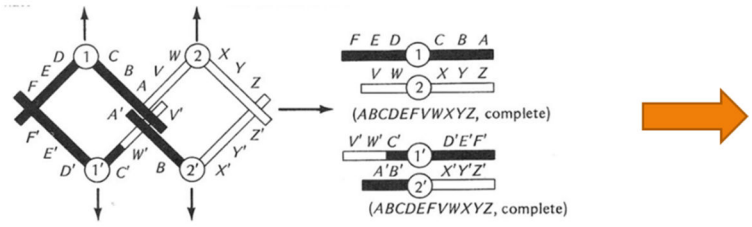



All gametes abort

## Alternate separation



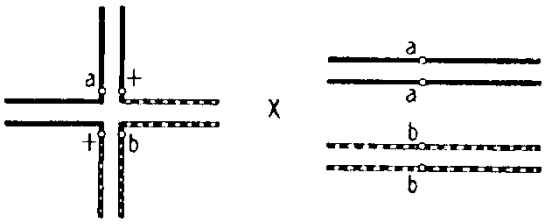


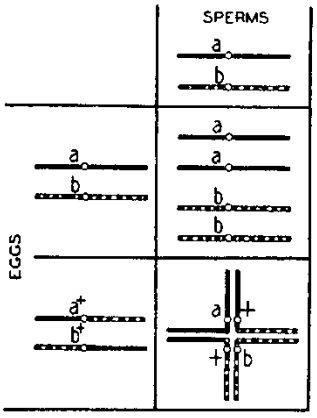

## Translocation separations

| Type: | Expected | Drosophila | Maize | Barley |
|---|---|---|---|---|
| Adjacent 1 | $^1/_3$ | 30 | 30 | 30 |
| Adjacent 2 | $^1/_3$ | 20 | 20 | - |
| Alternate | $^1/_3$ | 50 | 50 | 70 |

## Pseudolinkage

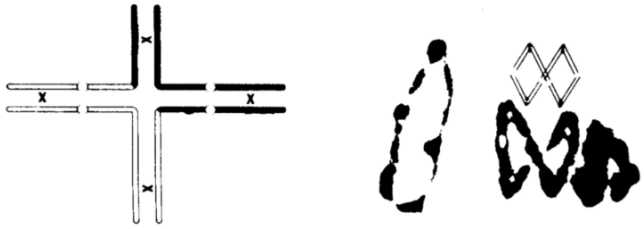
From **Sturtevant & Beadle, 1939**



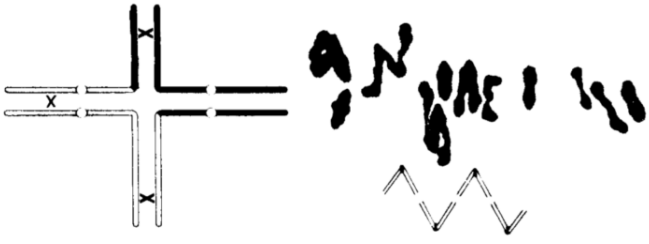



## Effect on linkage maps

## Effect of crossover number

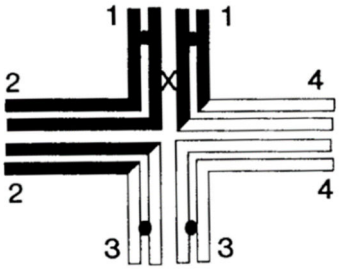


*Two rings of 4 in barley, one undergoing adjacent (left) and the other alternate (center) separation. From **Hagberg, 1960**.*

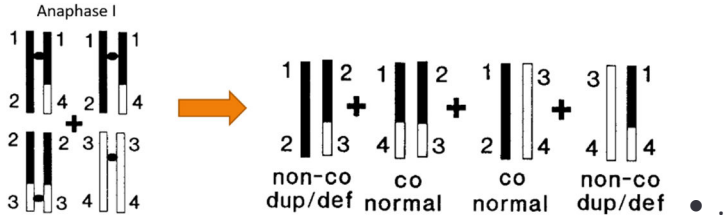


*Two chains of 4 in Agrostis. After **Jones, 1956**.*

## Case 2 – Crossovers in the interstitial region

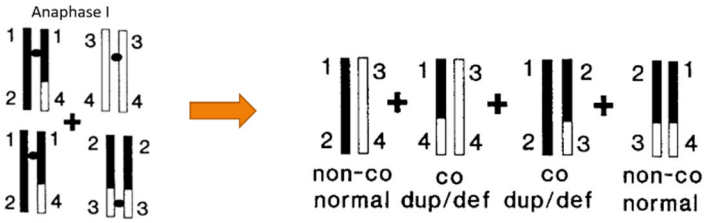



### Adjacent 1 separation




### Adjacent 2 separation

### Alternate

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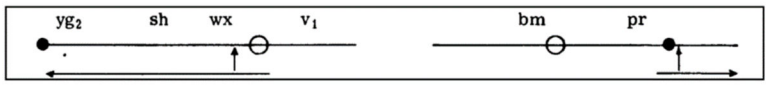
| | Alternate | Adjacent 1 | Adjacent 2 |
|---|---|---|---|
| Short interstitial | 50-57% | 19-31% | 19-26% |
| Long interstitial | 55-56% | 41-45% | 0-3% |

## Effect of Translocations on recombination

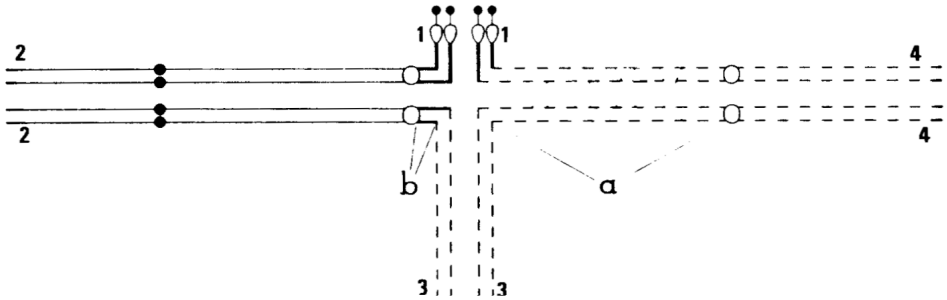



*Chromosome 5 (R) and part of chromosome 9 (L) showing break points. Horizontal arrows indicate regions showing variable pairing.*

| Chromosome | Standard | Heterozygous T5-9a as male | Homozygous T5-9a |
|---|---|---|---|
| Chromosome 9 | | | |
| *yg₂-sh* | 23 | 11 | -- |
| *sh-wx* | 20 | 5 | 18.6 |
| *wx-v₁* | 12 | 11 | independent |
| Chromosome 5 | | | |
| *bm-pr* | 27 | 32 | -- |
| *pr-wx* | independent | 28 | 23.8 |

# Frequency of crossing over in the interstitial region

- Worked out by McClintock (unpublished) and Burnham, 1950, using the NOR (chromosome 6) at the tetrad stage and pollen abortion as markers in translocations between chromosomes 6 & 5



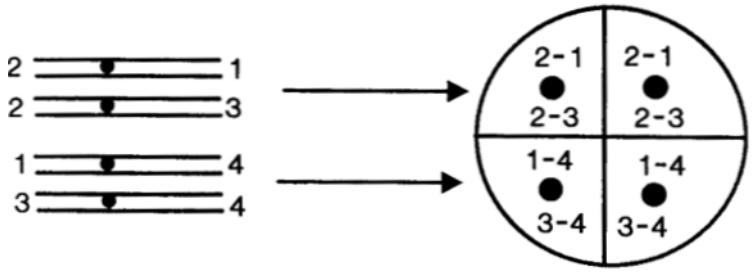

*Pachytene configuration of a 5-6 translocation. The interstitial regions are denoted as a and b. (Burnham, 1960).*

- Number of NOR = number of nucleoli
- If no NOR is present, nucleolar material remains scattered in small droplets

## IF NO CROSSING OVER OCCURS:

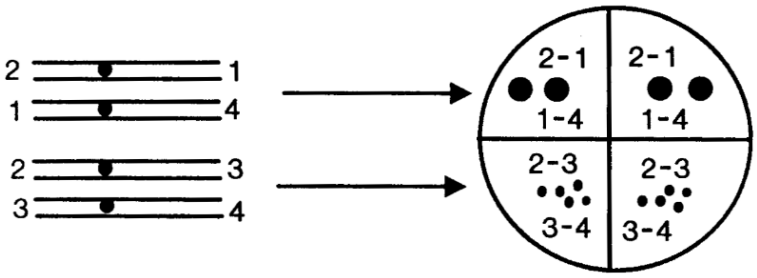
**1) Adjacent 1:**

- 2 have 2 nucleoli
- 2 have diffuse nucleolus
- All abort



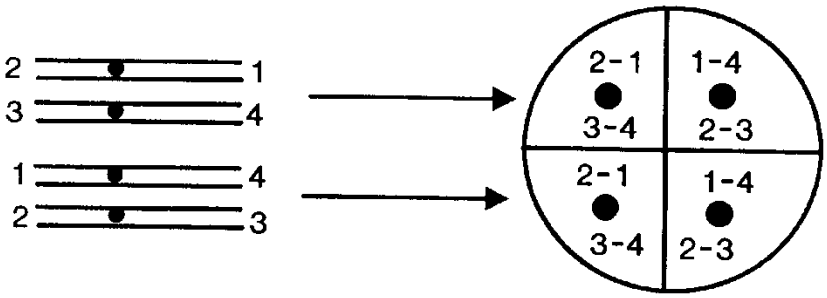

**2) Adjacent 2:**

- All microspores have 1 nucleolus
- All abort




**3) Alternate:**

- All have 1 nucleolus
- All are viable
- Can't tell from adjacent 2 by looking at tetrad



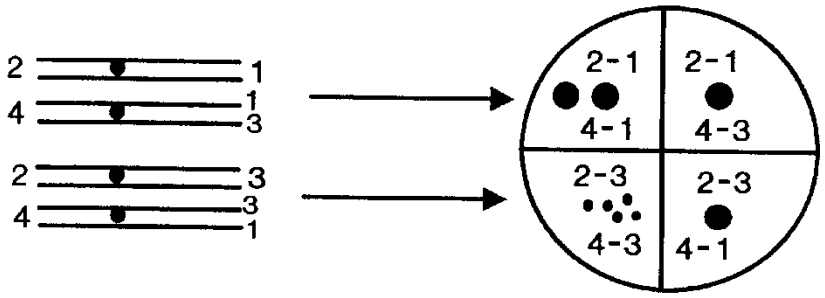
## IF A SINGLE CROSSOVER TAKES PLACE AT a:

**Adjacent 2** - will not occur

**Adjacent 1:**

- 2 are viable

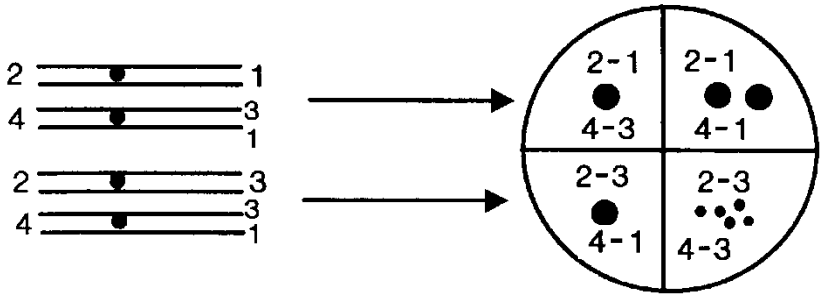
- 2 abort (1 diffuse)




**Alternate:**

- 2 viable

- 2 abort (1 diffuse)



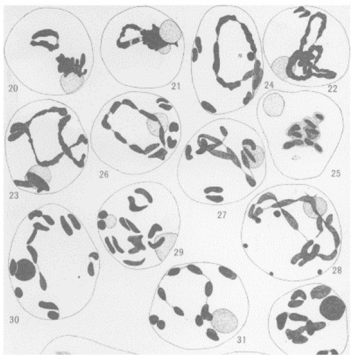

**Problem:** Cannot tell adjacent 1 apart from alternate, as both tetrads are the same.

-The # of tetrads with 1 diffuse nucleolus gives the # of crossover tetrads
- The # of NCO separations is made of 3 types:
    - Adjacent 1 = frequency of tetrads with 2 diffuse nucleoli
    - Alternate = amount of viable pollen [alternate] - viable pollen from crossover tetrads [adj1 with CO + alternate dis] = % tetrads with 1 diffuse × 2
    - Adjacent 2 = amount of aborted pollen - adjacent 1 - aborted pollen from crossover

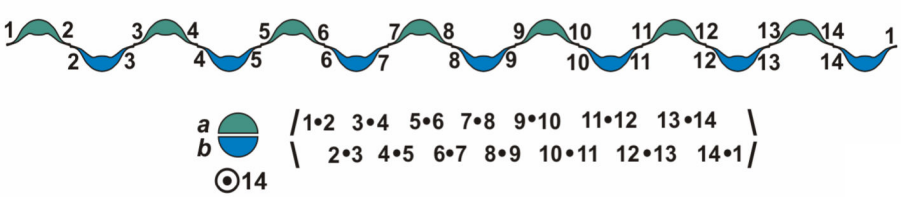
# Permanent translocation heterozygotes

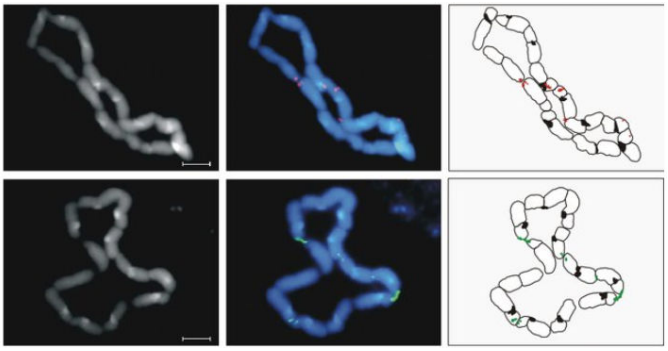
**Gates 1908; Golczyk, Massouh & Greiner, 2014**

(see section 5d on *Oenothera* cytogenetics)



*Oenothera*



## Use of translocations in mapping & breeding

**Burnham 1946, Sisodia & Shebeski, 1965;** review by **Farré et al., 2014**

*⊙14 in barley, Sisodia & Shebeski, 1965*

- Also found in *Rhoeo discolor*, *Paeonia californica*, *Viscum fischeri*, and *V. engleri* (East African mistletoes).
  - In these mistletoes, 2n = 23♂, 22♀.
  - The ♂ has 4 X and 5 Y chromosomes, all involved in translocations with the autosomes, so its gametes have 12 chromosomes.
  - The ♀ has 8 X chromosomes, none of which are involved in translocations.
    - It forms 11 II, and its gametes have 11 chromosomes.