

Mitosis and Meiosis

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All cells come from pre-existing cells. Cell division creates two new cells, and the cell that divides ceases to exist. Cell division serves three major functions:

- Unicellular organisms reproduce via cell division.
- Multicellular organisms use cell division for growth and development.
- Multicellular organisms use cell division for tissue renewal, replacing dead or destroyed cells and cells that are lost from the organism.

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In a eukaryotic cell, DNA is complexed with histone proteins, forming a mixture called chromatin. When a cell nears the time of cell division, the chromatin condenses into more compact strands that become visible microscopically. These strands continue to condense into a species-dependent number of much more compact structures called chromosomes.

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By the time chromosomes appear, the DNA has already been replicated in the cell, producing enough DNA for two cells. A replicated chromosome consists of two genetically identical halves, called sister chromatids, that are connected to each other at a region called the centromere. Later, the sister chromatids will separate and be placed in separate daughter cells that are created when the original cell divides. After separation, they are no longer chromatids, but rather chromosomes, though they are then non-replicated, because each is just one copy of DNA (enough for one daughter cell).

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In G_2 , chromatin is not yet condensed, so no chromosomes appear in the nucleus. Mitosis includes five phases:

- Prophase - The two centrosomes begin to move toward opposite poles within the cell. They are pushed apart by interaction between non-kinetochore microtubules that grow from each centrosome. The combination of the two centrosomes and the microtubules is called the mitotic spindle. The nuclear envelope is still intact. Within the nucleus, the chromatin is condensing into chromosomes.
- Prometaphase - The centrosomes have now finished moving to opposite poles. The chromosomes continue to condense. The nuclear envelope has disintegrated, allowing kinetochore microtubules (growing from the centrosomes) to connect to the kinetochores found on either side of the centromere of each replicated chromosome.
- Metaphase - The replicated chromosomes move along the mitotic spindle's microtubules until all chromosomes are in the metaphase plate, a plane that is midway between the two centrosomes. The replicated chromosomes are now maximally condensed.
- Anaphase - Each replicated chromosome splits, and its two sister chromatids separate, becoming non-replicated chromosomes that move in opposite directions. Each non-replicated chromosome moves along the spindle to one of the two poles, so that each of the two cells that will be created will receive one of the two copies of the DNA.
- Telophase - The non-replicated chromosomes reach the poles. A new nuclear envelope forms around each pole's set of chromosomes, forming two nuclei. The chromosomes in each nucleus begin to uncoil, so their genes can begin to be transcribed.

Cytokinesis begins before telophase ends. Cytokinesis ends in the full separation of the two daughter cells. The original cell no longer exists.

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An ordered, pictorial arrangement of an organism's replicated chromosomes (from one cell) is called a karyotype. Each species has a characteristic number of different chromosomes, which are different from each other, because they carry genes for different characteristics. Ploidy refers to the number of sets of chromosomes contained in a cell. A diploid cell is one that contains two versions of each type of chromosome. One version of each type was donated by one of the organism's parents; the other version was donated by the other parent. A haploid cell is one that contains just one of each type of chromosome. A human (like all animals) contains two types of cells:

- Somatic cells - These are most of the cells of the body. They are diploid, and when they divide, they do so by mitosis to produce genetic duplicates of themselves.
- Germ line cells - These are specialized cells within the gonads. They are diploid, and when they divide, they do so by meiosis to produce genetically distinct, haploid gametes.

The two versions of each type of chromosome (one from each parent) are homologous to one another. Each version within that homologous pair is called a homolog.

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The haploid number for any given species is designated as N . The diploid number is therefore $2N$. For any diploid cell, there are N homologous pairs, because each homologous pair is two chromosomes.

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For humans, $N=23$. Humans are diploid organisms, so their bodies are made out of cells with 46 chromosomes each. When a human reaches sexual maturity, its germ line cells undergo meiosis to produce haploid gametes (eggs or sperm), each with 23 chromosomes. Fertilization is the union of two unicellular, haploid gametes to produce one unicellular, diploid zygote. If two humans mate, a sperm and egg can fuse in the process of fertilization to produce a diploid zygote (46 total chromosomes, 23 from each of the haploid gametes). That diploid zygote then divides by mitosis to produce a multicellular human of the next generation, completing one life cycle.

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All sexually reproducing species undergo a generation-to-generation alternation between meiosis and fertilization. This is necessary, because fertilization doubles the ploidy. Without meiosis to cut the ploidy in half again, each generation would produce cells with twice as many chromosomes as the previous generation. Animals spend most of the life cycle in the diploid condition, producing haploid gametes that exist only long enough for fertilization to occur. Fungi spend most of the life cycle in the haploid condition, as adult fungi are made of haploid cells. Since they are already haploid, they produce gametes by mitosis. Gametes fuse in fertilization to produce a diploid zygote, but that zygote immediately undergoes meiosis to produce haploid spores. These spores then undergo mitosis to produce the multicellular, haploid adult. Plants spend appreciable time in each of the two conditions. The haploid version of the plant produces gametes by mitosis (like a fungus) and is called a gametophyte. Fertilization produces a diploid zygote that undergoes mitosis to produce the diploid version of the plant, called a sporophyte, which then produces haploid spores by meiosis.

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Meiosis involves two cell-division events, so the overall process is divided into meiosis I and meiosis II. Each of these is subdivided into subphases with names corresponding to the subphases of mitosis. In metaphase of meiosis I (i.e., metaphase I), N pairs of homologous, replicated chromosomes line up at the metaphase plate. This is different from metaphase of mitosis, in which $2N$ individual, replicated chromosomes line up. In anaphase I, the homologs in each pair separate, so that each daughter cell gets just one of the two chromosomes in each pair. Therefore meiosis I is the part of meiosis in which the ploidy is reduced from $2N$ to N . Meiosis II is effectively identical to mitosis, because metaphase II lines up individual, replicated chromosomes, and anaphase II separates sister chromatids. The resulting cells are gametes.

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Sexual reproduction has the advantage of greatly increasing genetic diversity beyond the diversity caused just by mutation. There are three sources of additional genetic diversity in sexual reproduction:

- Crossing over
- Independent assortment
- Random fertilization

The first two of these occur within meiosis I. Each of the two major phases of meiosis is subdivided into prophase, metaphase, anaphase, and telophase. There are important differences compared to mitosis:

- Prophase I - The two homologs for each kind of chromosome find each other and come together, forming a homologous pair. This is called synapsis. Because each of the two homologs in the pair is already replicated (from having gone through the S phase of interphase), the pair consists of four chromatids (two pairs of sister chromatids). Therefore, a homologous pair is also called a tetrad. Synapsis results in N tetrads. At the time of synapsis, two non-sister chromatids (one from each homolog) can cross over and trade corresponding portions of the DNA sequence. The location at which the non-sister chromatids cross is called a chiasma. Crossing over is the first important source of additional genetic diversity.
- Metaphase I - By now there are N tetrads, each consisting of two replicated homologs, and those N tetrads line up at the metaphase plate. Independent assortment refers to the fact that each tetrad lines up independently of other tetrads with respect to which pole the maternal homolog faces and which pole the paternal homolog faces. Independent assortment is the second important source of additional genetic diversity. The current cell has 2N total chromosomes, but they are paired up as N tetrads.
- Anaphase I - The tetrads divide, with each homolog of a tetrad moving toward its own pole. Each daughter cell of meiosis I will get just one of the two chromosomes from each tetrad, so meiosis I reduces the ploidy. Each of the two daughter cells coming out of meiosis I will contain N chromosomes, but those chromosomes are still replicated (consisting of two sister chromatids).
- Metaphase II - The N replicated chromosomes line up at the metaphase plate. The same thing occurs in the other cell produced by meiosis I.
- Anaphase II - Sister chromatids separate and become unreplicated chromosomes on their own.

Therefore, meiosis starts with one diploid germ line cell, and it produces four haploid gametes. Because of crossing over and independent assortment, each gamete is genetically different from the other gametes. When two parents mate, a gamete is randomly chosen from each parent, and those gametes fuse in the process of fertilization. Because each gamete is genetically distinct, this random fertilization is the third important source of additional genetic diversity.

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The important differences between mitosis and meiosis are illustrated.

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Independent assortment adds genetic diversity to gametes. The greater the value of N for a species, the greater the number of different ways in which assortment can occur.

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Crossing over adds genetic diversity to gametes. Because there are so many locations along a chromosome at which crossing over can occur, the number of possibilities is astronomically high.

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Nondisjunction is accidental failure of separation during anaphase. If nondisjunction occurs during meiosis I, two homologs in a tetrad will fail to separate. If nondisjunction occurs during meiosis II, two sister chromatids will fail to separate. In either case, aneuploid gametes are produced.

Nondisjunction can occur also in mitosis of a somatic cell, but that defect is not passed on to the offspring, because only gametes are involved in formation of the zygote.