15.8: Meiosis

In metazoa, there are two situations in which a cell gives rise to daughter cells. The first, and by far most common, is mitosis. The second is meiosis. Meiosis is the process by which gametes (sex cells) are generated. Animals and plants are generated by sexual reproduction (if this is news to you, please consider majoring in something other than biology). These organisms start life through the fusion of two cells: a sperm and an egg. Both contribute genetic material to the new organism. In order to maintain the proper number of chromosomes in each generation, the gametes each contribute one set of chromosomes, so that the fertilized egg and all other cells in the organism have two sets of chromosomes — one from each parent. The purpose of meiosis, and its primary difference with mitosis, is not generating daughter cells that are exact replicates, but generating daughter cells that only have half the amount of genetic material as the original cell.

Let us take a look at this situation selfishly: meiosis in human beings. Almost every cell in your body has a nucleus containing 46 chromosomes, a set of 23 from your father, and a set of 23 from your mother. The only exceptions are the gametes: the spermatocytes in men and the oocytes in women. The somatic cells are said to be 2n or diploid, that is having 2 sets of chromosomes, and the gametes are 1n or haploid, having only one set of chromosomes. Sometimes, meiosis can be a little confusing to students because it occurs in the same part of the cell cycle as mitosis, which is to say after G2. Because of this, the cell entering meiosis actually has 4 sets of chromosomes, since the DNA has already undergone replication in S phase.

Mature red blood cells contain no nucleus, and some muscle cells, while multinucleated because they form from the fusion of several myoblasts, nevertheless have 46 chromosomes in each of the nuclei. Polyploidy, while uncommon in humans, is a normal state for many organisms. The frog, *Xenopus laevis*, a common research animal, is tetraploid.

Meiosis consists of two consecutive meiotic divisions each of which has phases similar to mitosis: prophase, metaphase, anaphase, telophase, and each of which finishes with complete cytokinesis. Note that immediately following
meiotic telophase I, the cell divides, and both daughter cells are immediately in prophase II. There is no intervening G₁, S, or G₂ phase.

Prophase I of meiosis begins very similarly to prophase of mitosis: MPF (mitotic-cdk) activation, chromosome condensation, spindle formation and nuclear envelope breakdown. However, compared to mitosis, meiotic prophase I lasts for a very long time and can be subdivided into five stages: leptotene, zygotene, pachytene, diplotene, and diakinesis. During leptotene, the two sets (maternal and paternal) of sister chromatids for each chromosome condense, align and form a structure known as a bivalent. To clarify, this bivalent consists of four copies of a given chromosome: two copies each of the maternal chromosome and of the paternal chromosome. Because the maternal and paternal versions of a given chromosome are kept in extremely close proximity for an extended period of time, there is a greater chance of a recombination, or crossing over and exchange of homologous pieces of each chromosome.

![Figure 16](https://bio.libretexts.org/Bookshelves/Cell_and_Molecular_Biology/Book%3A_Cells_-_Molecules_and_Mechanisms_(Wong)/1…)

Recombination occurs when a piece of the paternal chromosome is swapped for the homologous piece of DNA on the matching maternal chromosome (or vice versa). Note that sister chromatids (i.e. exact copies) do not recombine - only homologous non-sister chromatids can recombine. Obviously, this kind of a DNA swap must be done carefully and with equivalence, so that the resultant DNA on each side contains all the genetic information it is supposed to, and no more information than it is supposed to. In order to ensure this precision in recombination, the non-sister homologous chromatids are held together in a synaptonemal complex (SC). This ladder-like complex begins to form in the zygotene stage of prophase I and completes in pachytene. The complete SC consists of proteinaceous lateral elements (aka axial elements) that run along the length of the chromatids and a short central element composed of fibrous proteins forming the rungs of the ladder perpendicular to the two lateral elements. The central element is formed of transverse lament dimers that interact with one another in offset fashion, as well as with the lateral elements. These lament proteins (e.g. SCP1 (mouse), Zip1p (yeast)) have central coiled-coil regions that function as protein interaction domains. Although SCP3 and therefore complete lateral element formation are unnecessary for a functional synaptonemal complex, condensin and cohesin do appear to be necessary for proper transverse lament attachment of the lateral elements.

Recombination may occur with or without the formation of double-strand breaks, and in fact, can occur without the formation of the synaptonemal complex, although the SC probably enhances the efficiency of recombination. In S. pombe, meiosis occurs without the formation of a synaptonemal complex, but there are small discontinuous structures somewhat similar to parts of the SC. In the fruit fly, Drosophila melanogaster, females undergo meiosis using a synaptonemal complex, but males do not undergo meiotic recombination, and their chromosomes do not form synaptonemal complexes. In most cases, recombination is preceded by the formation of recombination nodules, which
are protein complexes that form at potential points for recombination. The best studied mechanism for meiotic recombination involves a double-stranded break of one of the chromosomes initiated by the meiosis-specific endonuclease, Spo11. The 5’ ends (one in each direction) of this cut are degraded slightly to form 3’ single-stranded overhangs. This leads to the formation of Holliday junctions with a strand from one chromosome acting as a template for a missing portion of the homologous cut chromosome. This may be resolved one of two ways, with or without a crossover, as illustrated (Figure \(\PageIndex{17}\)).

![Figure \(\PageIndex{17}\). Recombination of homologous chromosomes.](image)

The recombination is initiated in pachytene and completes in diplotene, at which time the synaptonemal complex breaks down. As the chromatids begin to separate, chiasmata become apparent at some of the recombination sites. As prophase completes, the chiasmata resolve from the center of the chromosomes to the ends.

As the cell goes from meiotic prophase I to meiotic metaphase I, another difference between mitosis and meiosis is revealed: the chromosomes line up at the metaphase plate as tetrads rather than as pairs. Because of this, when they pull apart in anaphase, sets of sister chromatids segregate to opposite poles. Of course, due to recombination, the sister chromatids are unlikely to still be identical.
Figure \(\PageIndex{18}\). Meiosis generates 4 haploid daughter cells from one diploid precursor. To do so, it undergoes a two rounds of meiotic nuclear and cell division.

After a conventional anaphase and telophase, the cell splits, and immediately the daughter cells begin the second meiotic division (Figure \(\PageIndex{18}\), right side). In some cell types, chromosomes do not decondense in meiotic telophase I, but if they have, they re-condense in meiotic prophase II. Prophase II proceeds similarly to mitotic prophase, in that there is no formation of synaptonemal complexes or recombination. At metaphase II, the sister chromatids line up along the metaphase plate just as in mitosis, although now there are only 2n chromosomes in the cell, while in mitosis there would have been 4n (because the DNA has replicated). Again, nishing the rest of the division almost exactly like mitosis, the sister chromatids pull apart in anaphase II, the nucleus reforms in telophase II, and the final cytokinesis generates a total of four cells from the original one that entered into meiosis, each containing 1n chromosomes.

Egg cells, as genetic and bulk material donors, need to be large but sperm cells, as genetic donors only, do not. The diagram below depicts the generation of the egg cells. Only one oocyte is generated from a meiotic event; the other three daughter cells are termed polar bodies, and contain so little cytoplasmic material that they are only viable for a short time. The asymmetric distribution of cytoplasm in the first meiotic division for oocytes is due to the position of the meiotic spindle in the periphery of the cell rather than centered. Since the center of the spindle determines the position of the contractile ring for cytokinesis, this leads to unevenly sized daughter cells.
The generation of the very small sperm is a different mechanism altogether. In the meiotic steps of spermatogenesis, the cell divisions are equal, with the meiotic spindle aligned with the center of the cell, and the cells have equal amounts of cytoplasm, much like an average cell that has undergone mitosis. The streamlined, minimal-cytoplasm mature sperm is a product of post-meiotic differentiation, in which it gains the flagellar tail, and ejects most of its cytoplasmic material, keeping only some mitochondria to power the flagella, and an acrosomal vesicle, that contains the enzymes and other molecules needed to reach and fuse with (i.e. fertilize) an egg.

Not all organisms reproduce with the human-like egg and sperm mechanism, i.e. gametic meiosis. As just described, in a gametic meiosis life cycle, meiosis generates haploid gametes, which then fuse/fertilize to become a diploid zygote. The zygote becomes a multicellular diploid organism, and once it reaches sexual maturity can make more haploid
gametes via meiosis. The only multicellular state is diploid, and the gametes are haploid.

A common variation is sporic meiosis, used in all plants and many types of algae. In this usage, "spore" refers to eukaryotic spores, and not to bacterial endospores, which are simply dormant bacteria. Sporic meiosis does not directly produce gametes. Instead, meiosis produces haploid spores, which can develop by mitosis in haploid multicellular organisms. These organisms (termed gametophytes) can produce (still haploid) gametes by mitosis, that when fused/fertilized form a diploid zygote. This zygote can then develop into a diploid multicellular form called the sporophyte. Finally, the sporophyte is able to generate more spores by meiosis.

Figure \(\PageIndex{21}\). Gametic meiosis (left) and Sporic meiosis (right).

An example of this type of life-cycle and the role of meiosis is found in moss. What we think of as the body of the moss is actually a gametophyte, made up of haploid cells generated by mitotic division of a haploid spore. These gametophytes generate either sperm or eggs in specialized structures in their distal tips, and under the right conditions (e.g. rain) the sperm is carried to the eggs and fertilization occurs. The fertilized (diploid) egg now develops by mitotic division and differentiation into a sporophyte. In this case, the sporophyte is a specialized reproductive structure on the tip of the moss, and is also diploid. On the tip of the sporophyte is the sporangium, which is where meiosis takes place to generate haploid spores. The spores may then be dispersed (by wind or rain) and begin the cycle again by dividing and forming a new gametophyte.