

CHAPTER-10

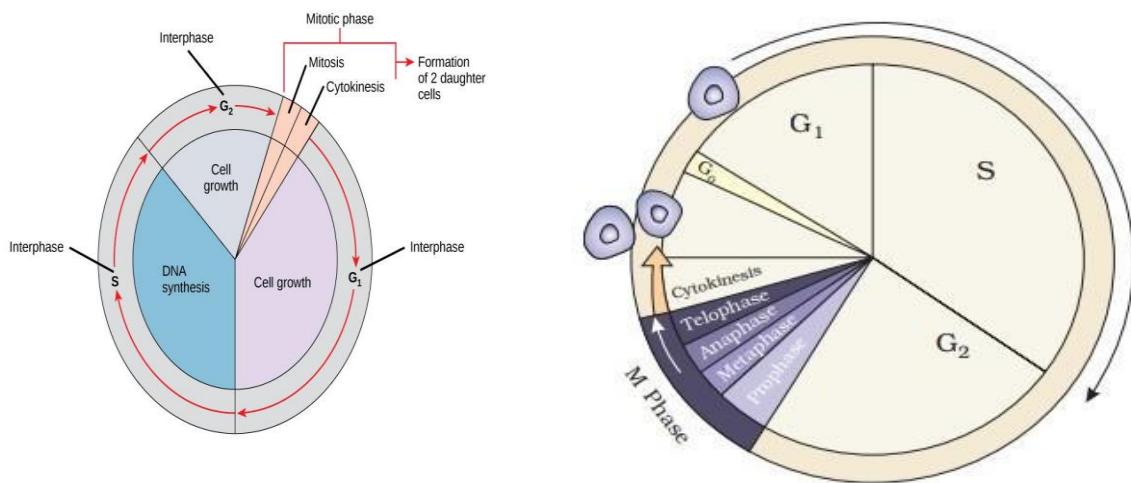
CELL CYCLE AND CELL DIVISION

Cell division is a very important process in all living organisms. During the division of a cell, DNA replication and cell growth also take place. All these processes, i.e., cell division, DNA replication, and cell growth, hence have to take place in a coordinated way to ensure correct division and formation of progeny cells containing intact genomes.

Phases of the cell cycle have severed

A typical eukaryotic cell cycle is illustrated by human cells in culture. These cells divide once in approximately every 24 hours as shown in the figure below. However, this duration of the cell cycle can vary from organism to organism and also from cell type to cell type. Yeast, for example, can progress through the cell cycle in only about 90 minutes.

- The cell cycle is an ordered series of events involving cell growth and cell division that produces two new daughter cells. Cells on the path to cell division proceed through a series of precisely timed and carefully regulated stages of growth, DNA replication, and division that produces two identical (clone) cells.
- The cell cycle has two major phases: interphase and the mitotic phase (Figure 1). During interphase, the cell grows and DNA is replicated. During the mitotic phase, the replicated DNA and cytoplasmic contents are separated, and the cell divides.

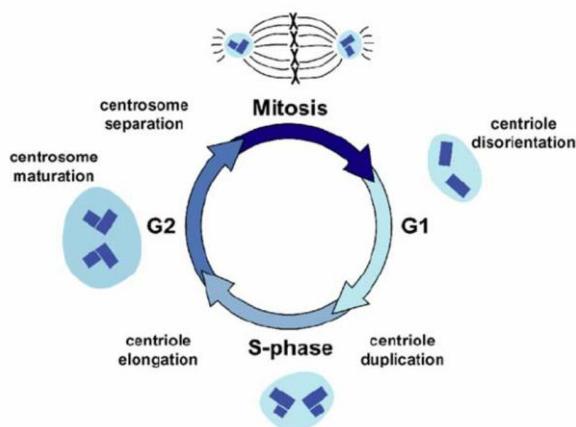


- Like a clock, the cell cycles from interphase to the mitotic phase and back to interphase. Most of the cell cycle is spent in interphase, which is subdivided into G₁, S, and G₂ phases. Cell growth occurs during G₁, DNA synthesis occurs during S, and more growth occurs during G₂.
- The mitotic phase consists of mitosis, in which the nuclear chromatin is divided, and cytokinesis, in which the cytoplasm is divided, resulting in two daughter cells.

The cell cycle consists of interphase and the mitotic phase.

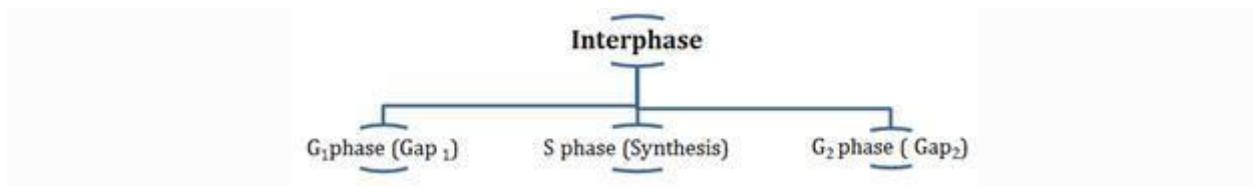
- During interphase, the cell grows and the nuclear DNA is duplicated. Interphase is followed by the mitotic phase.
- During the mitotic phase, the duplicated chromosomes are segregated and distributed into daughter nuclei. The cytoplasm is usually divided as well, resulting in two daughter cells.

Centrosome cycle during the cell cycle



Interphase

During interphase, the cell undergoes normal growth processes while also preparing for cell division. For a cell to move from interphase into the mitotic phase, many internal and external conditions must be met. The three stages of interphase are called G₁, S, and G₂.



• G₁ Phase (First Gap)

This phase corresponds to the interval between mitosis and initiation of DNA replication. The cell is metabolically active and continuously grows but does not replicate its DNA. The first stage of interphase is called the G₁ phase (first gap) because, from a microscopic aspect, little change is visible.

However, during the G₁ stage, the cell is quite active at the biochemical level. The cell is accumulating the building blocks of chromosomal DNA and the associated proteins as well as accumulating sufficient energy reserves to complete the task of replicating each chromosome in the nucleus.

• S Phase (Synthesis of DNA)

Throughout interphase, nuclear DNA remains in a semi-condensed chromatin configuration. DNA synthesis or replication takes place. In the S phase, DNA replication can proceed through the mechanisms that result in the formation of identical pairs of DNA molecules—sister chromatids—that are firmly attached to the centromeric region.

During this time thus the amount of DNA doubles. If the initial amount of DNA is denoted as 2C then it increases to 4C. However, there is no increase in chromosome number, if the cell had haploid or 2n number of the chromosome at G₁, even after S phase the number of chromosomes remains the same, i.e., 2n.

The centrosome is duplicated during the S phase. The two centrosomes will give rise to the mitotic spindle, the apparatus that orchestrates the movement of chromosomes during mitosis.

At the centrefibresfibres of each animal cell, the centrosomes of animal cells are associated with a pair of rod-like objects, the centrioles, which are at right angles to each other. Centrioles help organize cell division. Centrioles are not present in the centrosomes of other eukaryotic species, such as plants and most fungi.

- **G2 Phase (Second Gap)**

In the G2 phase, the cell replenishes its energy stores and synthesizes proteins necessary for chromosome manipulation. Some cell organelles are duplicated, and the cytoskeleton is dismantled to provide resources for the mitotic phase. There may be additional cell growth during G2. The final preparations for the mitotic phase must be completed before the cell can enter the first stage of mitosis.

In adult animals, some cells do not appear to exhibit division (e.g., heart cells) and many other cells divide or may divide occasionally, as needed to replace cells that have been lost because of injury or cell death. These cells do not divide further and exit the G1 phase to enter an inactive stage called the **Quiescent Stage (G0)** of the cell cycle. Cells in this stage remain metabolically active but no longer proliferate unless called on to do so depending on the requirement of the organism.

Cell Cycle Checkpoints

There exists a series of checkpoints which refer to the points of monitoring of cell cycle events such as DNA replication, DNA damage repair, spindle assembly, coming together of chromosomes, and separation of chromatids/chromosomes to opposite poles, generating signals in case of errors in processes and halting the cell cycle at specified points. Thus in the cell cycle, there are three main types of checkpoints:

- (i) DNA damage checkpoint,
- (ii) DNA replication checkpoint,
- (iii) Spindle checkpoint.

Divisional phase or M phase

- M phase involves the division of the nucleus (**karyokinesis**) and the division of cytoplasm (**cytokinesis**). The cell division in the plant kingdom, especially in eukaryotes, are of two types – Mitosis and Meiosis.

- Mitotic division occurs in somatic or body cells and is responsible for maintaining the constancy in chromosome numbers in all cells of an individual.
- The meiosis, on the other hand, occurs in reproductive organs and is responsible for the formation of gametes or spores after halving the chromosome number. The former is also known as equational, whereas the latter is termed as reductional cell division.

*** In animals, mitotic cell division is only seen in the diploid somatic cells. Against this, the plants can show mitotic divisions in both haploid and diploid cells.

Cell Division

There are many reasons for the division of cells as cells divide to replace old, dead, or damaged cells. Cells divide so that living things can grow. Organisms grow not because cells are getting larger but because cells are dividing to produce more and more cells. In the human body, about two trillion cells divide every day. In cell division, the cell that is dividing is called the 'parent' cell. The parent cell divides into daughter cells and this process is repeated known as the cell cycle.

How do cells divide?

There are two types of cell division: mitosis and meiosis. Most of the time when people refer to "cell division," they mean mitosis, the process of making new body cells. Meiosis is the type of cell division that creates egg and sperm cells.

Mitosis is a fundamental process for life. During mitosis, a cell duplicates all of its contents, including its chromosomes, and splits to form two identical daughter cells. Because this process is so critical, the steps of mitosis are carefully controlled by several genes. When mitosis is not regulated correctly, health problems such as cancer can result.

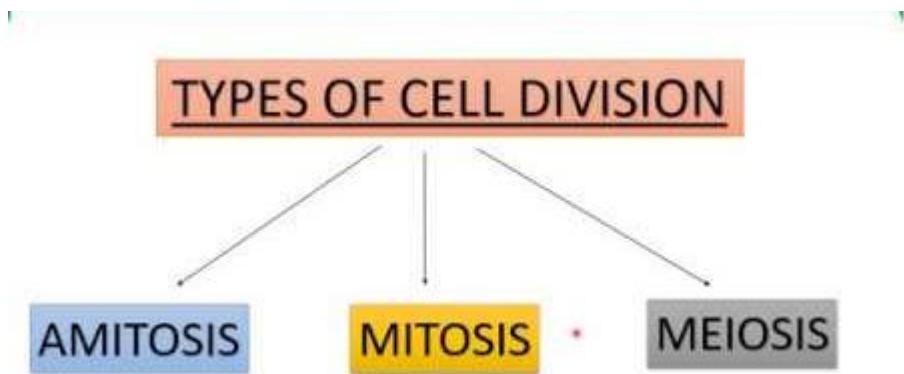
The other type of cell division, meiosis, ensures that humans have the same number of chromosomes in each generation. It is a two-step process that reduces the chromosome number by half—from 46 to 23—to form sperm and egg cells. When the sperm and egg cells unite at conception, each contributes 23 chromosomes so the resulting embryo will have the usual 46. Meiosis also allows genetic variation through a process of DNA shuffling while the cells are dividing.

According to the theory, old cells split into new cells and the formation of new cells is known as cell division or cell production. This was firstly observed by Flemming in 1882 but an extension in detail was given by Belar in 1920.

There are three ways for a cell to divide depending upon its type of cell- Amitosis, Mitosis, and Meiosis. Each of these methods of cell division has special characteristics.

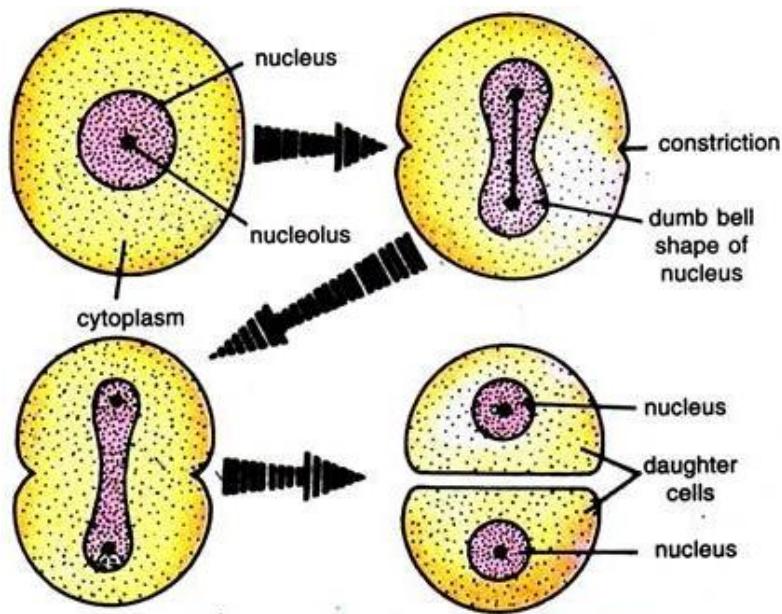
Usually, cell division is of three types:

- (i) Amitosis (ii) Mitosis (iii) Meiosis



Amitosis

Amitosis, also called 'karyostenosis' or direct cell division or binary fission. It is cell proliferation that does not occur by mitosis, the mechanism is usually identified as essential for cell division in eukaryotes. The polyploid macronucleus found in ciliates divides amitotically.



Diagrammatic representation of amitosis.

Mitosis

This is one of the two types of cell division where a single cell divides into two genetically identical daughter cells. In unicellular organisms, this type of cell division typically contributes to asexual reproduction. In multicellular organisms, mitosis is helpful for the growth and repair of damaged cells. Mitosis is also called equational division.

Meiosis

Also called reduction division, meiosis is another type of cell division that commonly occurs during sexual reproduction. Here, the chromosomes in the parent cell reduce by half, forming four gamete cells that are genetically distinct from the parent cells. Meiosis is very significant as it provides genetic diversity among a population.

When Cell Division Goes Wrong

Cells have many mechanisms that dictate when to divide and when to stop. When these mechanisms fail, the result is usually cancer. Cells divide at the right time and in the right order. Such abnormalities can result in the chromosomes being damaged or destroyed. When cancer cells that are initially benign lose or gain faulty chromosomes, it can become malignant, often becoming life-threatening.

Mitosis Definition

“Mitosis is that step in the cell cycle where the newly formed DNA is separated and two new cells are formed with the same number and kind of chromosomes as the parent nucleus.”

Mitosis is a process of asexual reproduction observed in unicellular organisms.

What is Mitosis? (Gk. Mitos-thread or fibril)

Cell division is the driving process of reproduction at the cellular level. Most eukaryotic cells divide in a manner where the ploidy or the number of chromosomes remains the same, except in the case of germ cells where the number of chromosomes is halved.

Depending upon the type of cell and the species, mitosis takes 30 minutes to 3 hours for completion.

Mitosis consists of two steps-**karyokinesis** and **cytokinesis**

Mitosis is the phase of the cell cycle where the nucleus of a cell is divided into two nuclei with an equal amount of genetic material in both the daughter nuclei. It succeeds in the G2 phase and is succeeded by cytoplasmic division after the separation of the nucleus.

Mitosis is essential for the growth of the cells and the replacement of worn-out cells. Abnormalities during mitosis may alter the DNA, resulting in genetic disorders.

Features of Mitosis

- In each cycle of cell division, two daughter cells are formed from the parent cell.
- The cell is also known as **equational cell division** because the chromosome number in the parent cell and daughter cell is the same.
- In plants, mitosis leads to the growth of vegetative parts of the plant like root tip, stem tip, etc.
- Mitosis occurs in the formation of somatic body cells and hence often named as **somatic cell division**.
- Mitosis occurs in the formation of somatic body cells and hence often named as **somatic cell division**.
- The sites of mitotic cell division in the plant are meristematic regions like the stem tip, root tip.
- Segregation and combination do not occur in this process.

The processes occurring during mitosis have been divided into different stages.

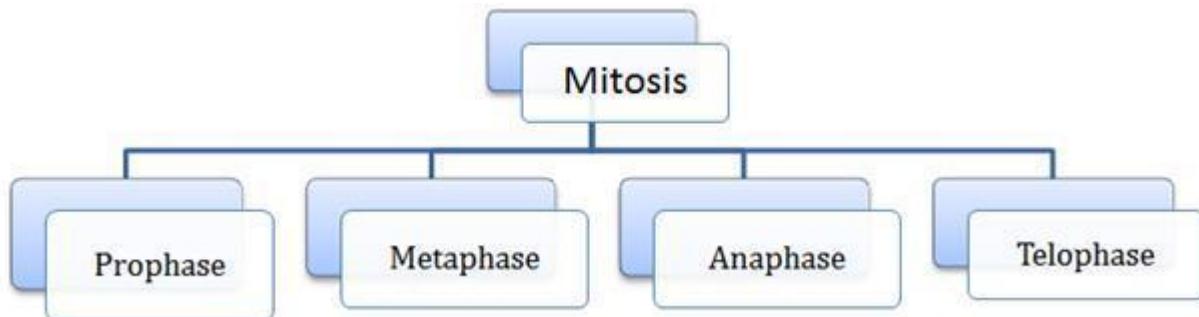
Phases of mitosis

Mitosis consists of four basic phases: prophase, metaphase, anaphase, and telophase. Some textbooks list five, breaking prophase into an early phase (called prophase) and a late phase (called prometaphase). These phases occur in strict sequential order, and cytokinesis - the process of dividing the cell contents to make two new cells - starts in anaphase or telophase.

Stages of Mitosis

Right before prophase, the cell spends most of its life in the interphase, where preparations are made before the beginning of mitosis (the DNA is copied). However, since the actual process involves the division of the nucleus, prophase is technically the first stage of this process.

The different stages of mitosis occurring during cell division are given as follows-



Interphase

Before entering mitosis, a cell spends a period of its growth under interphase. It undergoes the following phases when in interphase:

- **G1 Phase:** This is the period before the synthesis of DNA.
- **S Phase:** This is the phase during which DNA synthesis takes place.
- **G2 Phase:** This is the phase between the end of DNA synthesis and the beginning of prophase.

The cell in interphase (late G2 phase) and has already copied its DNA, so the chromosomes in the nucleus each consist of two connected copies, called **sister**

chromatids. The chromosomes are very clearly at this point, because they are still in their long, stringy, decondensed form.

This animal cell has also made a copy of its **centrosome**, an organelle that will play a key role in orchestrating mitosis, so there are two centrosomes. (Plant cells generally don't have centrosomes with centrioles, but have a different type of **microtubule organizing centre** that plays a similar role.)

Karyokinesis (Mitosis) **Karyokinesis**, (Gk. Karyon-nucleus, kinesis-movement) also known as **mitosis**, is divided into a series of phases (prophase, prometaphase, metaphase, anaphase, and telophase) that result in the division of the cell nucleus.

Prophase (Gk. Karyon-nucleus, kinesis-movement)

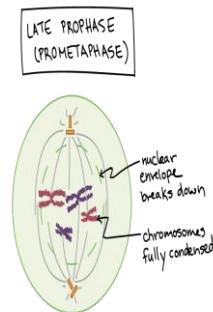
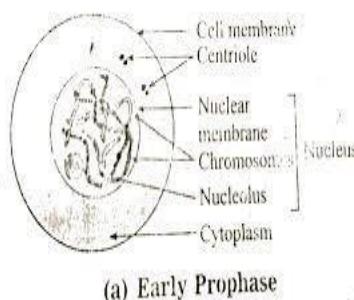
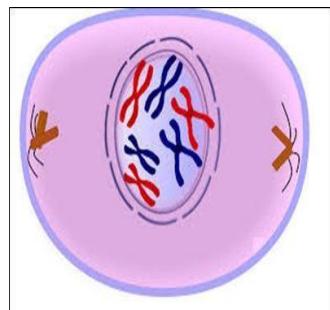
Prophase immediately follows S and G2 phase of the cycle and is marked by condensation of the genetic material to form compact mitotic chromosomes composed of two chromatids attached at the centromere.

Chromosomal material condenses to form compact mitotic chromosomes. Chromosomes are seen to be composed of two chromatids attached at the centromere. Centrosome which had undergone duplication during interphase begins to move towards opposite poles of the cell.

Each centrosome radiates out microtubules called asters. The two asters together with spindle fibres form mitotic apparatus.

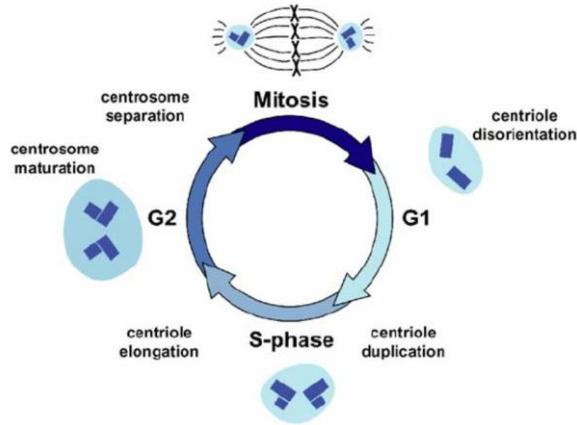
The completion of prophase is characterized by the initiation of the assembly of the mitotic spindle, the microtubules, and the proteinaceous components of cytoplasm that help in the process.

The nuclear envelope starts disintegrating.



Prophase

Centrosome cycle during the cell cycle



Prometaphase (Gk. Pro-before, meta-second, phasis-stage)

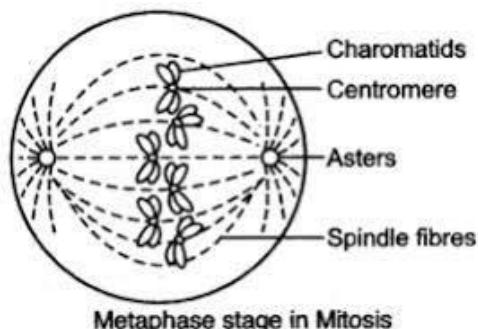
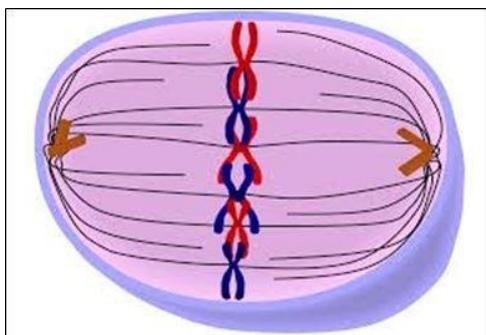
In the prometaphase, the nuclear envelop disintegrates. Now the microtubules are allowed to extend from the centromere to the chromosome. The microtubules attach to the kinetochores which allow the cell to move the chromosome around.

At this stage, the metaphase chromosome is made up of two sister chromatids, which are held together by the centromere.

Small disc-shaped structures at the surface of the centromeres are called kinetochores. These structures serve as the sites of attachment of spindle fibres (formed by the spindle fibres) to the chromosomes that are moved into position at the centre of the cell.

Metaphase (Gk. meta-second, phasis-stage)

At this stage, the microtubules start pulling the chromosomes with equal force, and the chromosome ends up in the middle of the cell. This region is known as the metaphase plate. Thus, each cell gets an entire functioning genome.

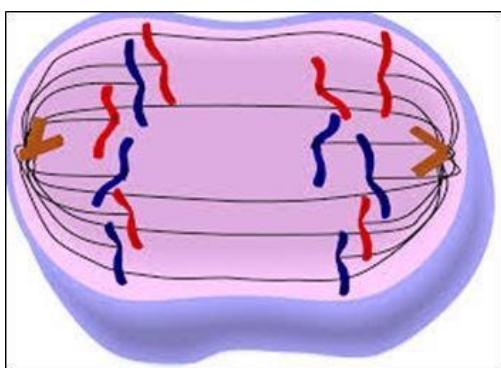


Metaphase

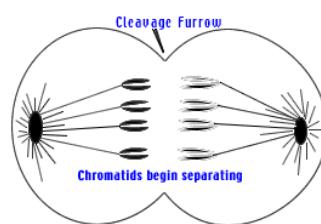
Before proceeding to anaphase, the cell will check to make sure that all the chromosomes are at the metaphase plate with their kinetochores correctly attached to microtubules. This is called the spindle checkpoint and helps ensure that the sister chromatids will split evenly between the two daughter cells when they separate in the next step. If a chromosome is not properly aligned or attached, the cell will halt division until the problem is fixed.

Anaphase (Gk. Ana-up, phasis-stage)

The splitting of the sister chromatids marks the onset of anaphase. These sister chromatids become the chromosome of the daughter nuclei. The chromosomes are then pulled towards the pole by the fibres favourfibres attached to the kinetochores of each chromosome. The centromere of each chromosome leads at the edge while the arms trail behind it.



Animal Cell In Anaphase



During this phase, the spindle fibers contract, pulling the chromatids apart. In animal cells, a small cleavage furrow may appear as cytokinesis (cytoplasm division) begins.

Anaphase

All of these processes are driven by motor proteins, molecular machines that can “walk” along microtubule tracks, and carry cargo. In mitosis, motor proteins carry chromosomes or other microtubules as they walk.

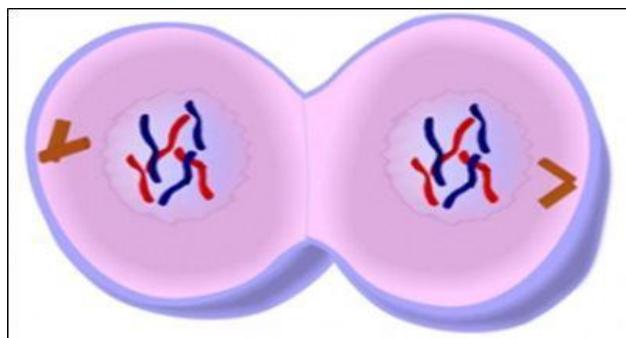
Telophase (Gk, telos-end, phasis-stage)

The chromosomes that cluster at the two poles start coalescing into an undifferentiated mass, as the nuclear envelope starts forming around it.

Chromosomes cluster at opposite spindle poles and their identity is lost as discrete elements.

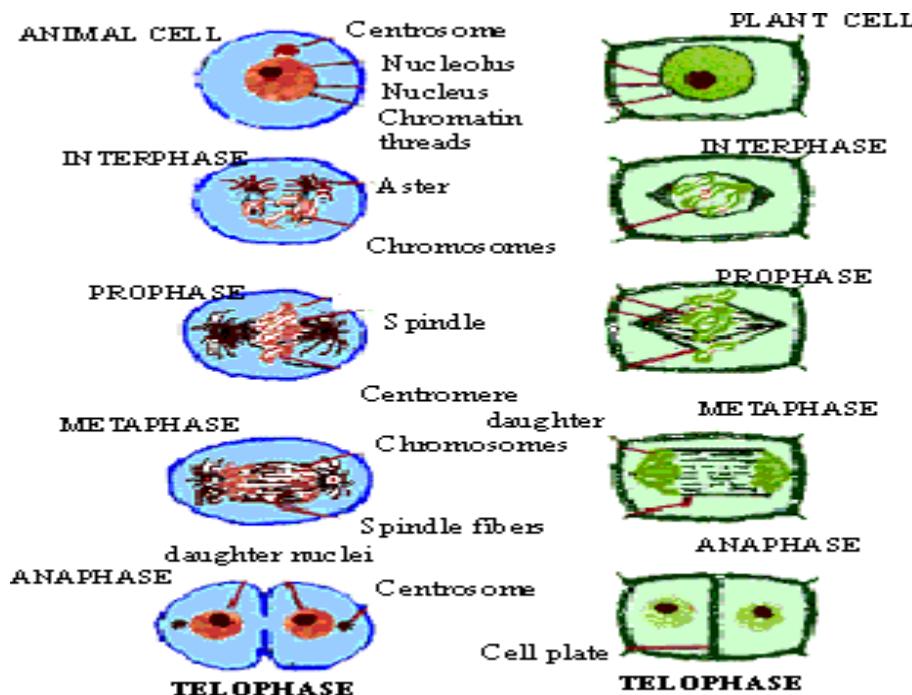
Nuclear envelope develops around the chromosome clusters at each pole forming two daughter nuclei.

The nucleolus, Golgi bodies, and ER complex, which had disappeared after prophase start to reappear.



Telophase

Telophase is followed by cytokinesis, which denotes the division of the cytoplasm to form two daughter cells. Thus, it marks the completion of cell division.



Cytokinesis, the division of the cytoplasm to form two new cells, overlaps with the final stages of mitosis. It may start in either anaphase or telophase, depending on the cell, and finishes shortly after telophase.

This is also often known as cytoplasmic division or cell cleavage.

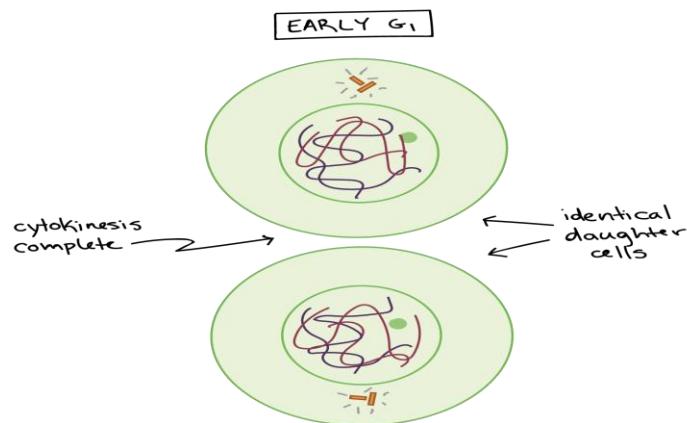
Cytokinesis begins in anaphase in animal cells and prophase in plant cells, and terminates in telophase in both, to form the two daughter cells produced by mitosis. In essence, cytokinesis is the partitioning of the cytoplasm into two equal parts, each of which contains a diploid chromosomal set identical to that of the parent cell.

Once this cytoplasmic material is divided, a plasma membrane (cell membrane) is formed around each new cell and organelles within the cytoplasm form through replication or synthesis.

Because the cytoplasmic material is not doubled in mitosis, unlike nuclear material, the resulting daughter cells are approximately half the volume of the parent cell. However, the nucleus of each daughter cell is roughly the same size as that of the parent cell, due to the chromosome replication which occurs before mitosis. Cytokinesis takes place in four stages: initiation,

contraction, membrane insertion, disorders, and completion. The events occurring within these stages differ in animal and plant cells.

In animal cells, cytokinesis is contractile, pinching the cell in two like a coin purse with a drawstring. The “drawstring” is a band of filaments made of a protein called actin, and the pinch crease is known as the **cleavage furrow**. Plant cells can't be divided like this because they have a cell wall and are too stiff. Instead, a structure called the **cell plate** forms down the middle of the cell, splitting it into two daughter cells separated by a new wall.



When division is complete, it produces two daughter cells. Each daughter cell has a complete set of chromosomes, identical to that of its sister (and that of the mother cell). The daughter cells enter the cell cycle in G₁.

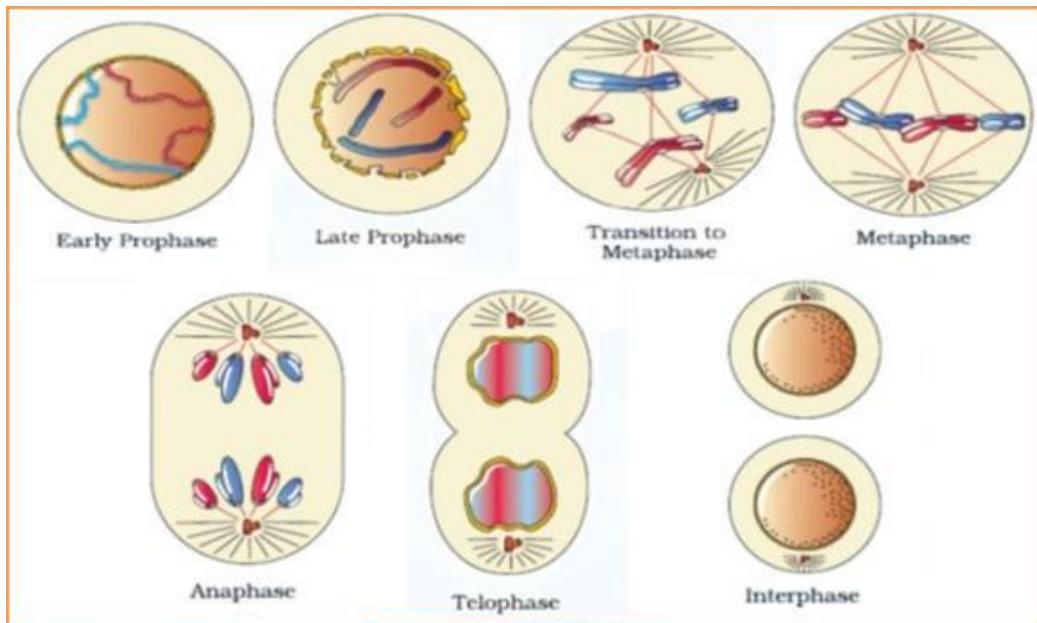
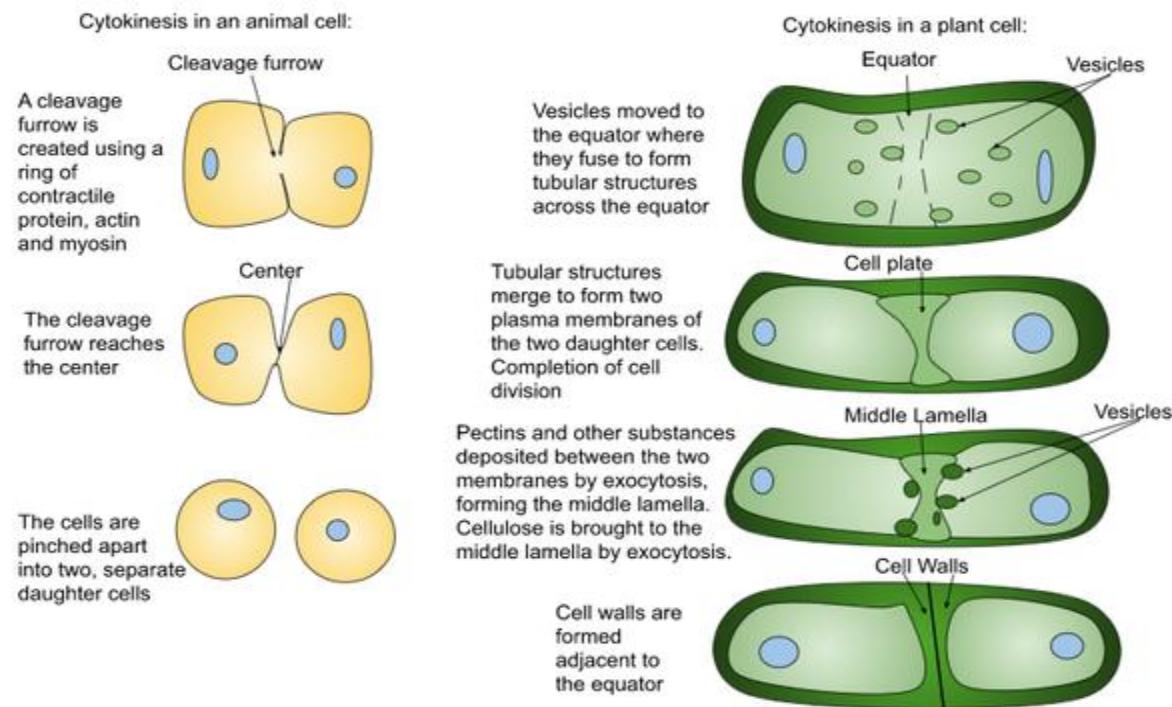
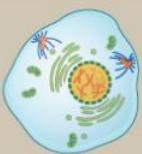
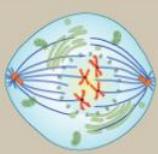
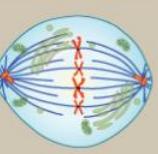
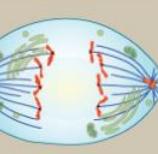
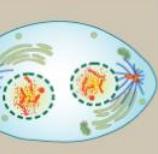
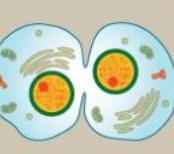
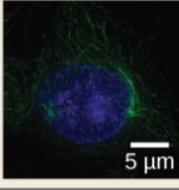
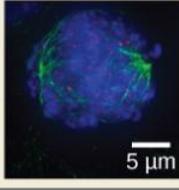
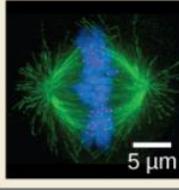
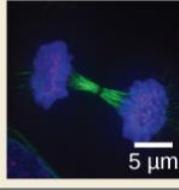
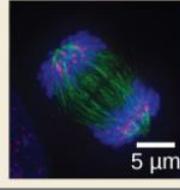
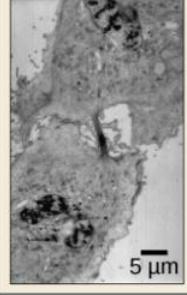


Fig: Different stages of Mitosis

When cytokinesis finishes, we end up with two new cells, each with a complete set of chromosomes identical to those of the mother cell. The daughter cells can now begin their own cellular “lives,” and – depending on what they decide to be when they grow up – may undergo mitosis themselves, repeating the cycle.



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Prophase	Prometaphase	Metaphase	Anaphase	Telophase	Cytokinesis
					
<ul style="list-style-type: none"> Chromosomes condense and become visible Spindle fibers emerge from the centrosomes Nuclear envelope breaks down Nucleolus disappears 	<ul style="list-style-type: none"> Chromosomes continue to condense Kinetochores appear at the centromeres Mitotic spindle microtubules attach to kinetochores Centrosomes move toward opposite poles 	<ul style="list-style-type: none"> Mitotic spindle is fully developed, centrosomes are at opposite poles of the cell Chromosomes are lined up at the metaphase plate Each sister chromatid is attached to a spindle fiber originating from opposite poles 	<ul style="list-style-type: none"> Cohesin proteins binding the sister chromatids together break down Sister chromatids (now called chromosomes) are pulled toward opposite poles Non-kinetochore spindle fibers lengthen, elongating the cell 	<ul style="list-style-type: none"> Chromosomes arrive at opposite poles and begin to decondense Nuclear envelope material surrounds each set of chromosomes The mitotic spindle breaks down 	<ul style="list-style-type: none"> Animal cells: a cleavage furrow separates the daughter cells Plant cells: a cell plate separates the daughter cells
					

MITOSIS

When Things Go Wrong

Cytokinesis needs to occur at the right time and place, so that each daughter cell has a complete diploid set of chromosomes, and so that chromosome movement is not interrupted. If cytokinesis occurs at the wrong time or in the wrong place, it can lead to cells with an abnormal amount of chromosomes. This leads to conditions such as aneuploidy, where a cell has several extra or missing chromosomes; polyploidy, where cytokinesis does not occur and a cell has more than a diploid set of chromosomes; or multinucleated cells, where more than one nucleus is present in a cell. These can lead to genetic disorders even cancers.

Cytokinesis does not occur in the process of mitosis leading to **multinucleate cells**. In this process, cytokinesis is skipped in favour of rapid development. This occurs in *Drosophila*, commonly known as the fruit fly, embryos as well as in certain types of mammalian cells, such as heart muscle cells and some liver cells, both of which need to be regenerated rapidly.

On some occasions, the location of the contractile ring in animal cells and the cell plate in plant cells is not centred, leading to the creation of cells of unequal volumes or unequal cytoplasmic

content. This is controlled through the movement of the mitotic spindle and is used to create cells that will serve different functions, such as the division of a fertilized egg cell in meiosis.

In conclusion, cytokinesis is central to mitosis and therefore to the maintenance of the Eukaryota taxon.

Functions of Mitosis

The following are the two important functions of mitosis:

- Mitosis helps in the development of an organism. In single-celled organisms, mitosis is the process of asexual reproduction.
- Mitosis helps in the replacement of damaged tissues. The cells near the damaged cells begin mitosis when they do not sense the neighbouring cells. The dividing cells reach each other and cover the damaged cells.

Significance of Mitosis

- Mitosis is responsible for the development of the zygote into an adult.
- The chromosomes are distributed equally to the daughter cells after each cycle.
- It is responsible for a definite shape, and proper growth and development of an individual.
- It maintains the constant number of chromosomes in all body cells of an organism.
- In plants, mitosis helps in the formation of new parts and the repairing of damaged parts. Mitosis helps in the vegetative propagation of crops also.
- Since no recombination and segregation occurs in the process, it helps in maintaining the purity of types.
- It helps in maintaining a balance between the DNA and RNA contents as well as the nuclear and cytoplasmic contents of the cell.
- It is responsible for replacing dead and old cells in the animals: Eg., gut epithelium, and blood cells.

Meiosis (Gk.meioum or meio-to lessen)

Mitosis is used for almost all of your body's cell division needs. It adds new cells during development and replaces old and worn-out cells throughout your life. The goal of mitosis

is to produce daughter cells that are genetically identical to their mothers, with not a single chromosome more or less.

Meiosis, on the other hand, is used for just one purpose in the human body: the production of **gametes**—sex cells, or sperm, and eggs. Its goal is to make daughter cells with exactly half as many chromosomes as the starting cell.

To put that another way, **meiosis** in humans is a division process that takes us from a diploid cell—one with two sets of chromosomes—to haploid cells—ones with a single set of chromosomes. In humans, the haploid cells made in meiosis are sperm and eggs. When a sperm and an egg join in fertilization, the two haploid sets of chromosomes from a complete diploid set: a new genome.

“Meiosis is the type of cell division that results in four daughter cells each with half the number of chromosomes of the parent cell.”

What is Meiosis?

Meiosis is the process in which a single cell divides twice to form four haploid daughter cells. These cells are the gametes – sperms in males and eggs in females. The process of meiosis is divided into 2 stages. Each stage is subdivided into several phases.

Phases of meiosis

In many ways, meiosis is a lot like mitosis. The cell goes through similar stages and uses similar strategies to organize and separate chromosomes. In meiosis, however, the cell has a more complex task. It still needs to separate **sister chromatids** (the two halves of a duplicated chromosome), as in mitosis. But it must also separate **homologous chromosomes**, the similar but nonidentical chromosome pairs an organism receives from its two parents.

These goals are accomplished in meiosis using a two-step division process. Homolog pairs separate during the first round of cell division, called **meiosis I**. Sister chromatids separate during a second round, called **meiosis II**.

The first division of meiosis (**meiosis I**) is called **heterotypic or reduction division** as the chromosomes are reduced to half.

The second division of meiosis (**meiosis II**) is called **homotypic or educational division** as the number of the chromosome remains the same.

Since cell division occurs twice during meiosis, one starting cell can produce four gametes (eggs or sperm). In each round of division, cells go through four stages: prophase, metaphase, anaphase, and telophase.

Meiosis I:

- Prophase I
- Metaphase I
- Anaphase I
- Telophase I
- Cytokinesis I

Meiosis II:

- Prophase II
- Metaphase II
- Anaphase II
- Telophase II
- Cytokinesis II

Interkinesis or **interphase II** is a period of rest that cells of some species enter during **meiosis**, between **meiosis I** and **meiosis II**. However, it does occur during the **interphase I** stage of **meiosis**.

Meiosis I

Before undergoing **meiosis**, a cell goes through an **interphase** period in which it grows, replicates its chromosomes, and checks all of its systems to ensure that it is ready to divide.

Prophase I

Prophase I is typically the longest phase of meiosis. During prophase I, homologous chromosomes pair and exchange genetic information (homologous chromosomes). This often results in the chromosomal crossover. This process facilitates pairing between homologous chromosomes and hence accurate segregation of the chromosomes at the first meiosis division.

The new combinations of DNA created during crossover are a significant source of variation and result in new combinations of alleles which may be beneficial. The paired and replicated chromosomes are called bivalents or tetrads, which have two chromosomes and four chromatids, with one chromosome coming from each parent.

The process of pairing the homologous chromosomes is called synapsis. At this stage, non-sister chromatids may cross-over at points called chiasmata (plural; singular chiasma).

Prophase I have historically been divided into a series of substages that are named according to the appearance of chromosomes.

For instance, in the image below, the letters A, B, and C represent genes found at particular spots on the chromosome, with capital and lowercase letters for different forms, or alleles, of each gene. The DNA is broken at the same spot on each homologous—here, between genes B and C—and reconnected in a criss-cross pattern so that the homologues exchange part of their DNA.

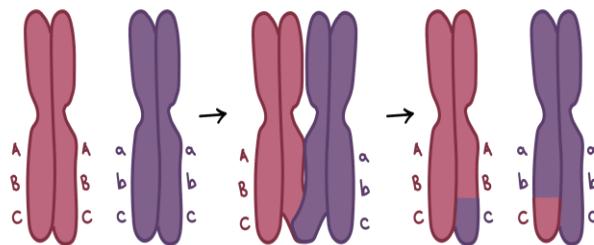


Image of crossing over.

Two homologous chromosomes carry different versions of three genes. One has the A, B, and C versions, while the other has the a, b, and c versions. A crossover event in which two chromatids—one from each homologue—exchange fragments swaps the C and c genes.

Now, each homologue has two dissimilar chromatids.

One has A, B, C on one chromatid and A, B, c on the other chromatid.

The other homologue has a, b, c on one chromatid and a, b, C on the other chromatid.

This process, in which homologous chromosomes trade parts, is called **crossing over**. It's helped along by a protein structure called the **synaptonemal complex** that holds the homologues together. The chromosomes would be positioned one on top of the other—as in the image below—throughout crossing over; they're only shown side-by-side in the image above so that it's easier to see the exchange of genetic material.

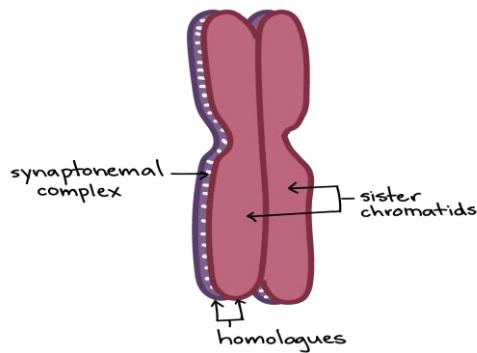


Image of two homologous chromosomes positioned one on top of the other and held together by the synaptonemal complex.

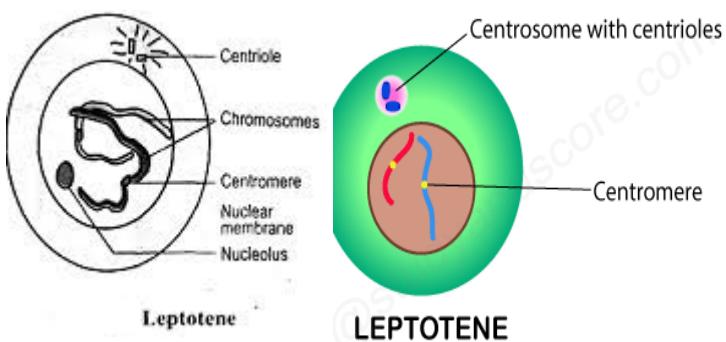
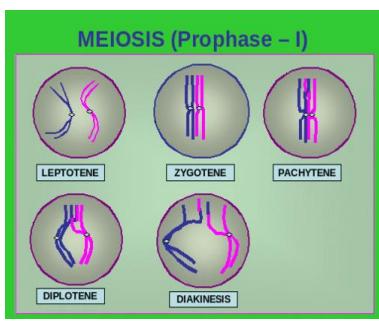
A crossover under a microscope is known as **chiasmata**, cross-shaped structures where homologues are linked together. Chiasmata keep the homologues connected after the synaptonemal complex breaks down, so each homologous pair needs at least one. It's common for multiple crossovers (up to 252525!) to take place for each homologue pair.

The spots where crossovers happen are more or less random, leading to the formation of new, "remixed" chromosomes with unique combinations of alleles.

Leptotene

The first stage of prophase I is the *leptotene* stage, also known as *leptonema*, from Greek words meaning "thin threads". In this stage of prophase I, individual chromosomes—each consisting of two sister chromatids—become "individualized" to form visible strands within the nucleus.

The two sister chromatids closely associate and are visually indistinguishable from one another. During leptotene, lateral elements of the synaptonemal complex assemble. Leptotene is of very short duration and progressive condensation and coiling of chromosome fibres take place.



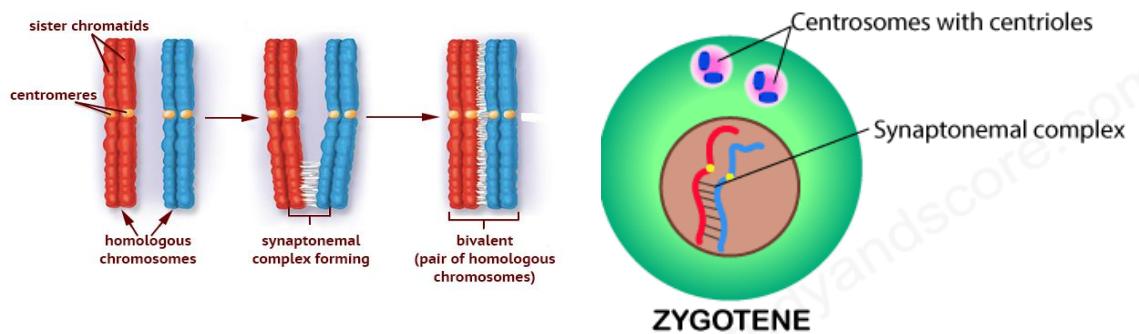
Zygotene

The *zygotene* stage, also known as *zygonema*, from Greek words meaning "paired threads", occurs as the chromosomes approximately line up with each other into homologous

chromosome pairs. In some organisms, this is called the bouquet stage because of the way the telomeres cluster at one end of the nucleus.

At this stage, the synapsis (pairing/coming together) of homologous chromosomes takes place, facilitated by the assembly of the central element of the synaptonemal **complex**. Pairing is brought about in a zipper-like fashion and may start at the centromere (procentric), at the chromosome ends (proterminal), or any other portion (intermediate).

Individuals of a pair are equal in length and position of the centromere. Thus pairing is highly specific and exact. The paired chromosomes are called **bivalent** or **tetrad** chromosomes.



Pachytene

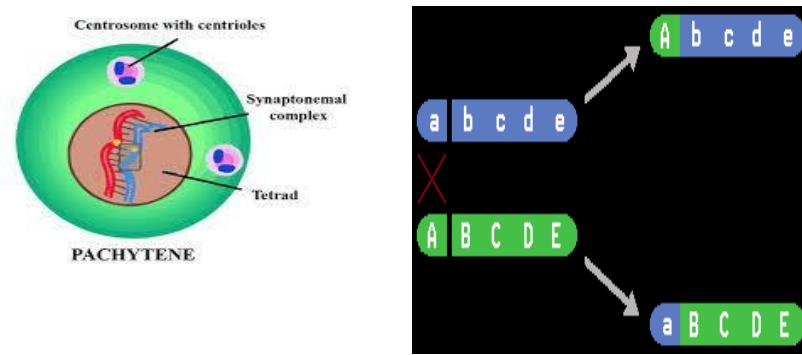
The *pachytene* stage also is known as *pachynema*, from Greek words meaning "thick threads".

At this point, a tetrad of the chromosomes has formed known as a bivalent. This is the stage when homologous **recombination**, including chromosomal **crossover** (crossing over), occurs.

Thus this stage is characterized by the appearance of **recombination nodules**, the sites at which crossing over occurs between non-sister chromatids of the homologous chromosomes.

Crossing over is the exchange of genetic material between two homologous chromosomes. Crossing over is also an enzyme-mediated process and the enzyme involved is called **recombinase**.

At the sites where exchange happens, chiasmata form. The exchange of information between the non-sister chromatids results in a recombination of information; each chromosome has the complete set of information it had before, and there are no gaps formed as a result of the process. Because the chromosomes cannot be distinguished in the synaptonemal complex, the actual act of crossing over is not perceivable through the microscope, and chiasmata are not visible until the next stage.



genetic recombination

Diplotene

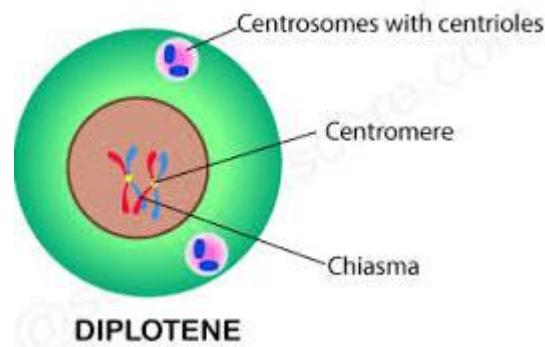
During the *diplotene* stage, also known as *diplonema*, from Greek words meaning "two threads", the synaptonemal complex degrades and homologous chromosomes separate from one another a little.

The chromosomes themselves uncoil a bit, allowing some transcription of DNA. However, the homologous chromosomes of each bivalent remain tightly bound at chiasmata, the regions where crossing-over occurred. The **chiasmata** remain on the chromosomes until they have severed at the transition to anaphase I.

*Thus the beginning of diplotene is recognized by the dissolution of the synaptonemal complex and the tendency of the recombined homologous chromosomes of the bivalents to separate from each other except at the sites of crossovers. These **X-shaped structures** are called **chiasmata**.*

In human fetal oogenesis, all developing oocytes develop to this stage and are arrested in prophase I before birth.

This suspended state is referred to as the pachytene stage or dictyate. It lasts until meiosis is resumed to prepare the oocyte for ovulation, which happens at puberty or even later.



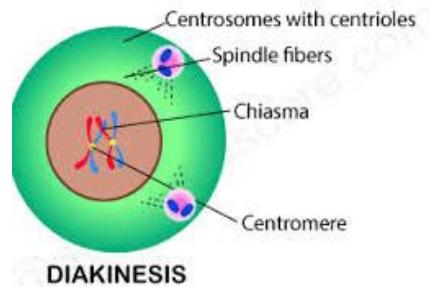
Diakinesis

Chromosomes condense further during the *diakinesis* stage, from Greek words meaning "moving through".

This is the first point in meiosis where the four parts of the tetrads are visible. Sites of crossing over entangle together, effectively overlapping, making chiasmata visible.

This is marked by terminalisation of chiasmata.

Other than this observation, the rest of the stage closely resembles the prometaphase of mitosis; the nucleoli disappear, the nuclear membrane disintegrates into vesicles, and the meiotic spindle begins to form.



Meiotic spindle formation

Unlike mitotic cells, human and mouse oocytes do not have centrosome to produce the meiotic spindle.

In human oocytes spindle microtubule nucleation begins on the chromosomes, forming an aster that eventually expands to surround the chromosomes.

Chromosomes then slide along the microtubules towards the equator of the spindle, at which point the chromosome kinetochores form end-on attachments to microtubules.

Meiosis I

Prophase I (leptotene, zygotene, pachytene, diplotene and diakinesis)

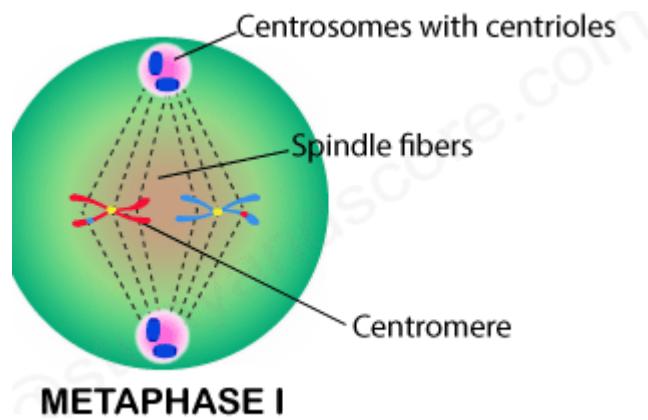
Metaphase I

Homologous pairs move together along the metaphase plate: As *kinetochore microtubules* from both spindle poles attach to their respective kinetochores, the paired homologous chromosomes align along an equatorial plane that bisects the spindle, due to continuous counterbalancing forces exerted on the bivalents by the microtubules emanating from the two kinetochores of homologous chromosomes.

This attachment is referred to as a bipolar attachment. The physical basis of the independent assortment of chromosomes is the random orientation of each bivalent along with the metaphase plate, concerning the orientation of the other bivalents along the same equatorial line.

The protein complex cohesion holds sister chromatids together from the time of their replication until anaphase. In mitosis, the force of kinetochore microtubules pulling in opposite directions creates tension.

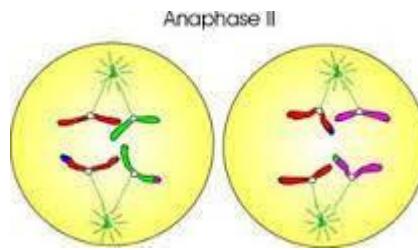
The cell senses this tension and does not progress with anaphase until all the chromosomes are properly bi-oriented. In meiosis, establishing tension ordinarily requires at least one crossover per chromosome pair in addition to cohesion between sister chromatids.



Anaphase I

Kinetochore microtubules shorten, pulling homologous chromosomes (which each consist of a pair of sister chromatids) to opposite poles. Non-kinetochore microtubules lengthen, pushing the centrosomes farther apart.

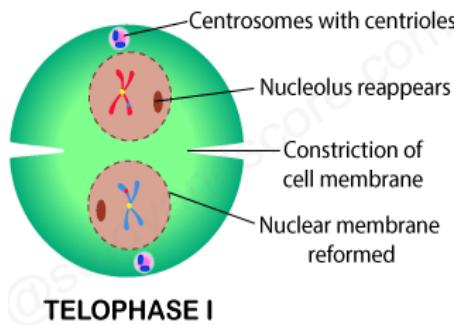
The cell elongates in preparation for division down the centre.



Unlike in mitosis, only the cohesin from the chromosome arms is degraded while the cohesin surrounding the centromere remains protected by a protein named Shugoshin (Japanese for "guardian spirit"), which prevents the sister chromatids from separating. This allows the sister chromatids to remain together while homologous are segregated.

Telophase I

The first meiotic division effectively ends when the chromosomes arrive at the poles. Each daughter cell now has half the number of chromosomes but each chromosome consists of a pair of chromatids. The microtubules that make up the spindle network disappear and a new nuclear membrane surrounds each haploid set. The chromosomes uncoil back into chromatin. Cytokinesis, the pinching of the cell membrane in animal cells or the formation of the cell wall in plant cells, occurs, completing the creation of two daughter cells. Sister chromatids remain attached during telophase I.



Cells may enter a period of rest known as interkinesis or interphase II. No DNA replication occurs during this stage.

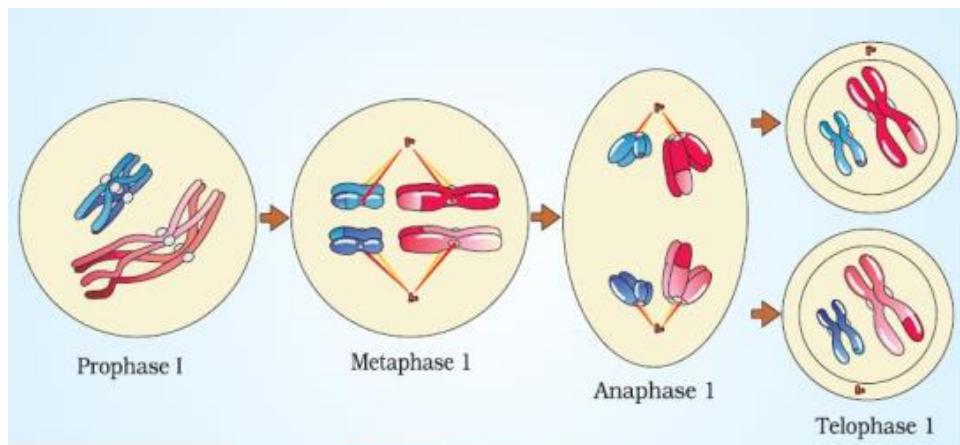
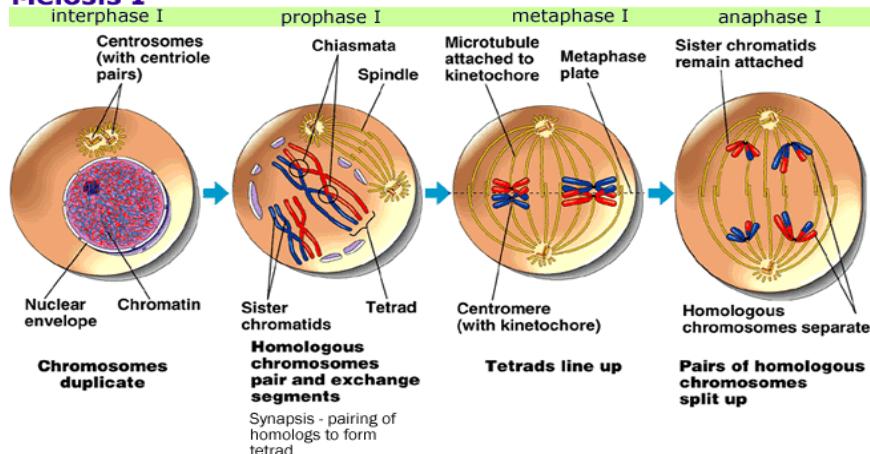
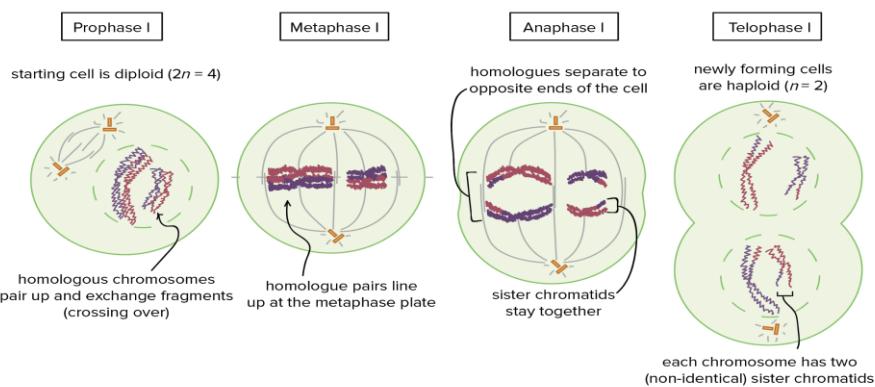


Fig: Different stages of Meiosis I

Meiosis I

PHASES OF MEIOSIS I



Meiosis II

The second division of meiosis (**meiosis II**) is called **homotypic or equational division** as the number of the chromosome remains the same.

Cells move from meiosis I to meiosis II without copying their DNA. Meiosis II is a shorter and simpler process than meiosis I, and you may find it helpful to think of meiosis II as "mitosis for haploid cells."

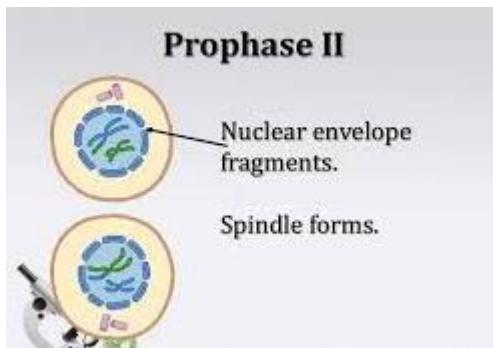
The cells that enter meiosis II are the ones made in meiosis I. These cells are haploid—have just one chromosome from each homologue pair—but their chromosomes still consist of two sister chromatids. In meiosis II, the sister chromatids separate, making haploid cells with non-duplicated chromosomes

Phases of meiosis II

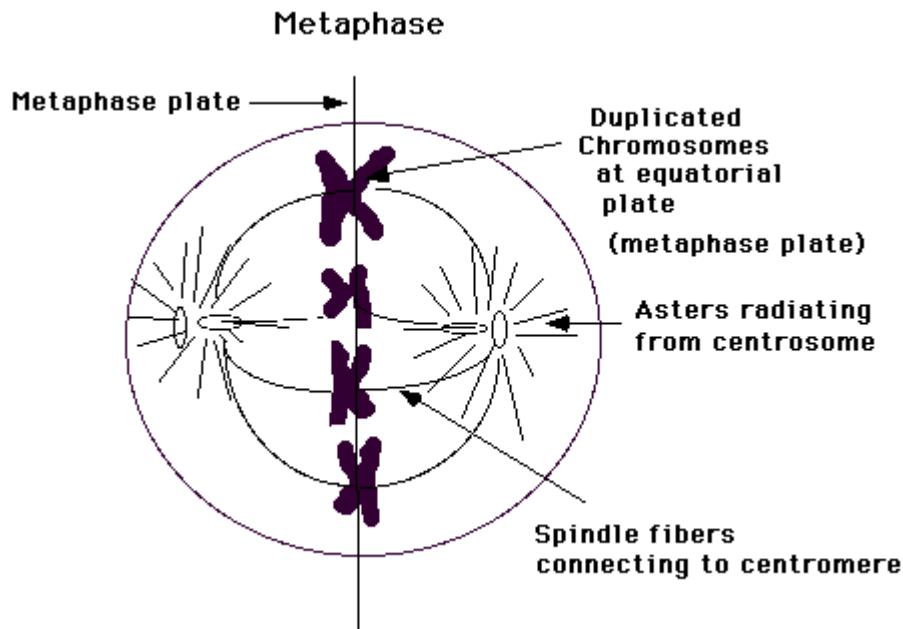
Prophase II

During **prophase II**, Starting cells are the haploid cells made in meiosis I. chromosomes condense and the nuclear envelope breaks down if needed. The centrosomes move apart, the spindle forms between them, and the spindle microtubules begin to capture chromosomes.

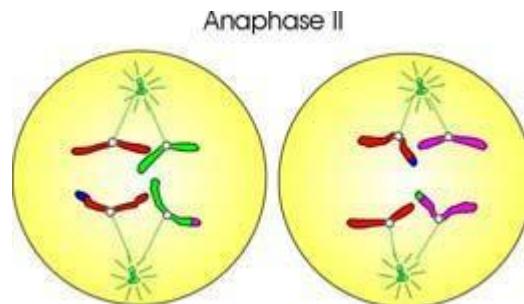
The two sister chromatids of each chromosome are captured by microtubules from opposite spindle poles.



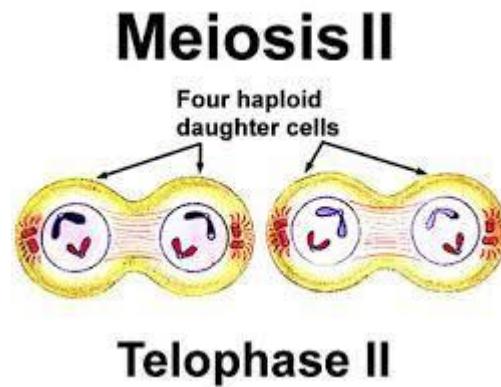
Metaphase II, the chromosomes line up individually along with the metaphase plate.



Anaphase II, the sister chromatids separate and are pulled towards opposite poles of the cell.



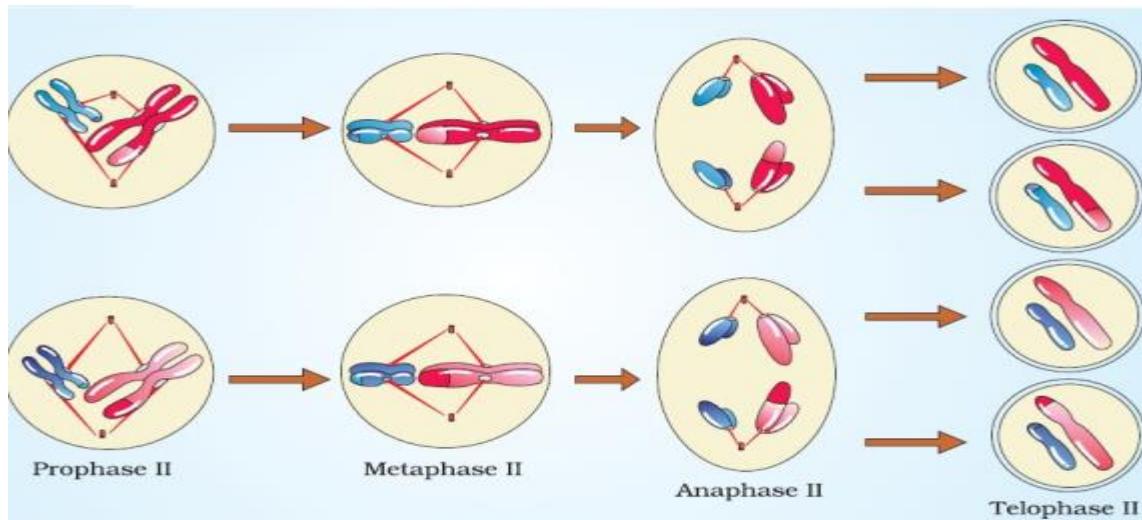
Telophase II, nuclear membranes form around each set of chromosomes and the chromosomes decondense.

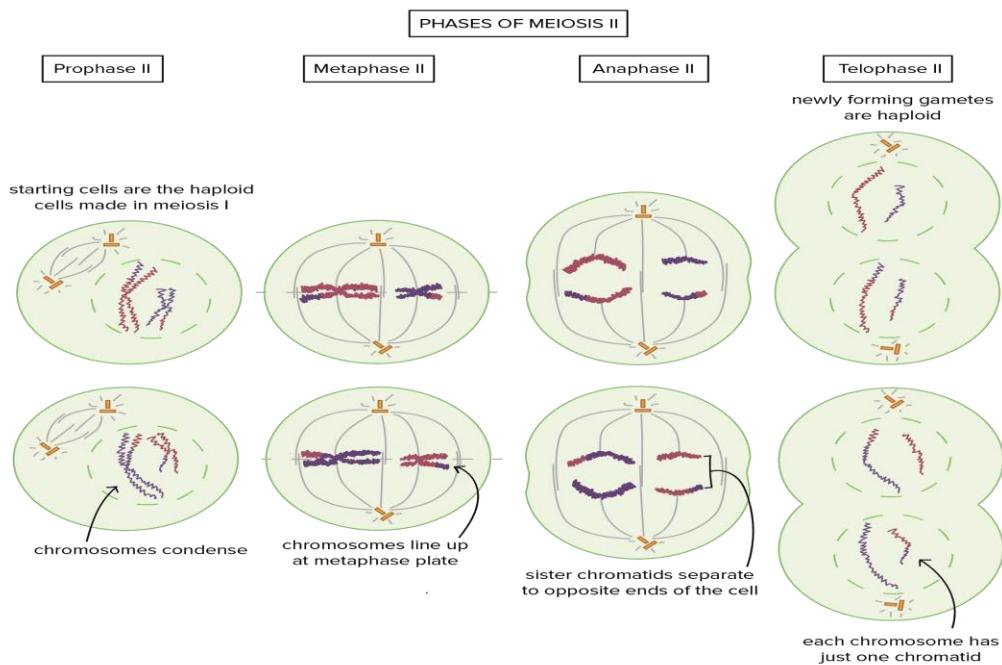


Cytokinesis II

The cytoplasm and cell divide producing 4 non-identical haploid daughter cells.

Cytokinesis splits the chromosome sets into new cells, forming the final products of meiosis: four haploid cells in which each chromosome has just one chromatid. In humans, the products of meiosis are sperm or egg cells.





How meiosis "mixes and matches" genes

The gametes produced in meiosis are all haploid, but they're not genetically identical. For example, take a look at the meiosis II diagram above, which shows the products of meiosis for a cell with $2n = 42$, $n = 21$, equal, 21 chromosomes. Each gamete has a unique "sample" of the genetic material present in the starting cell.

As it turns out, there are many more potential gamete types than just the four shown in the diagram, even for a cell with only four chromosomes. The two main reasons we can get many genetically different gametes are:

- **Crossing over.** The points where homologues cross over and exchange genetic material are chosen more or less at random, and they will be different in each cell that goes through meiosis. If meiosis happens many times, as in humans, crossovers will happen at many different points.
- **Random orientation of homologue pairs.** The random orientation of homologue pairs in metaphase I allow for the production of gametes with many different assortments of homologous chromosomes.

In a human cell, the random orientation of homologue pairs alone allows for over 8 million possible different gametes. When we layer crossing over on top of this, the number of genetically different gametes that you-or any other person- can make is effectively infinite.

Similarities between meiosis I meiosis II

Both Meiosis 1 and 2 have the same phases: Prophase, Metaphase, Anaphase, and Telophase. One difference is that Meiosis 1 starts with a diploid cell and Meiosis 2 starts with 2 haploid cells, each with a homologous pair. Meiosis 1 results in 2 daughter cells and Meiosis 2 results in 4.

Meiosis 2 is very similar to Mitosis.

Difference between meiosis I meiosis II

The difference between Anaphase 1 and Anaphase 2 in Meiosis is this: In Anaphase 1, the homologous pairs are broken up, but the chromosomes are not. In Anaphase 2, there are no homologous pairs: instead, the chromosomes (the sister chromatids) are separated. Probably the most important difference is that in Meiosis 1 since there are homologous pairs, homologous recombination occurs during Prophase 1. This chromosomal crossing over allows variation, which facilitates evolutionary adaptation. Since there are no homologous pairs (only chromatids), recombination can not occur.

Significances of meiosis

The process of meiosis is essential for all sexually reproducing organisms. It occurs in reproductive cells to form gametes that have half the number of chromosomes of the reproductive cells. The two gametes from reproductive cells fuse to form a zygote. As a result, the zygote comes to have a double number of chromosomes. Thus, meiosis maintains the chromosome number of organisms. Apart from this, there are other significances of meiosis also. Some of these are as follows

- Meiosis form gametes that are required for sexual reproduction
- Meiosis maintains the fixed number of chromosomes in sexually reproducing organisms by having the same during gametogenesis
- In meiosis, paternal and maternal chromosomes assort independently. It causes a reshuffling of chromosomes and the traits controlled by them. The variations help the breeders in improving the races of useful plants and animals.
- Meiosis introduces a new combination of traits or variations.
- Chromosomal and genomic mutations occur by irregularities of the meiotic division. Some of these mutations are useful to the organism.

The gametes produced in meiosis are all haploid, but they're not genetically identical. For example, take a look at the meiosis II diagram on the previous page, which shows the products of meiosis for a cell with $2n = 4$ chromosomes. Each gamete has a unique "sample" of the genetic material present in the starting cell.

As it turns out, there are many more potential gamete types than just the four shown in the diagram, even for a cell with only four chromosomes.

The two main reasons we can get many genetically different gametes are:

- Crossing over. The points where homologues cross over and exchange genetic material are chosen more or less at random, and they will be different in each cell that goes through meiosis. If meiosis happens many times, as in humans, crossovers will happen at many different points.
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Important terms

Cell cycle

The cell cycle, or cell-division cycle, is the series of events that take place in a cell that causes it to divide into two daughter cells.

Cell division

Cell division is the process by which a parent cell divides into two or more daughter cells. Cell division usually occurs as part of a larger cell cycle

Chromosomes

A thread-like structure of nucleic acids and protein found in the nucleus of most living cells, carrying genetic information in the form of genes.

Chromatids

A chromatid is a chromosome that has been newly copied or a copy of such a chromosome, the two of them still joined to the original chromosome by a single centromere. Before replication, one chromosome is composed of one DNA molecule.

Karyokinesis

Division of a cell nucleus during mitosis.

Cytokinesis

Cytokinesis is the part of the cell division process during which the cytoplasm of a single eukaryotic cell divides into two daughter cells. Cyttoplasmic division begins during or after the late stages of nuclear division in mitosis and meiosis.

Kinetochore

A complex of proteins associated with the centromere of a chromosome during cell division, to which the microtubules of the spindle attach.

Centromere

The region of a chromosome to which the microtubules of the spindle attach, via the kinetochore, during cell division.

Metaphase plate

A plane in the equatorial region of the spindle in dividing cells, along which the chromosomes become arranged during the **metaphase**.

Spindle fibre

the spindle apparatus refers to the cytoskeletal structure of eukaryotic cells that forms during cell division to separate sister chromatids between daughter cells.

Microtubule

A microscopic tubular structure present in numbers in the cytoplasm of cells, sometimes aggregating to form more complex structures.

Centriole

Each of a pair of minute cylindrical organelles near the nucleus in animal cells, involved in the development of spindle fibres in cell division.

Centrosome

An organelle near the nucleus of a cell which contains the centrioles (in animal cells) and from which the spindle fibres develop in cell division.

Synaptonemal complex

The synaptonemal complex is a protein structure that forms between homologous chromosomes during meiosis and is thought to mediate synapsis and recombination during meiosis I in eukaryotes.

Chiasmata

A point at which paired chromosomes remain in contact during the first metaphase of meiosis, and at which crossing over and exchange of genetic material occurs between the strands.

Bivalent

A pair of homologous chromosomes.

Tetrad

The tetrad is the four spores produced after meiosis of yeast or other Ascomycota, Chlamydomonas or other algae, or a plant. After parent haploids mate, they produce diploids. Under appropriate environmental conditions, diploids sporulate and undergo meiosis.

Synapsis

Synapsis is the pairing of two homologous chromosomes that occurs during meiosis. It allows matching-up of homologous pairs before their segregation and possible chromosomal crossover between them. Synapsis takes place during prophase I of meiosis.

Equational division

Mitosis is the process of **cell division** wherein the chromosomes replicate and get equally distributed into two daughter cells. The chromosome number in each daughter cell is equal to that in the parent cell, i.e., diploid. Hence, mitosis is known as **equational division**.

Reductional division

The first **division** of meiosis in which the number of chromosomes is reduced to half the original number. meiosis.

Mitosis

A type of cell division that results in two daughter cells each having the same number and kind of chromosomes as the parent nucleus, typical of ordinary tissue growth.

Meiosis

A type of cell division that results in four daughter cells each with half the number of chromosomes of the parent cell, as in the production of gametes and plant spores.

Amitosis

Amitosis, also called 'karyostenosis' or direct cell division or binary fission. It is cell proliferation that does not occur by mitosis, the mechanism is usually identified as essential for cell division in eukaryotes. The polyploid macronucleus found in ciliates divides amitotically.

Interphase

Interphase is the portion of the cell cycle that is not accompanied by observable changes under the microscope and includes the G1, S, and G2 phases. During interphase, the cell grows, replicates its DNA, and prepares for mitosis.

Checkpoint in cell cycle

A **checkpoint** is a stage in the eukaryotic **cell** cycle at which the **cell** examines internal and external cues and "decides" whether or not to move forward with the division.

Dyads

A secondary morphological unit, consisting of two monads: a chromosome **dyad**. the double chromosomes resulting from the separation of the four chromatids of a tetrad.

Interkinesis

Interkinesis or interphase II is a period of rest that cells of some species enter during meiosis between meiosis I and meiosis II.

Zygotic meiosis

Haplontic life cycle — the haploid stage is multicellular and the diploid stage is a single cell, meiosis is "**zygotic**". diplontic life cycle — the diploid stage is multicellular and haploid gametes are formed, meiosis is "**gametic**".

Sporic meiosis

In **sporic meiosis** (also commonly known as intermediary **meiosis**), the zygote divides mitotically to produce a multicellular diploid sporophyte

Gametic meiosis

In **gametic meiosis**, instead of immediately dividing meiotically to produce haploid cells, the zygote divides mitotically to produce a multicellular diploid individual or a group of more unicellular diploid cells.