Meiosis

General references: Schulz-Schaeffer (1980 Ch. 7)

In the absence of crossing over

- Meiosis I: "reductional"- homologous segments of non-sister chromatids disassociate.
- Meiosis II: "equational"- homologous segments of sister chromatids separate.

First division in particular, lasts considerably longer than mitosis.

Prophase I:

- Great increase in volume of the nucleus.
- Meiotic prophase nuclei in plants and animals is 3 to 4 times that of mitotic prophase nuclei.
- Is also of extremely long duration if it is compared with mitotic prophase.
- Chromosome pairing, chromatid exchange, repulsion, and terminalization.
- **5 substages**: leptotene, zygotene, pachytene, diplotene, and diakinesis

1. Leptotene
   - Meiotic prophase cells are larger than mitotic ones.
   - Chromosomes are longer and thinner than those in early mitotic prophase.
   - Bead-like structures, called chromomeres, appear along entire length of the chromosomes. These are regions of the chromatin threads (chromonemata) that are more tightly coiled than the interchromomeric regions.
   - An increase of size of the nucleolus during leptotene has been related to RNA and protein synthesis.

2. Zygotene
   - The chromosomes gradually become shorter in length and wider in diameter as a result of progressive coiling.
   - Pairing of homologous chromosomes in a zipper-like fashion starting at any or even at several "contact points" along the chromosomes.
   - Paring is not always completely finished; e.g. chromosomes that have non homologous sections such as the sex chromosomes.
   - chromosomepairing is remarkably precise and is called synapsis.
   - Moses in 1956 first discovered a tripartite ribbon at the site of synapsis in crayfish called the **synaptonemal complex**.

   The Synaptonemal Complex:
   - The 10 nm fibers of the chromosomes are comprised of three parallel, electron dense elements that are separated by less dense areas. Two lateral elements are wider than 10 nm and the central element is ladder-like in the center of the SC. Lateral elements are rich in DNA, RNA, and proteins (histones included) but the central element mainly RNA and protein and none or little DNA.
   - Carpenter (1975) described certain SC modifications at the crossover sites. She called these **recombination nodules** (RN) in order to indicate the correlation of their frequency and distribution with the crossover sites in female *Drosophila*. Similar RN's have been observed in the ascomycetous fungi, *Neurospora crasa*, yeast*, etc.*
   - Model of crossover position ***interference*** proposes (Holiday 1977) that a crossover between naked DNA molecules is initially weak in structure and subsequently stabilized by DNA binding

protein. The depletion of DNA binding protein in the neighborhood of a crossover prohibits the formation of a second crossover adjacent to it.

3. Pachytene
- The pairing of homologues is completed form bivalents.
- Chromosomes are shorter than during early prophase.
- The nucleoli are particularly evident during pachytene. In many species they have already all united into one big nucleolus by pachytene that is attached to the nucleolus organizer chromosomes.
- The major function of the chromosomes during late zygotene and pachytene is the phenomenon of crossing over.

4. Diplotene
- Chromosomes further contract and thicken and the chiasmata become apparent as visible evidence of crossing over.
- Synaptic attraction of the chromosomes suddenly comes to an end and the homologues move apart in **repulsion** and are held together at exchange points that are the result of crossing over.
- The longer the chromosome the more chiasmata are present. 12 chiasmata have been observed in the long chromosomes of the broad bean.
- As diplotene progresses, the chiasmata seem to move away from the centromere and diminish in number, called **chiasma terminalization.**
- One of the main forces during chiasma terminalization seems to be a strong repulsion force at the centromeres.
- As the chiasmata move toward the chromosome ends, they seem to become arrested there, forming **endchiasmata** and become locked in at the telomeres without being able to slide over these end structures.
- Hold the homologues together until metaphase orientation is completed and extreme tension is exerted on the endchiasmata, at which time a special trigger mechanism separates all chromosomes and at the same time ushers in anaphase I.

5. Diakinesis
- Bivalents have their greatest degree of terminalization and contraction in diakinesis. They become almost *spherical* configurations.
- If **interstitial chiasmata**, located close to the centromeres, remain localized, then the bivalents appear like *crosses*.
- Other possible chromosome associations in diakinesis are *rod bivalents* and *open ring bivalents*.
- At the end of diakinesis, the nucleolus begins to disappear.

Metaphase I
- End of prophase I is marked by the disappearance of the nuclear envelope and the nucleolus as well as by the division of the centrosome and formation of the spindle.
- Bivalents assemble at the equatorial plate and become oriented with their centromeres poleward.
- In mitosis the sister chromatids are held together by functionally undivided centromeres, which are located on the equatorial plate exactly halfway between the poles. In meiosis, the two centromeres of the homologues are not located on the equatorial plate but are oriented in the long axis of the spindle equidistant from the equator, while the endchiasmata are located in the equatorial plate.
- In general, the position of each chromosome of a bivalent with respect to the poles seems to be at random.

- The random orientation of the bivalents on the equatorial plate determines the meiotic segregation and distribution of the paternal and maternal chromosomes to the daughter cells of the meiotic division. Meiotic segregation is the key to the Mendel's second law, the law of independent assortment.

Anaphase I

- The tetrad chromosomes separate into dyad chromosomes, as the two cooriented centromeres move toward opposite poles.
- Typical meiotic anaphase I always has four chromosome arms dangling behind the centromere, while a mitotic anaphase has only two such arms showing.
- An anaphase I dyad chromosome consists of two chromatids, whereas a mitotic anaphase chromosome is really a single chromatid.
- Anaphase I is shorter in duration than metaphase I. Evenly distribute the partners of homologous chromosome pairs to the daughter nuclei, with the result of a reduction by half the number in each resulting nucleus. Original somatic chromosome number (2n) is reduced to a gametic chromosome number (n).

Telophase I

- Is similar to mitotic telophase in that the chromosomes assemble at the poles.

Interkinesis

- Is a short stage, the chromosomes do not synthesize new DNA and consequently there is no reduplication.
- In some species (maize for example) the chromosomes become partially uncoiled during interkinesis, and nuclear envelopes form.
- In some species (*Paeonia*) there is no cytokinesis after the first meiotic division. Cytokinesis is postponed until after the second meiotic division. This process is referred to as **quadripartioning**.
- In contrast, the normal process as found in many plants, where a cell plate forms between the telophase nuclei of the first division, is called **bipartitioning**.
- In some species following the disappearance of the spindle, the chromosomes orient themselves at the poles and pass directly to the equatorial plate of the second division.

Meiosis II

Is essentially mitosis except:

- The chromosomes are already prepared for the second division in that each of them consists of two chromatids only held together by a centromere.
- Chromosomes in haploid (n) not in diploid (2n) numbers.
- DNA synthesis does not precede meiosis II.
- Each chromatid at the end of meiosis II may be genetically distinct.

End results:

- Male--quartet of microspores from pollen mother cells (PMC)---->pollen.
- Female--linear quartet of megaspores from megaspore mother cells (MMC)---->embryo sac.