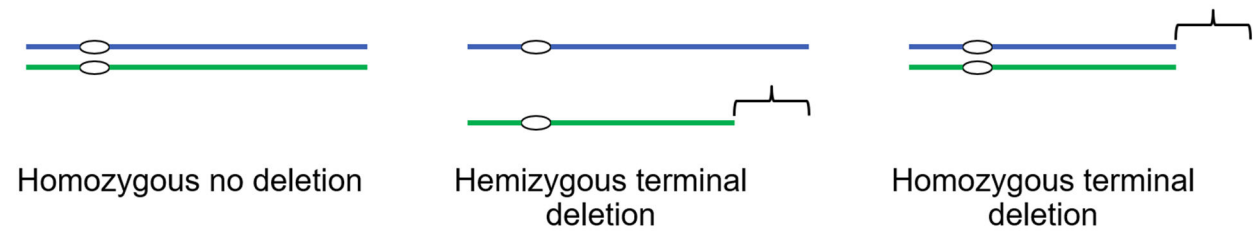


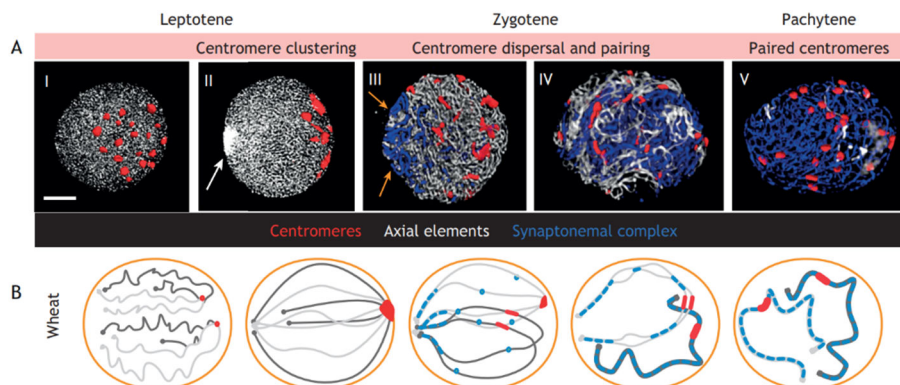
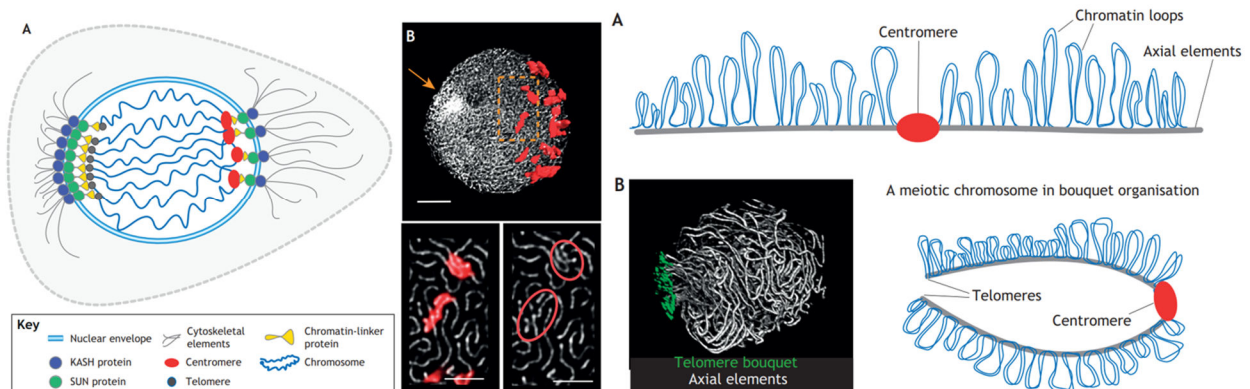
Pairing and crossing over

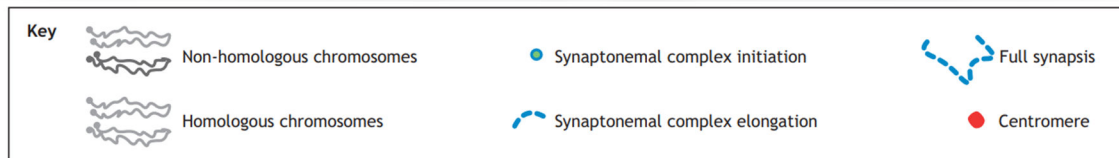
Synapsis

Lukaszewski, 1997; Abirached-Darmeny et al., 1983



Sepsi & Schwarzacher, 2020





The synaptonemal complex

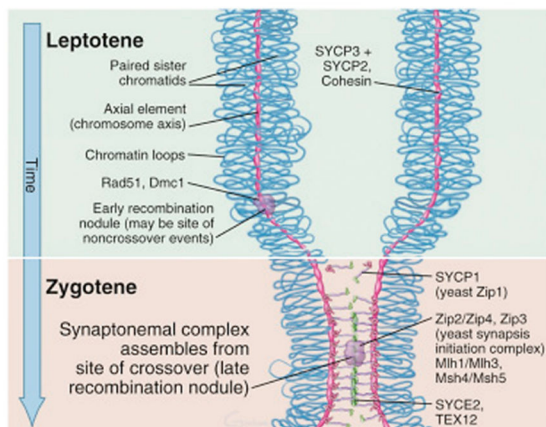


Figure 1. Cell Biology, third edition (2017)

Figure 2. Alexandra Popa. The evolution of recombination and genomic structures: a modeling approach.. Bioinformatics [q-bio.QM]. Université Claude Bernard - Lyon I, 2011. English. <tel-00750370>

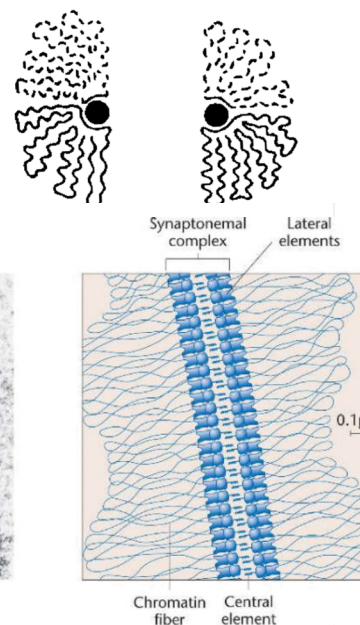
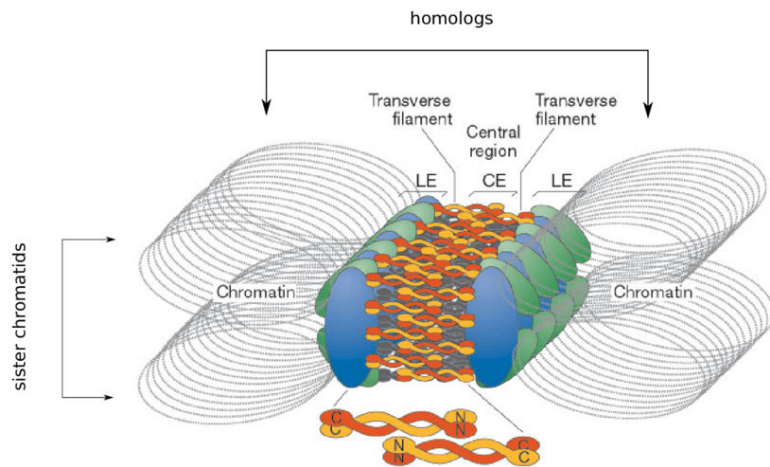


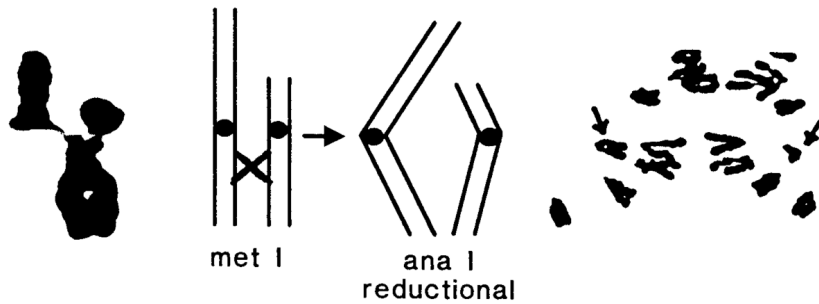
Figure 3.

http://bio3400.nicerweb.net/Locked/media/ch02/02_14-synaptonemal_complex.jpg

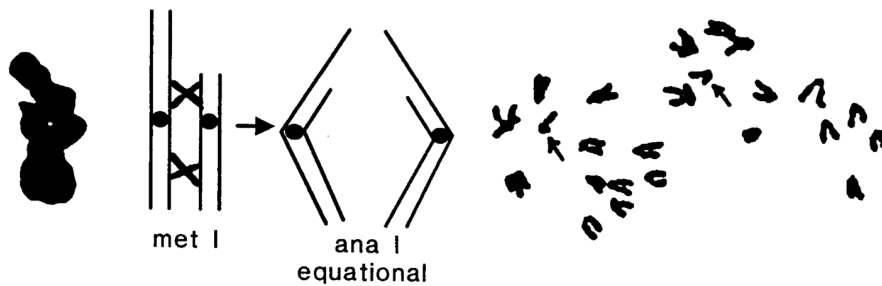
Fundamental concepts

Frequency of chiasmata = frequency of CO

Brown and Zohary, 1955



Photographs and interpretive drawing of events leading to a reductional anaphase I.

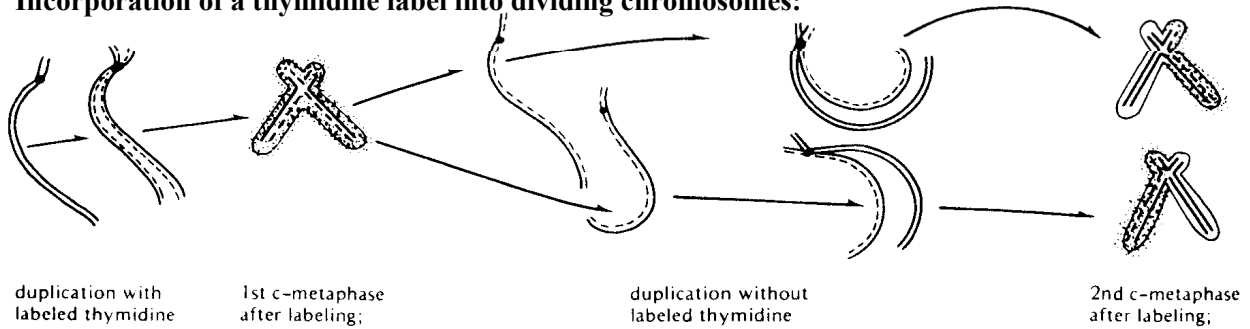


Photographs and interpretive diagram of events leading to equational anaphase I.

Behavior of the heteromorphic arms:

	Metaphase I		Anaphase I		
	Chiasmata	No chiasmata	Equational	Reductional	p=
Year: 1951	71%	29%	71%	29%	<0.05
Year: 1953	51%	49%	55%	45%	<0.05

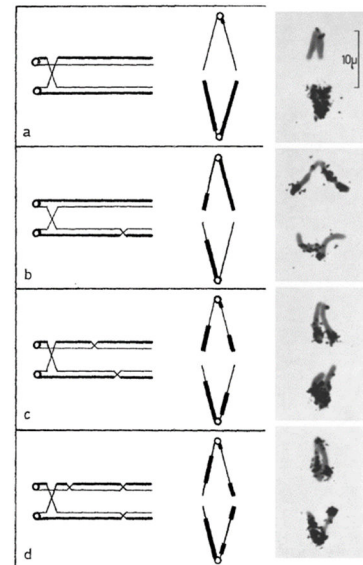
Jones, 1971

Incorporation of a thymidine label into dividing chromosomes:

Label Exchange Type	
Hidden	
Visible	



Stethophyma grossum
Wikipedia commons



Recombination takes place between homologs

Stern, 1931 (*Drosophila*)

Creighton & McClintock, 1931 (Maize)

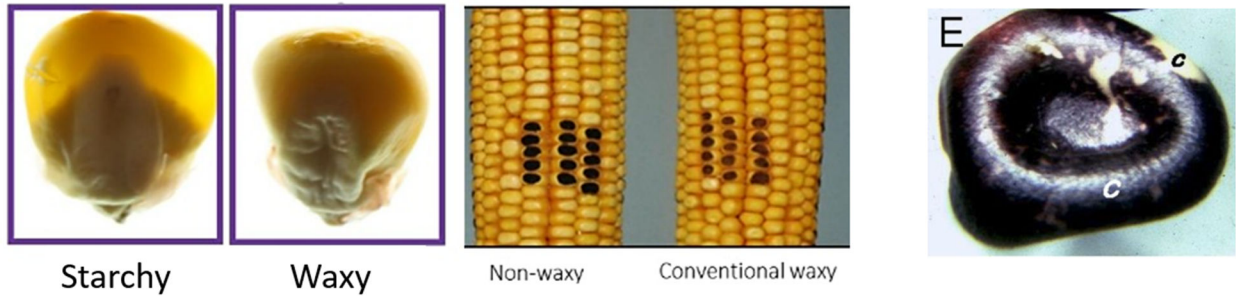
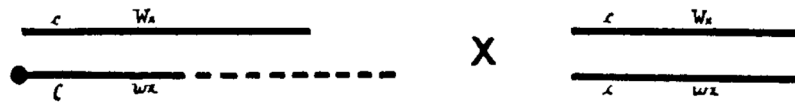
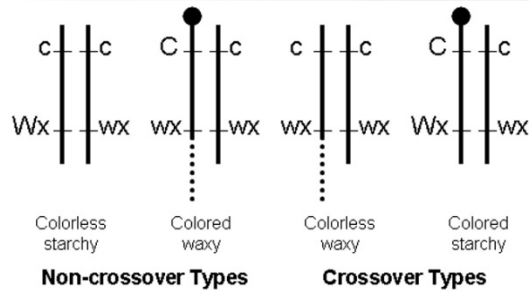


Figure 4. Corteva; Fedoroff NV. 2012. PNAS 109: 20200-20203; <https://doi.org/10.1073/pnas.1215482109>



Colored, starchy × colorless, starchy

$$\frac{\text{knobless} \cdot c \cdot Wx \cdot \text{normal}}{\text{knob} \cdot C \cdot wx \cdot \text{interchange}} \times \frac{\text{knobless} \cdot c \cdot Wx \cdot \text{normal}}{\text{knobless} \cdot c \cdot wx \cdot \text{normal}}$$



<https://www.nature.com/scitable/content/mcclintock-and-creighton-s-work-in-maize-41556/>

Progeny types	Cytological Features	Attributed cytological mechanism
Colored, waxy ($C_{-}, wxwx$)	Knob, Interchanged	Non-CO
Colorless, waxy ($cc, wxwx$)	Knobless, Interchanged	Crossovers
Colored, starchy (C_{-}, Wx_{-})	Knob, normal	Crossovers
Colorless, starchy (cc, Wx_{-})	Knobless, Interchanged	Crossovers
	Knobless, normal	Non-CO

Crossing over occurs at the 4-strand stage

The linear sporads of *Neurospora*

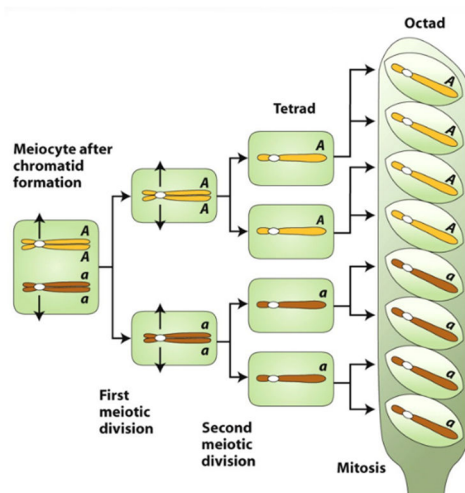


Figure 3-10b
Introduction to Genetic Analysis, Tenth Edition
© 2012 W. H. Freeman and Company

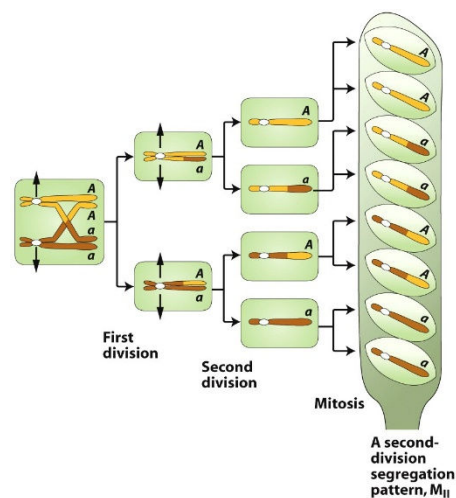


Figure 4-17
Introduction to Genetic Analysis, Tenth Edition
© 2012 W. H. Freeman and Company

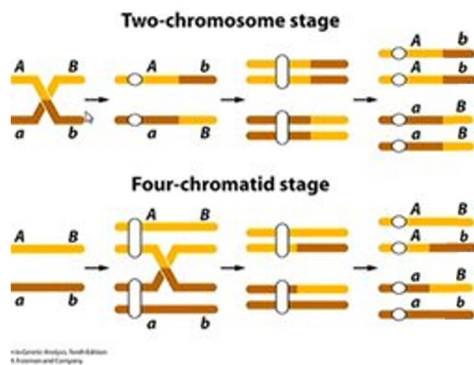


Figure 5. <https://quizlet.com/>

Models of chiasma

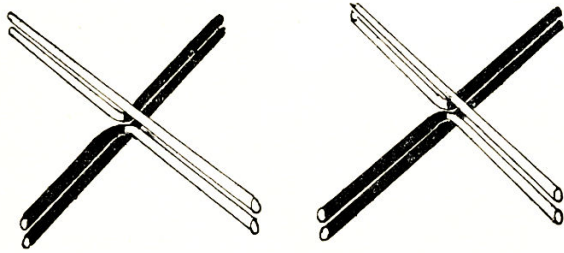
Sax, 1932

Any model of CO must account for these facts:



The chiasmotype or 1-plane model

Janssens, 1909

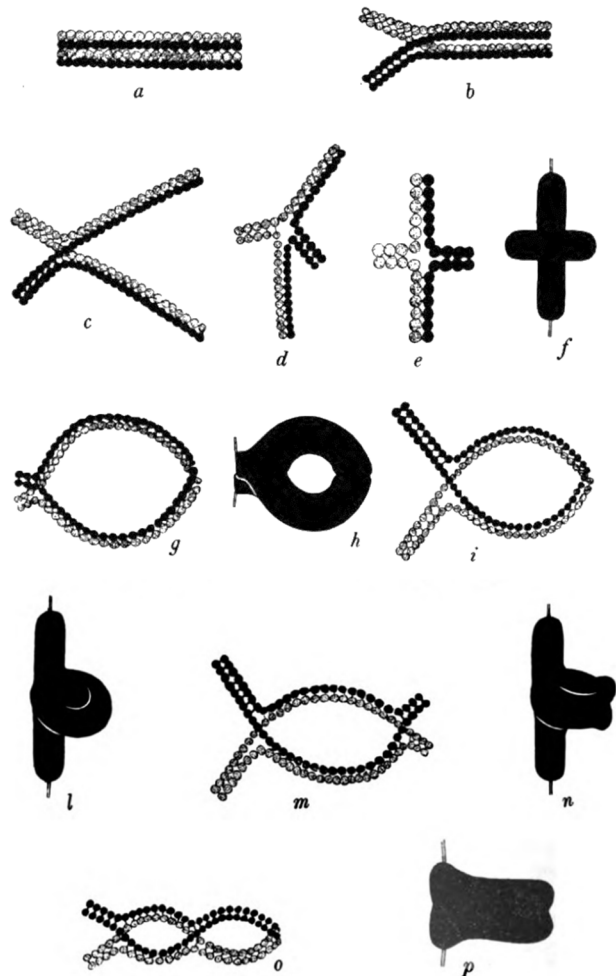


Frans Alfons Janssens
1865-1924



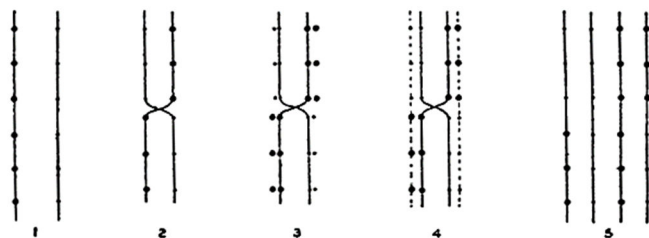
The 2-plane model

Granata, 1910

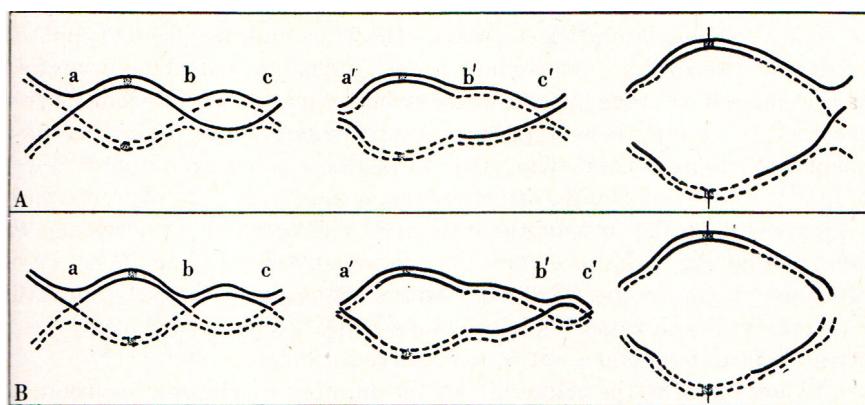


The copy choice model

Belling 1933; Freese 1957

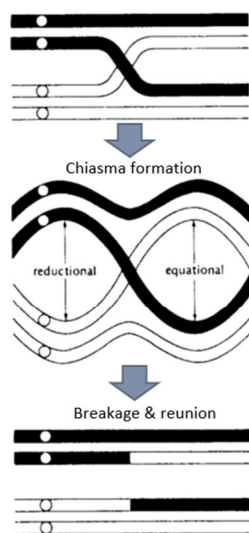


1 & 2-plane models summarized by Sharp, 1934



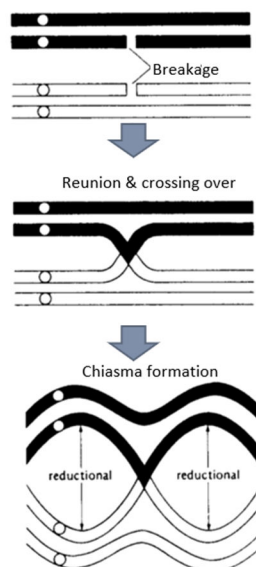
Classical or 2-plane model

Blamed on **Sharp, 1934**,
based on McClung and
Sax, but it precedes him
– he just explained what
others thought



Chiasmatype or 1-plane model

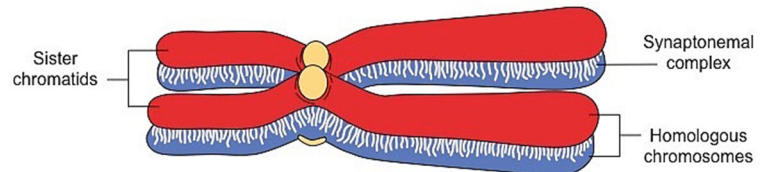
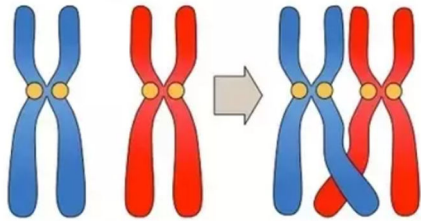
Janssens, 1909, with
follow-ups by Belling
and Darlington



Evidence for the chiasmotype hypothesis

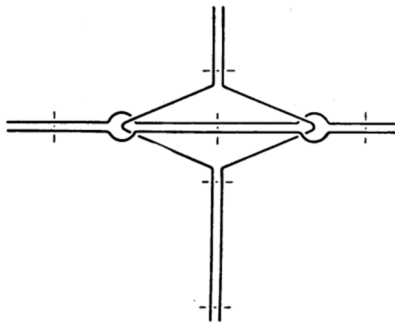
The synaptonemal complex

Pairing and chiasma as commonly depicted



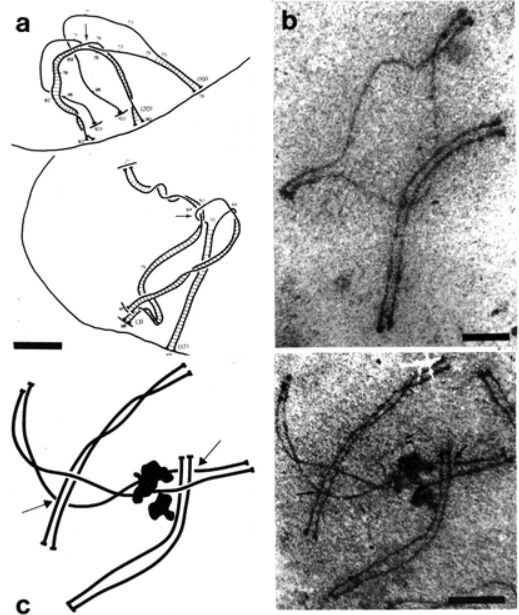
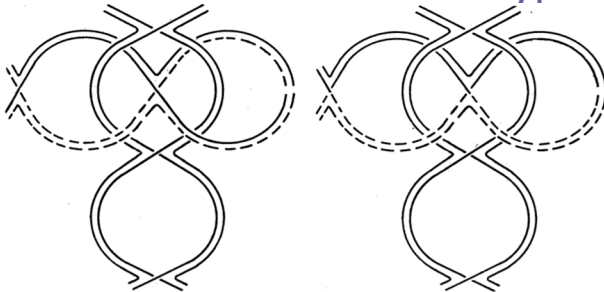
Interlocking bivalents

Mather, 1934



Classical

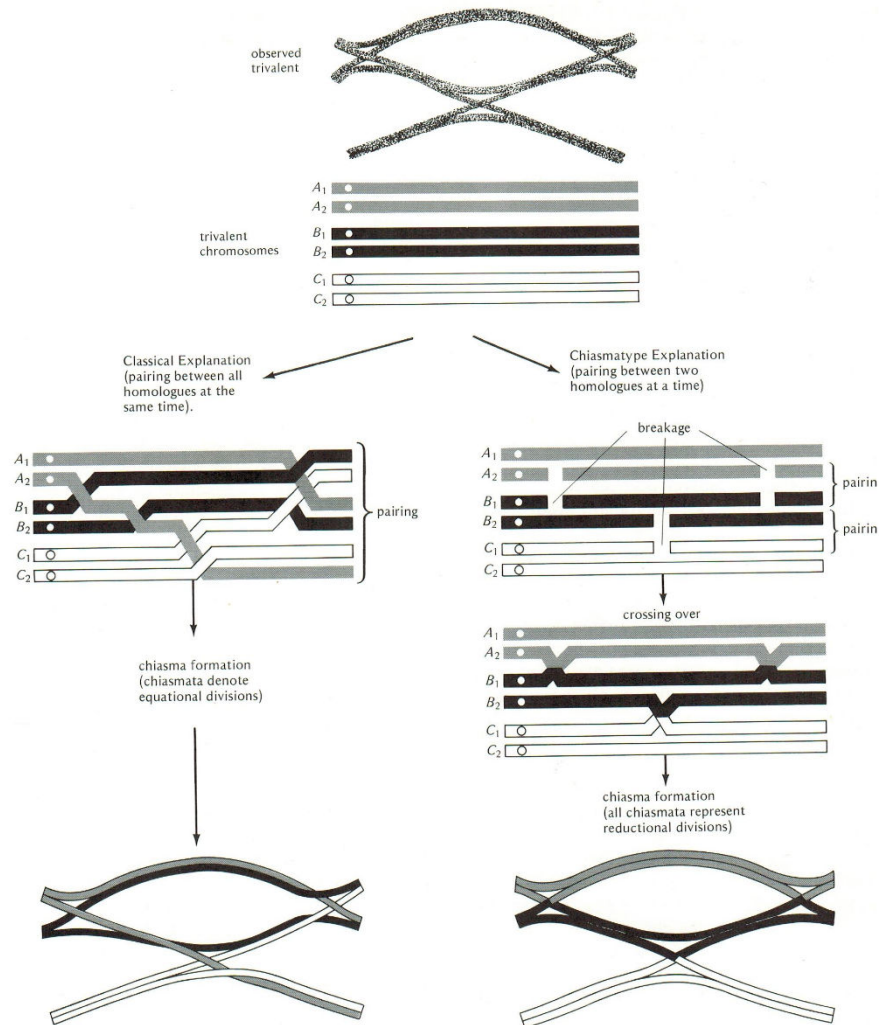
Chiasmotype



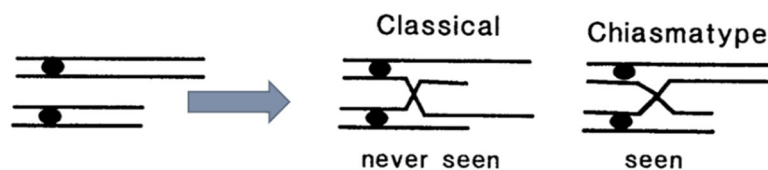
Examples of interlockings seen in *Bombyx mori*.
Zickler & Kleckner, 1999

Interlocking bivalent in *Lilium regale*. <https://www.jstor.org/stable/pdf/2471717.pdf>

Chiasmata in trisomics

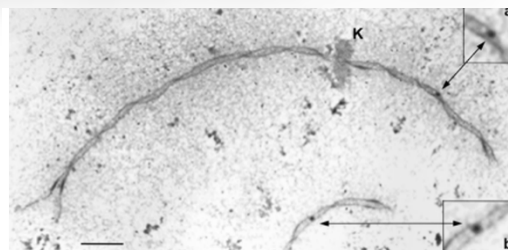


Heteromorphic pairs @ pachytene



Recombination nodules

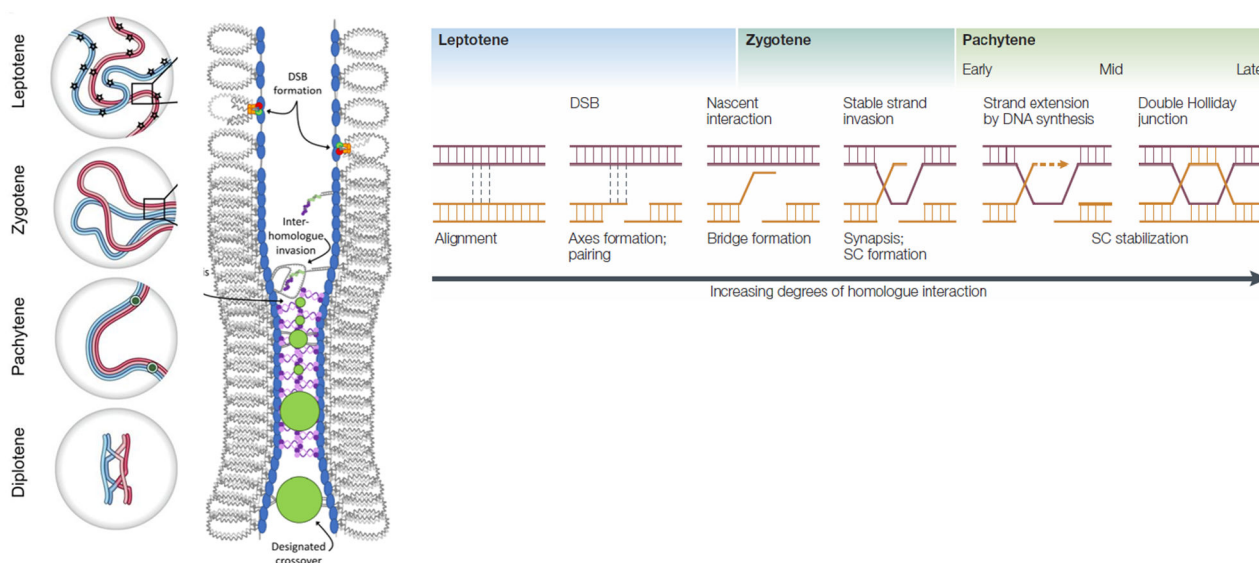
Sherman and Stack, 1995



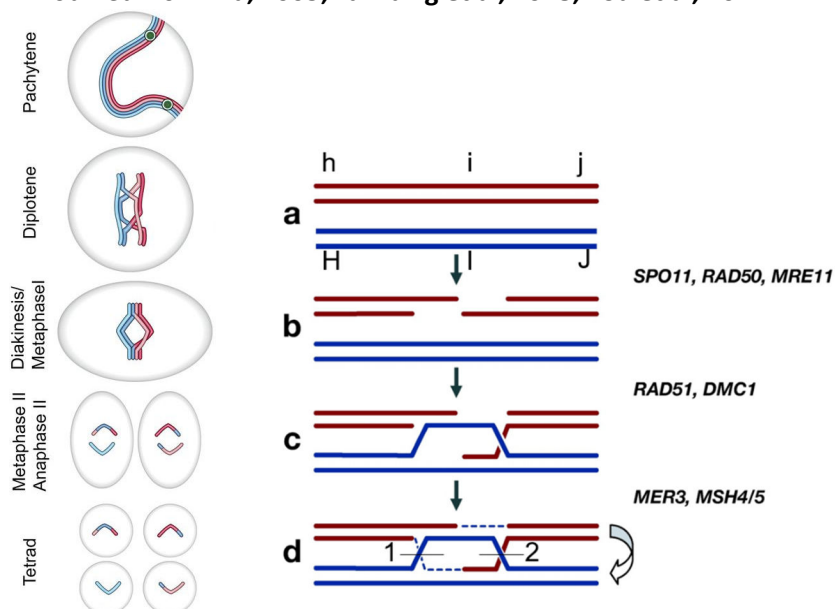
Anderson et al., 2003. Two recombination nodules in early diplotene chromosomes – note the large chromosome has started to desynapse.
K=kinetochore.

Crossing over

Gerton and Hawley, 2005; Lambing et al, 2018; Sepsi & Schwarzacher, 2020; Lloyd, 2022



Modified from Ma, 2005; Lambing et al, 2018; Zou et al, 2024



Holliday junction

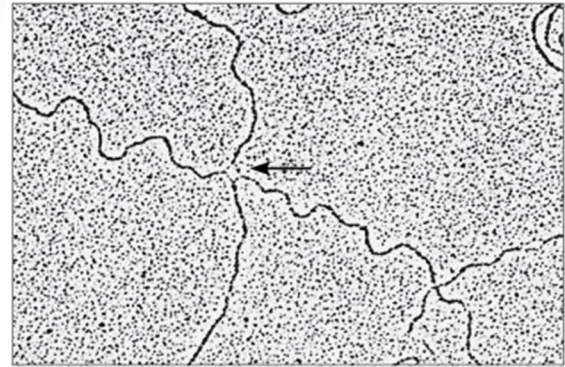
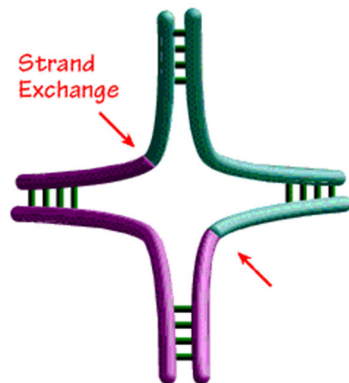
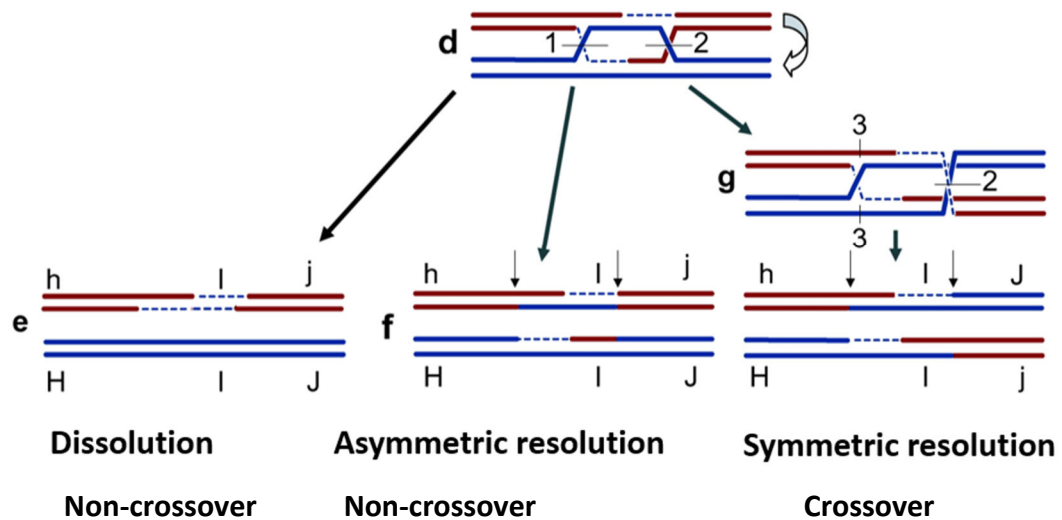
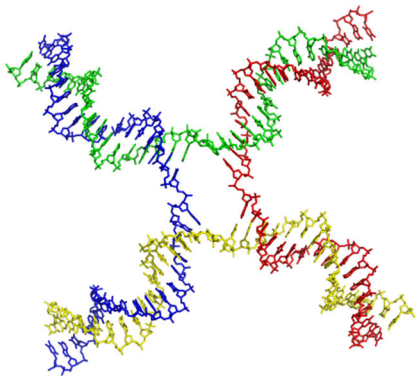
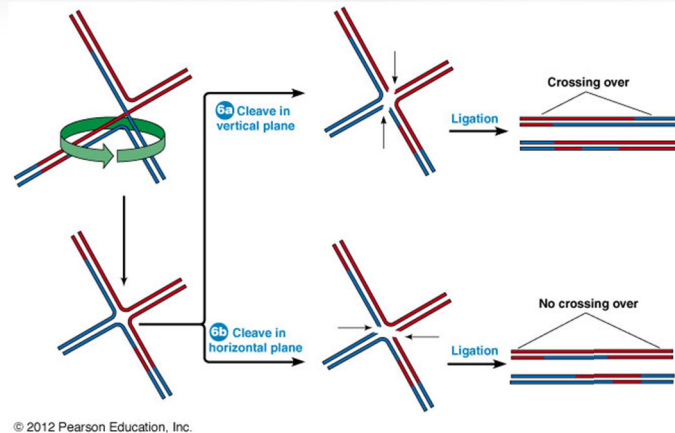


Figure 6. <http://engels.genetics.wisc.edu/Holliday/holliday3D.html>



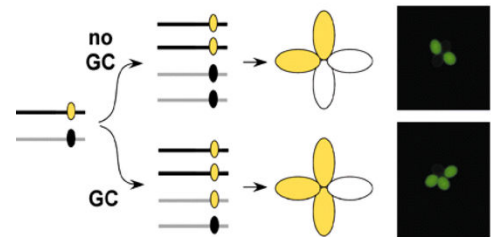


Gene conversion

Francis et al., 2007



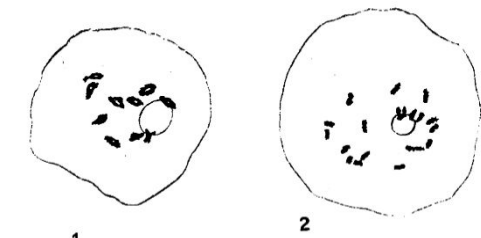
Pollen tetrad of Arabidopsis.
Preuss et al., 1994



Yang et al., 2012

Pairing mutants

Soost, 1951



Diakinesis in normal and asynaptic maize (Beadle, 1930).

Asynaptic mutants –

Desynaptic –

Synaptic -

Metanaphase

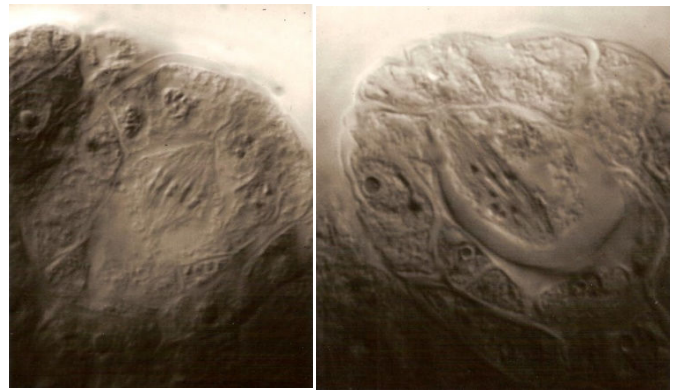


Figure 7. (left) Metaphase I in normal and (right) Metanaphase I in asynaptic megaspores of potato.

Behavior of univalents

Figure 8. Lagging chromosomes in a pollen mother cell of buffelgrass. Bar = 10 μ m

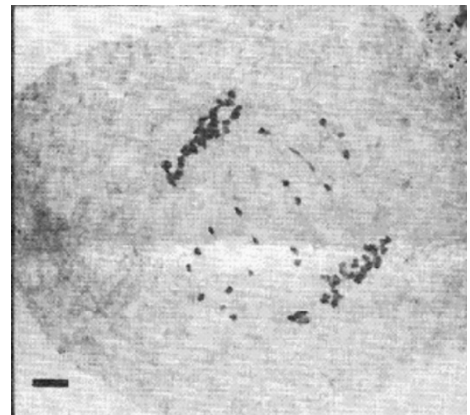


Photo: Visser NC, JJ Spies, and HJT Venter. The presence of synaptic and chromosome disjunction mutants in *Cenchrus ciliaris* (Poaceae: Paniceae). *Bothalia* 29:327-334.

Meiosis in synaptic mutants

Peloquin 1983

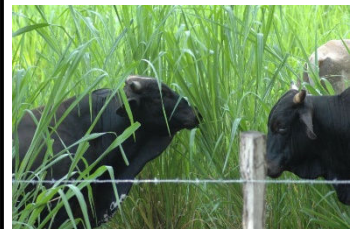
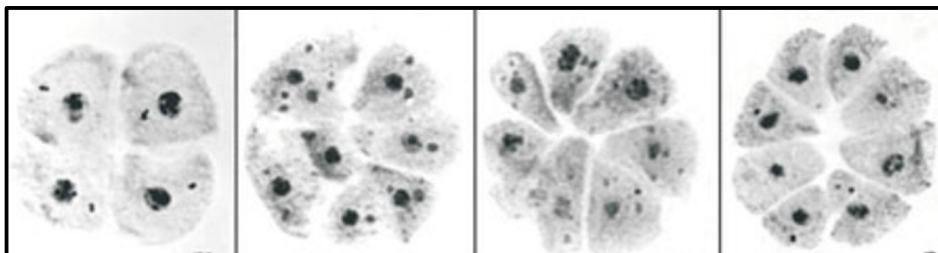
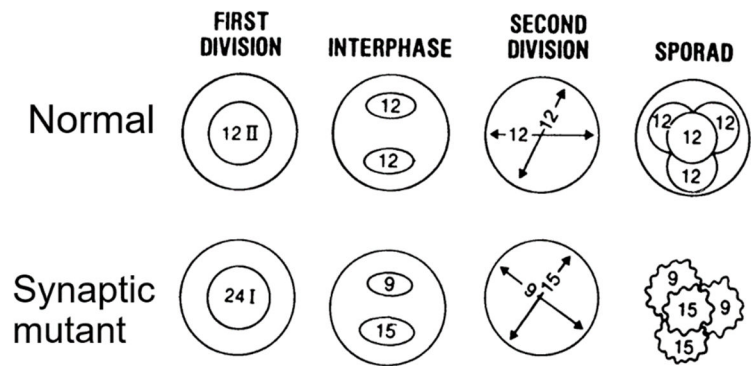


Figure 9. Polyads from 4x *Brachyaria brizantha*. Mendes-Bonato et al., 2009.

Disjunction in synaptic mutants

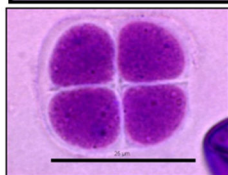
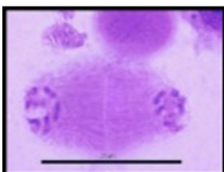
Belling & Blakeslee, 1927



Figure 10. Pollen from asynaptic (top) and normal maize. Notice even normal maize has some aborted pollen grains [Beadle, 1930]

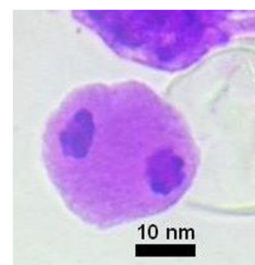
Correction for small n

Jackson and Jordan, 1975

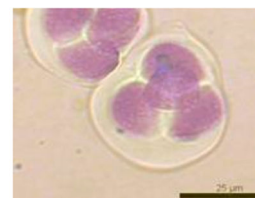


Class alum Doug Heckart
Seashore paspalum

$$\frac{4}{4(2^n) - 2}$$



Class alumnus Aaron Hoskins
Jalapeño pepper



Class alumna Rebecca Tashiro
White clover

$$\frac{4}{4(2^n) - 4}$$

Chromosome #	$(0.5)^n$	$4/[4(2^n)-2]$	$4/[4(2^n)-4]$
1	50.00	66.67	100.00
2	25.00	28.57	33.33
3	12.50	13.33	14.29
4	6.25	6.45	6.67
5	3.13	3.17	3.23
6	1.56	1.57	1.59
7	0.78	0.78	0.79
8	0.39	0.39	0.39
9	0.20	0.20	0.20
10	0.10	0.10	0.10
11	0.05	0.05	0.05
12	0.02	0.02	0.02
13	0.01	0.01	0.01