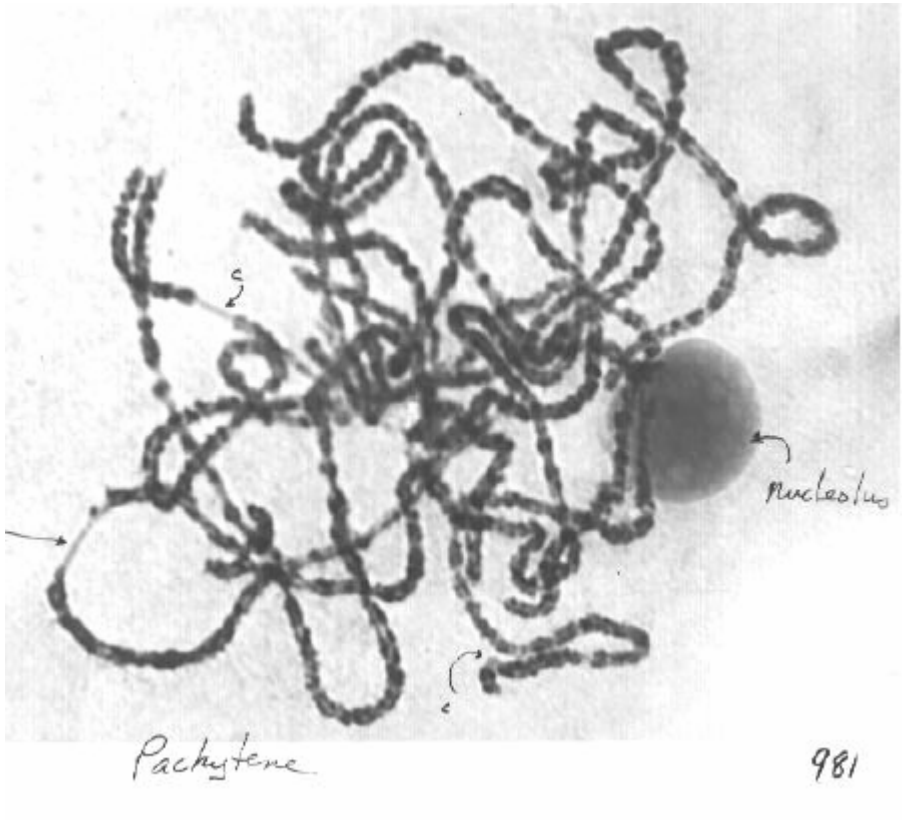
Meiosis



Meiotic chromosome dance

The function of meiosis is to generate cells that contain exactly half of the genetic materials of the parental cells and that develop into germ cells.

Chromosome rearrangements could occur during meiosis, get fixed in populations, and eventually can contribute to genetic diferentiation and speciation.

Meiotic prophase (diakinesis) in a sporocyte of *Ophioglossum reticulatum*, showing about 630 bivalents.

Meiotic phases

- premeiotic S-phase

Meiosis I (reductional division)

- **prophase**

leptotene

zygotene

pachytene

diplotene

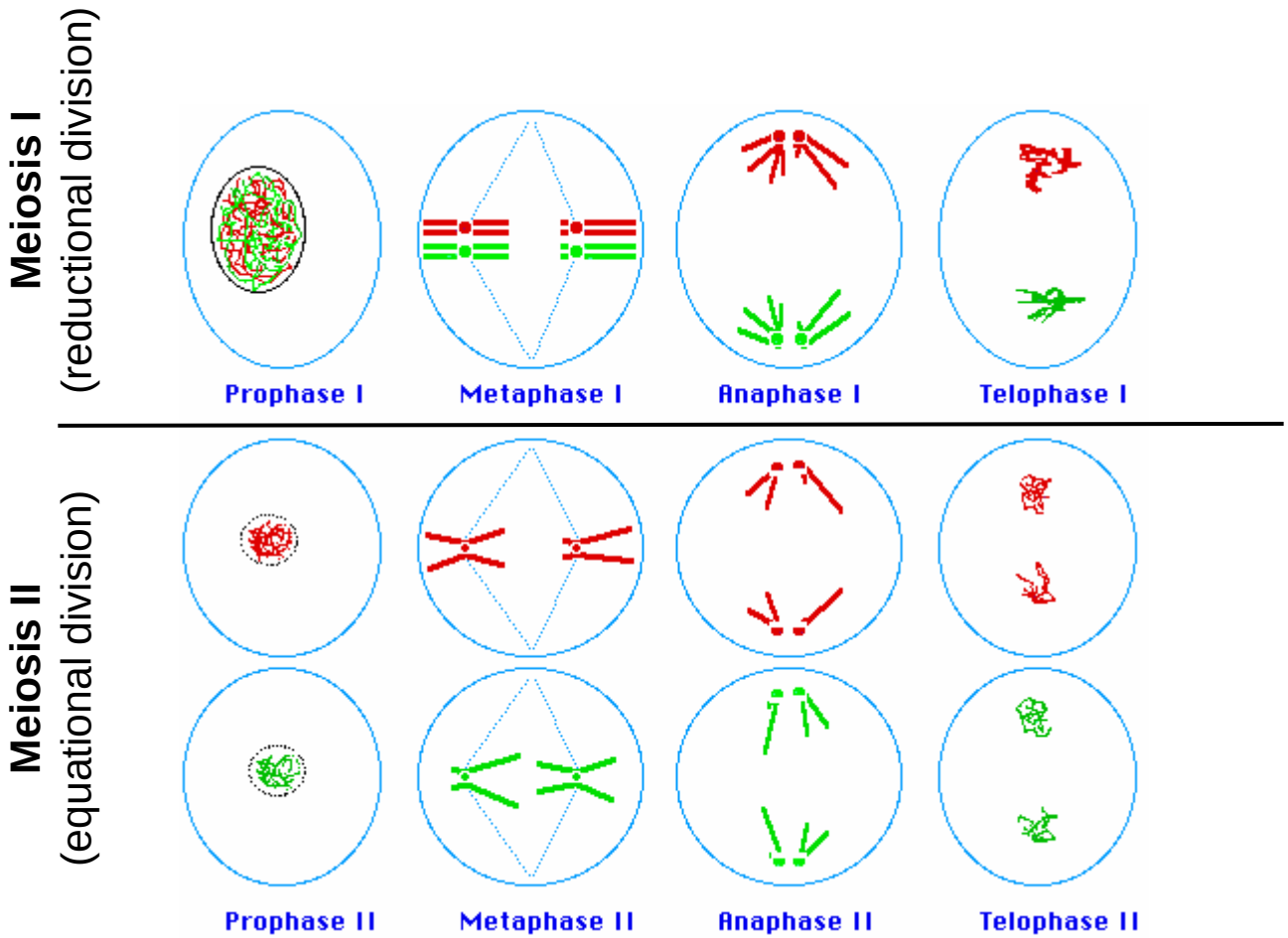
diakinesis

- **metaphase**
- **anaphase**
- **telophase**

Meiosis II (equational division)

- **prophase**
- **metaphase**
- **anaphase**
- **telophase**

Meiotic chromosome dance



Key events of meiosis I

Links between chromosome **pairing**, **synapsis** and **recombination** are not well undestood. Available data suggest that recombination plays a key role in unifying meiotic events in prophase I.

Chromosome pairing

- pairing of homologous chromosomes
- the mechanism is not known

Synapsis

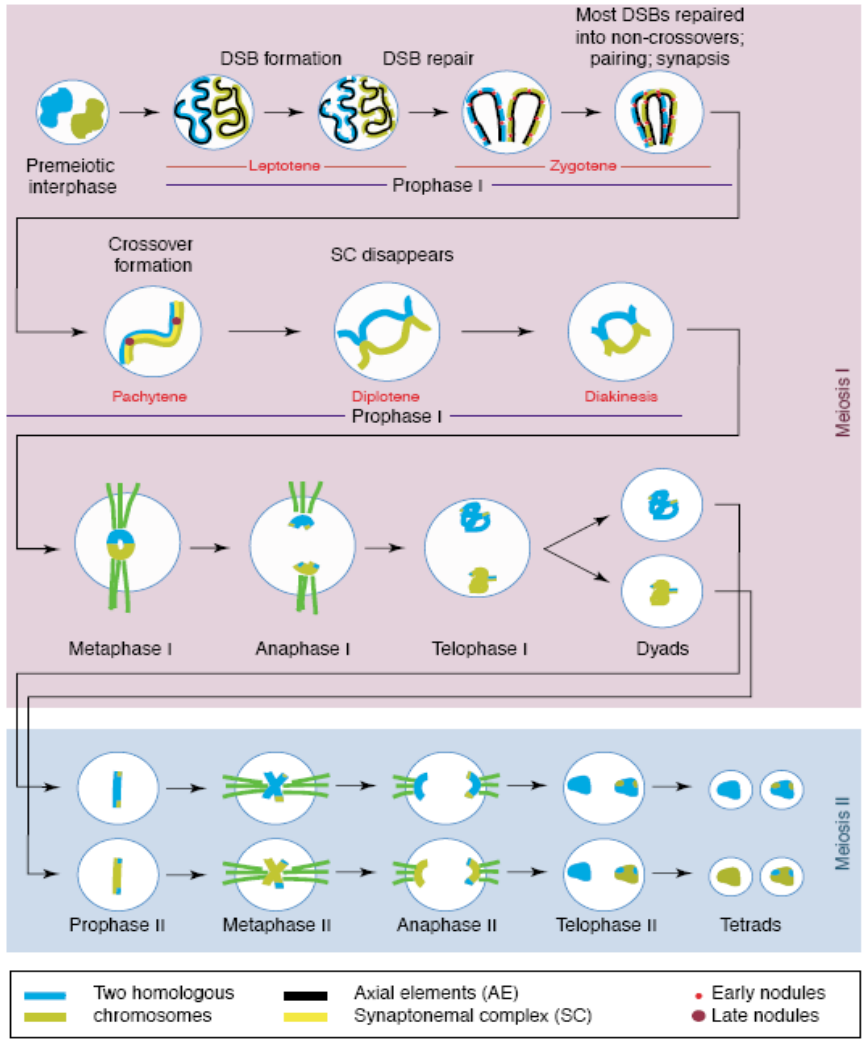
- synaptonemal complex (SC)

- the link between synapsis and recombination is not well understood

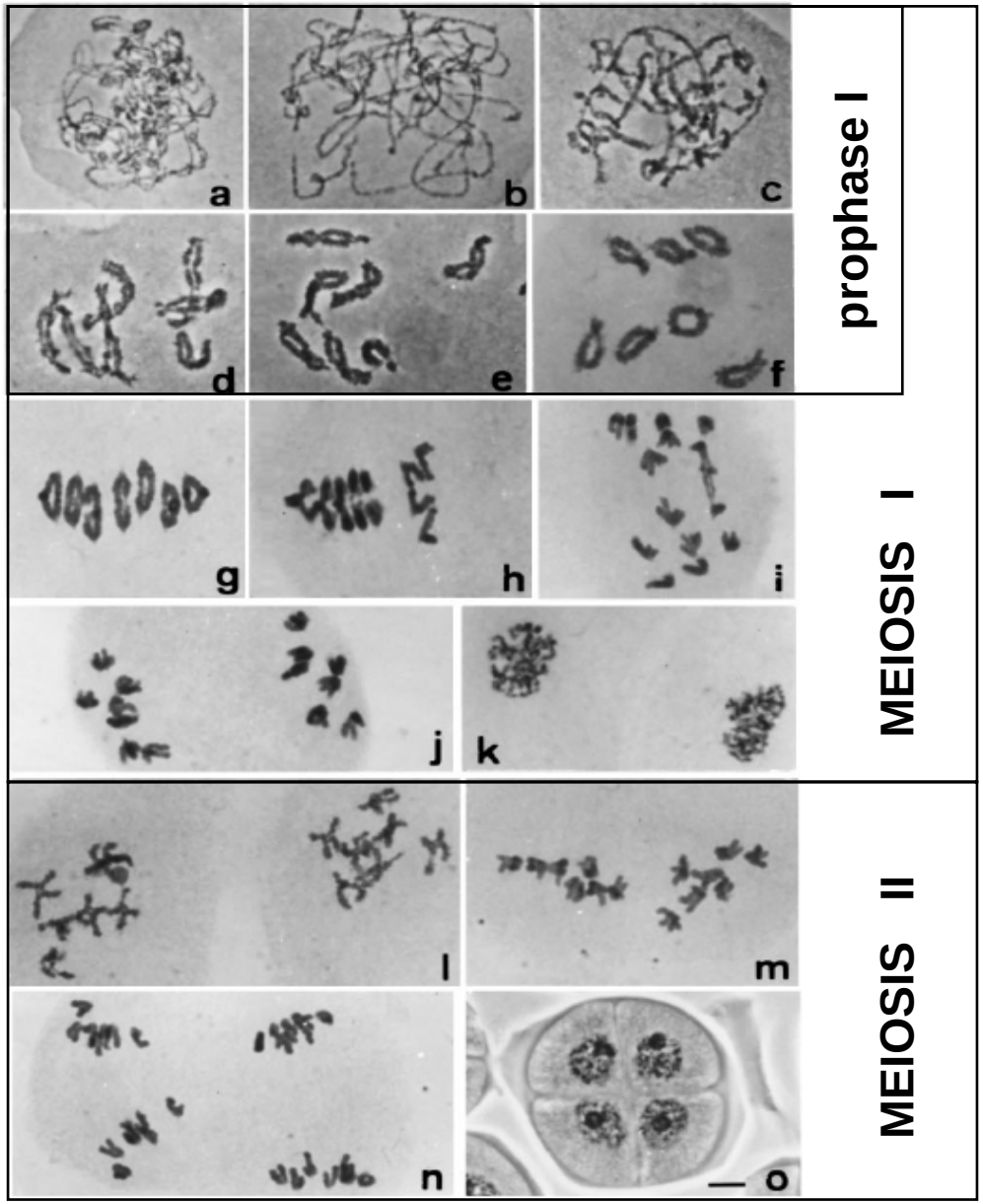
Meiotic recombination

- process of formation of double-strand breaks (DSBs) and their subsequent repair

- results in formation of crossover and non-crossover products



Meiotic divisions I and II in the rye (*Secale cereale*)



(a – f) prophase I

(*a*) early zygotene

(*b* - *d*) early to late pachytene

(*e*) diplotene

(*f*) diakinesis

(*g*, *h*) metaphase I

(*i*, *j*) anaphase I

(*k*) telophase I

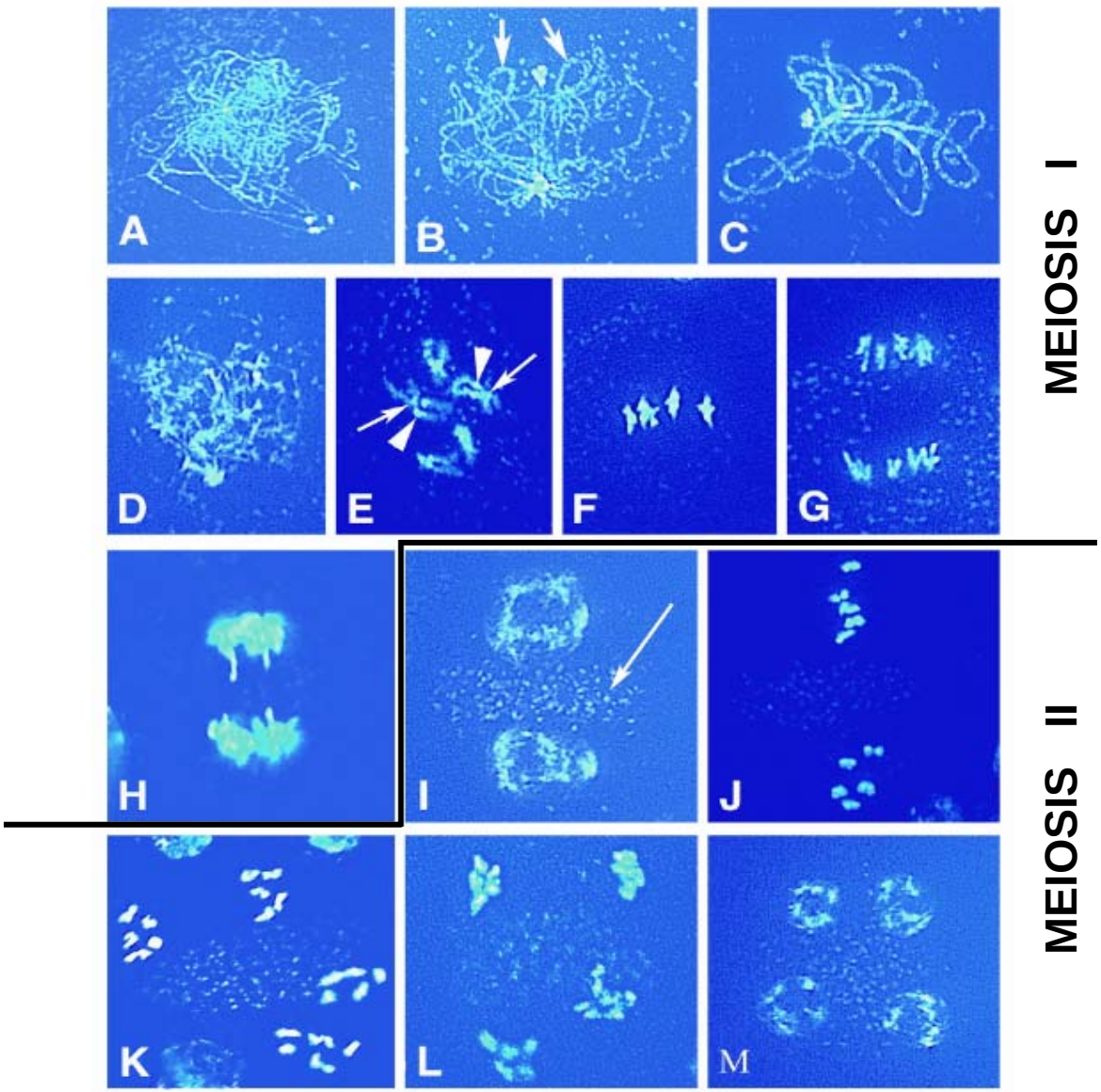
(*l*) prophase II

(*m*) metaphase II

(*n*) anaphase II

(*o*) telophase II (four haploid microspores - tetrad)

Meiotic divisions I and II in *Arabidopsis thaliana*



(A - H) prophase I

(A) leptotene

(B) zygotene

(C) pachytene

(D) diplotene

(E) diakinesis

(F) metaphase I

(G) anaphase I

(H) telophase I

(I) prophase II

(J) metaphase II

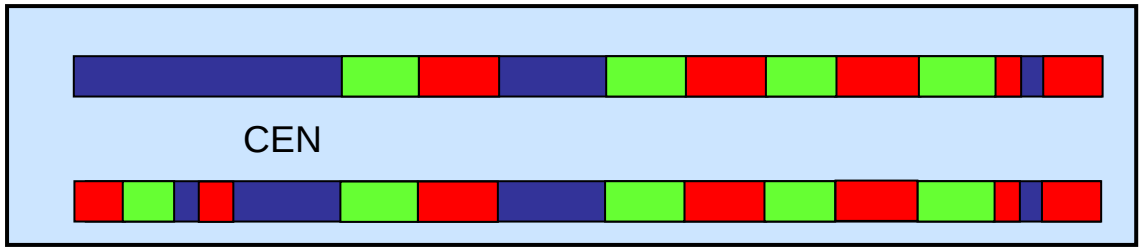
(K) anaphase II

(L) telophase II

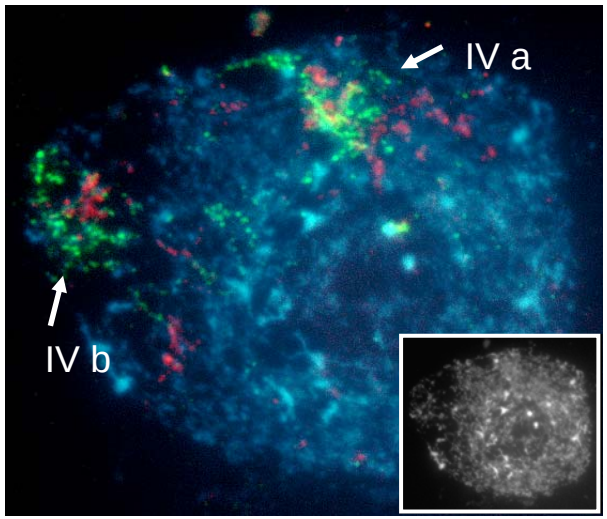
(M) four haploid formed nuclei

Prophase I in *Arabidopsis thaliana* revealed by bicolor chromosome painting

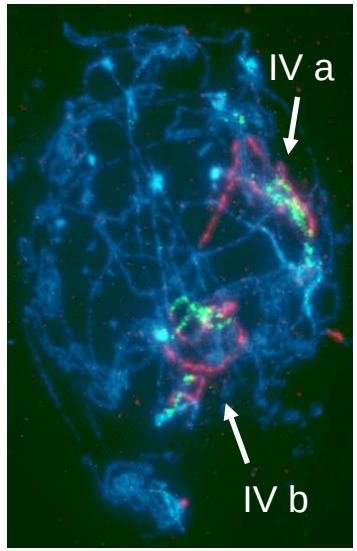
139 clones of a BAC tiling path covering *Arabidopsis* chromosome 4 were divided into 11 pools of 8-18 BACs. Individual pools were labelled either by biotin-dUTP (red) or digoxigenin-dUTP (green) for painting of either the long arm (113 BACs) or the entire chromosome (139 BACs).



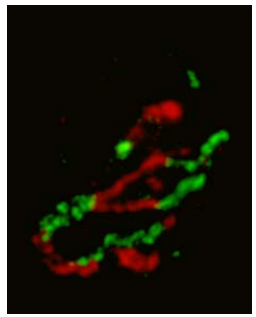
early prophase I

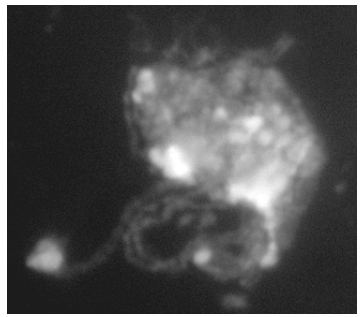


leptotene

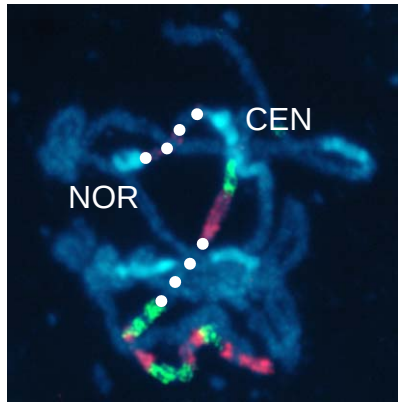


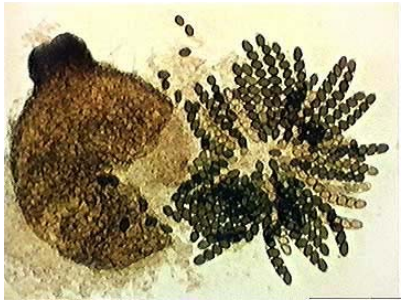
zygotene





pachytene





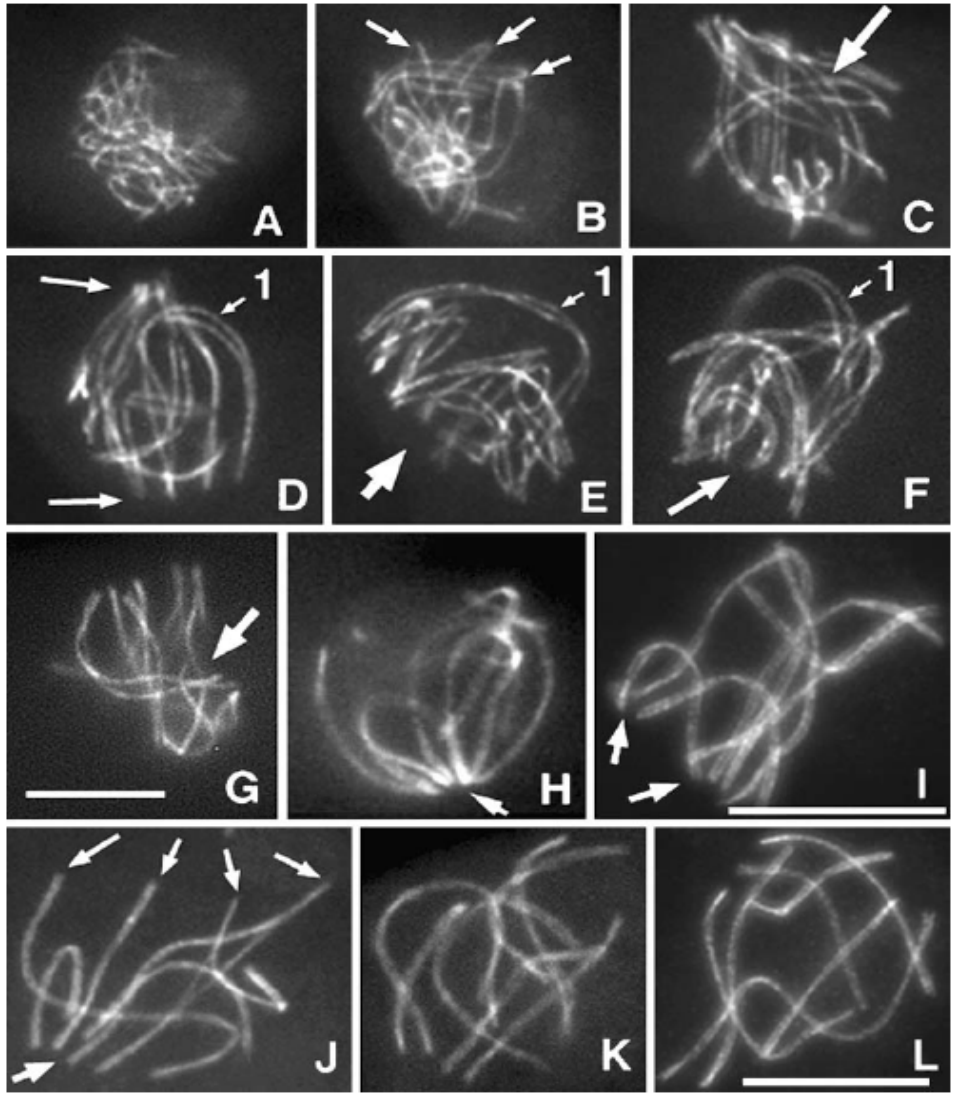
Prophase I in *Sordaria*

(A – C) early, mid- and late leptotene

(D - F) bouquet

(G) zygotene

(H - L) early, mid- and late pachytene



Small arrows: homologues 1 in D through F

Large arrows: telomeres

Chromosome structure at prophase I

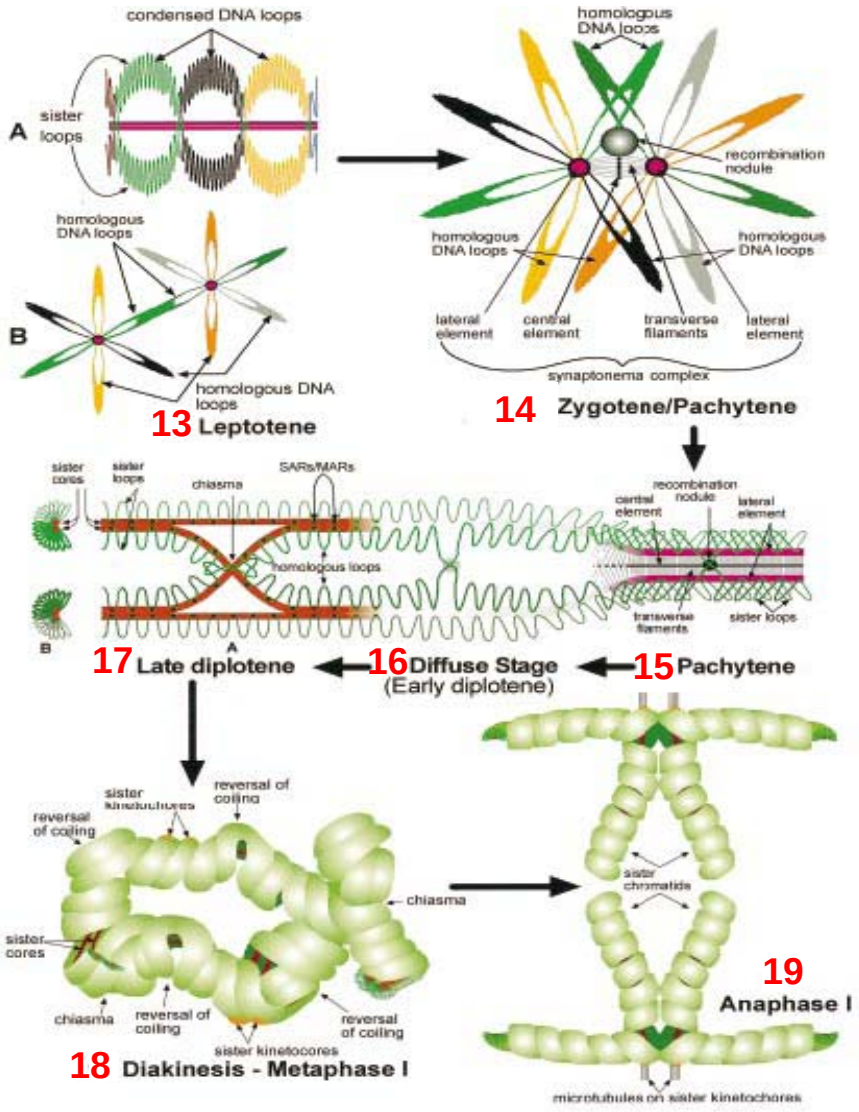


Fig. 13. Leptotene. Longitudinal (A) and end (B) views of a segment of a leptotene chromosome.

Fig. 14. Zygotene/pachytene. End view of a segment of synaptonemal complex (SC). Here a recombination nodule mediates a crossover between the two homologous green loops.

Fig. 15. Pachytene. Frontal view of a segment of synaptonemal complex. At the recombination nodule, DNA loops from two non-sister chromatids are involved in a crossover.

Fig. 16. Diffuse stage (early diplotene). Homologs de-synapse with the disintegration of the SC.

Fig. 17. Late diplotene. Transition from the diffuse stage to late diplotene showing new chromatid cores.

Fig. 18. Diakinesis - metaphase I. From diakinesis through metaphase I, sister chromatids are held together throughout their length (sister chromatid cohesion).

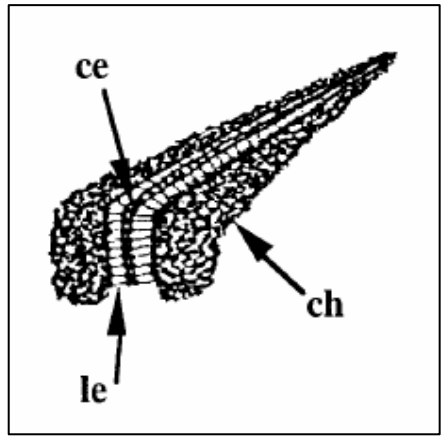
Fig. 19. Anaphase I. Sister chromatid cohesion is lost in the arms but maintained at centromeres. As a result, sister chromatid arms swing apart, chiasmata are lost, and homologous chromosomes are pulled to opposite poles by kinetochore microtubules.

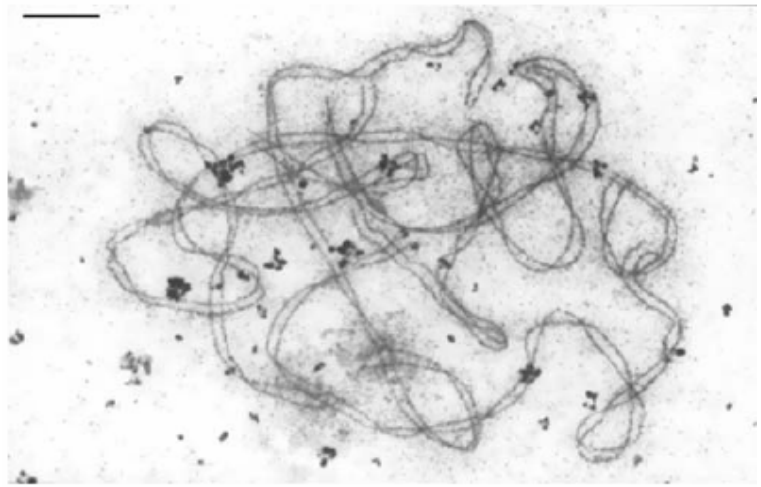
Synaptonemal complex (SC)

- synapsis

- consists of two lateral elements (**le**) connected by a central element (**ce**) [the lateral elements formed as axial elements (AEs, also called the chromosome axis) in leptotene]

- the central element assembles following chromosome pairing during zygotene





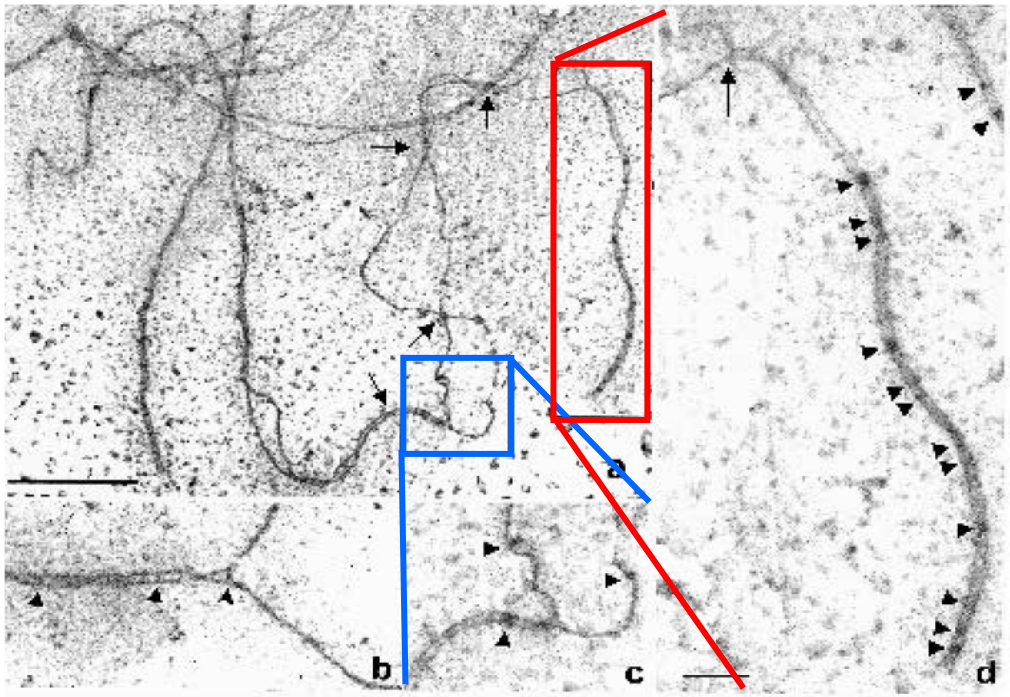
Synaptonemal complex in *Arabidopsis thaliana*

Synaptonemal complex and recombination nodules (RNs)

SCs at zygotene

(a) A complete bivalent with synapsed ends and interstitial sites of synaptic initiation (arrows).

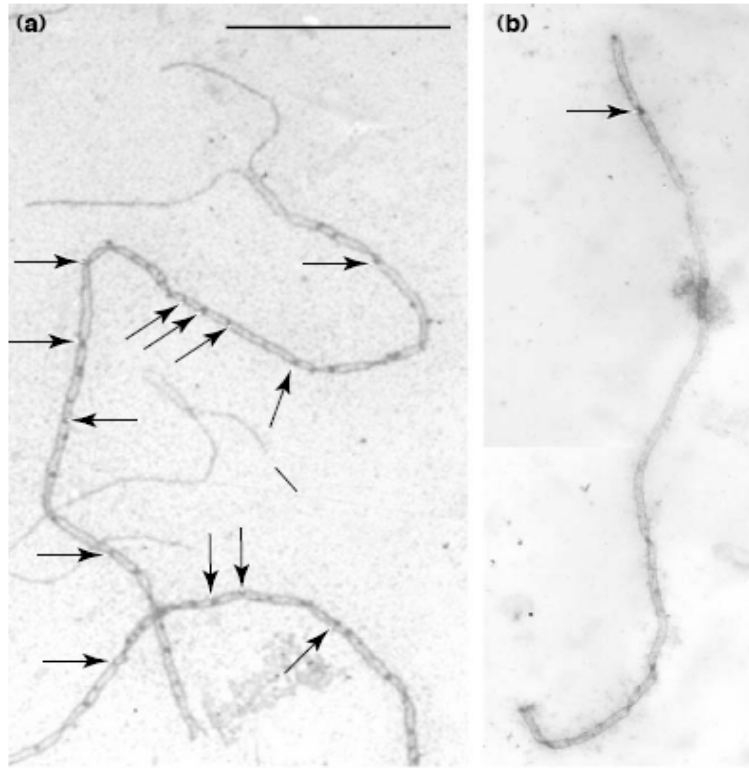
(d) Early nodules (ENs) on SC (arrowheads). Note the synaptic fork without an EN (arrow).



(b) Segment of an SC with ENs (arrowheads).

(c) A synaptic fork without an EN. ENs on SC and on axial elements are indicated by arrowheads.

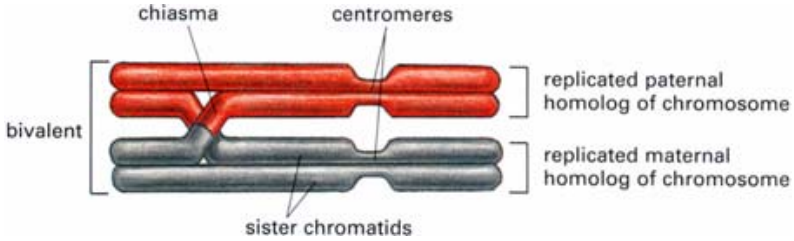
SC spreads of tomato showing recombination nodules



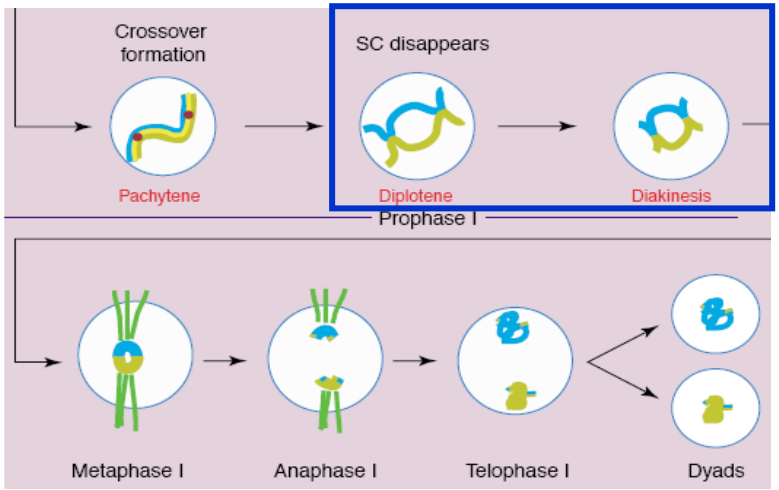
(a) Early nodules in zygotene. Arrows indicate several nodules.

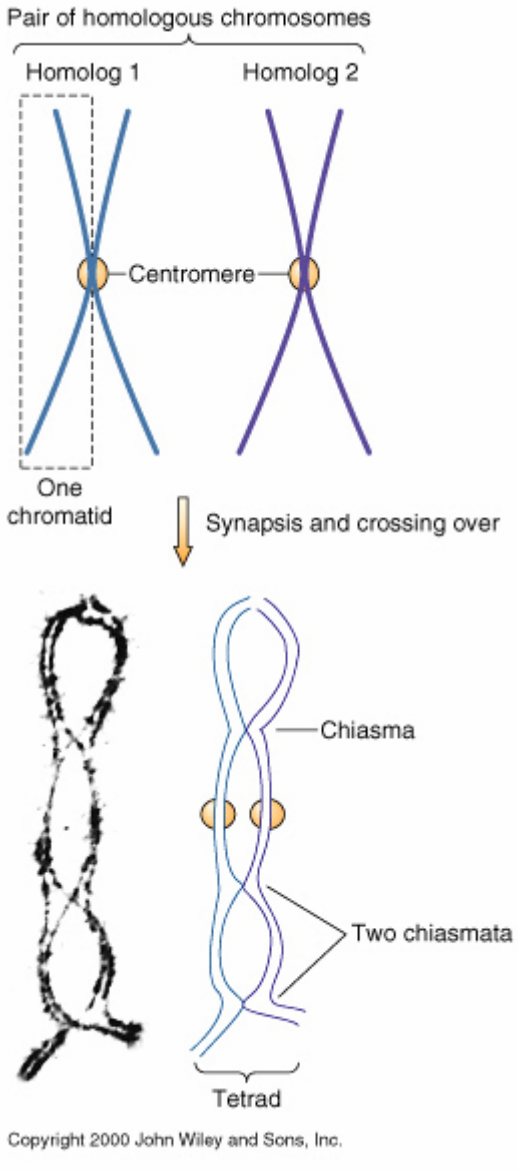
(b) A late nodule in pachytene indicated by an arrow.

Recombination and chiasmata



chiasma formation





Meiotic recombination

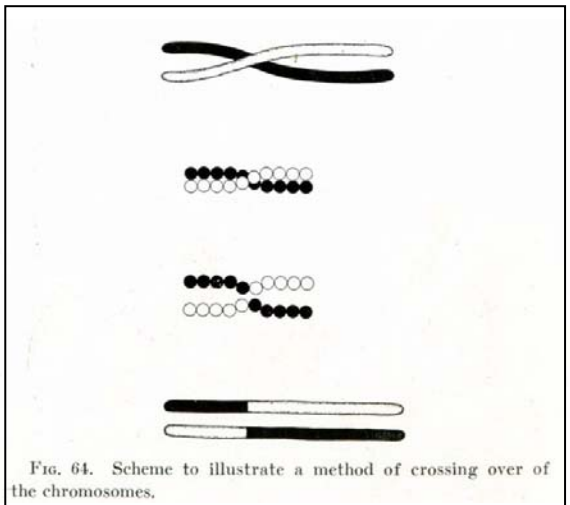


Fig. 64. Scheme to illustrate a method of crossing over of the chromosomes.

Thomas Hunt Morgan's illustration of crossing over (1916)

- usually via homologous recombination (HR)

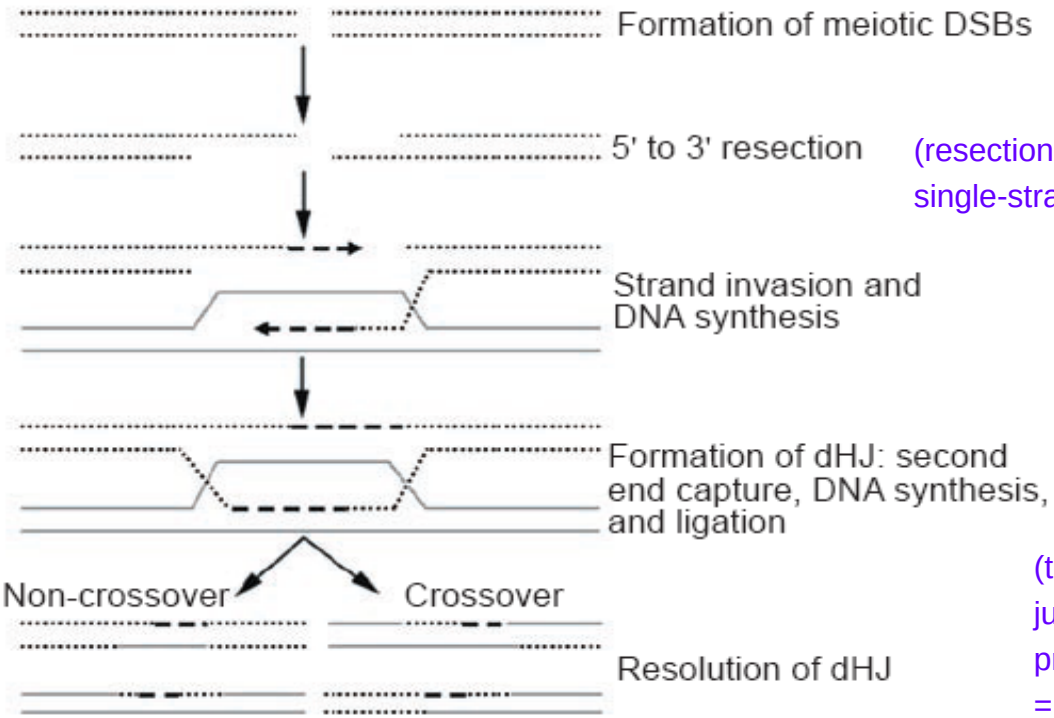
- the double-strand break repair (DSBR) model of HR generally accepted

- double-strand breaks (DSBs) introduced by topoisomerase Spo11 (and other proteins)

- the resection of the DSBs by the MRN (Mre11-Rad50-Nbs1) complex to produce 3' single-stranded DNA ends, the invasion of one of the 3' ssDNA ends is catalyzed by a group of proteins (e.g. DMC1, RAD51)

- recombination probably occurs at the sites of recombinational nodules (RNs) associated with syneptonemal complexes (distinct foci on prophase chromosomes in maize: 500 foci in zygotene, 10-20 foci in pachytene; no. of pachytene foci corresponds to the number of cross-overs)

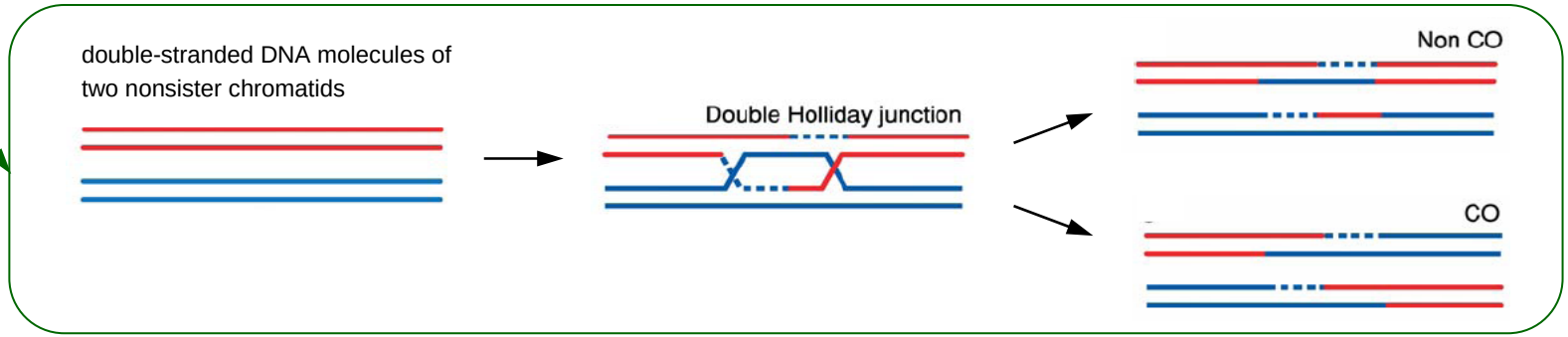
The double-strand break repair (DSBR) model of HR



(resection of the 5' strand ends ⇒ two 3' single-stranded DNA overhangs)

.[one of the 3'overhangs invades the partner chromatid and forms a D-loop. DNA synthesis from the 3' ends using the partner as a template and subsequent ligation form a double Holliday junction (dHJ)]

(the pattern of resolution of this double-Holliday junction determines whether the recombination product is a crossover or a non-crossover; crossovers = chiasmata holding two homologs together from late prophase I to metaphase I/anaphase I)



Some unanswered and new questions about meiosis

(Hamant et al. 2006)

• the mechanisms underlying homology recognition before and during pairing is mostly unknown (premeiotic pairing of homologues ?)

• despite decades of analysis, the role of the synaptonemal complex (SC) in relationship with pairing and recombination is still under debate

• how the meiocyte decides between a crossover or a non-crossover event is poorly understood

• the centromere, with little sequence data available, remains an obstacle to understanding the biology of the meiotic chromosome