
Meiosis - Part 1

Objectives

After going through this lesson, the learners will be able to understand the following:

- Meiosis
- Prophase 1
- Metaphase 1
- Anaphase 1
- Telophase 1

Content Outline

- Introduction
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- Meiosis 1
- Prophase 1
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- Telophase 1
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Introduction

The production of offspring by sexual reproduction includes the fusion of two gametes, each with a complete haploid set of chromosomes. Gametes are formed from specialised diploid cells. This specialised kind of cell division that reduces the chromosome number by half results in the production of haploid daughter cells. This kind of division is called meiosis. Meiosis ensures the production of haploid phase in the life cycle of sexually reproducing organisms whereas fertilisation restores the diploid phase. We come across meiosis during gametogenesis in plants and animals. This leads to the formation of haploid gametes. The key features of meiosis are as follows:

- Meiosis involves two sequential cycles of nuclear and cell division called meiosis I and meiosis II but only a single cycle of DNA replication.
- Meiosis I is initiated after the parental chromosomes have replicated to produce identical sister chromatids at the S phase.

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- Meiosis involves pairing of homologous chromosomes and recombination between them.
 - Four haploid cells are formed at the end of meiosis II.

Meiosis

Meiotic events can be grouped under the following phases:

- Meiosis I Meiosis II
- Prophase I Prophase II
- Metaphase I Metaphase II
- Anaphase I Anaphase II
- Telophase I Telophase II

Meiosis I

Prophase I: Prophase of the first meiotic division is typically longer and more complex when compared to prophase of mitosis. It has been further subdivided into the following five phases based on chromosomal behaviour, i.e., Leptotene, Zygotene, Pachytene, Diplotene and Diakinesis.

During the leptotene stage the chromosomes become gradually visible under the light microscope. The compaction of chromosomes continues throughout leptotene. This is followed by the second stage of prophase I called zygotene. During this stage chromosomes start pairing together and this process of association is called synapsis. Such paired chromosomes are called homologous chromosomes. Electron micrographs of this stage indicate that chromosome synapsis is accompanied by the formation of a complex structure called synaptonemal complex. The complex formed by a pair of synapsed homologous chromosomes is called a bivalent or a tetrad. However, these are more clearly visible at the next stage. The first two stages of prophase I are relatively short-lived compared to the next stage that is pachytene. During this stage bivalent chromosomes now clearly appear as tetrads. This stage is characterised 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. Crossing over leads to recombination of genetic material on the two chromosomes.

Recombination between homologous chromosomes is completed by the end of pachytene, leaving the chromosomes linked at the sites of crossing over. The beginning of diplotene is recognised 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 oocytes of some vertebrates, diplotene can last for months or years.

The final stage of meiotic prophase I is diakinesis. This is marked by terminalisation of chiasmata. During this phase the chromosomes are fully condensed and the meiotic spindle is assembled to prepare the homologous chromosomes for separation. By the end of diakinesis, the nucleolus disappears and the nuclear envelope also breaks down.

Diakinesis represents transition to metaphase.

Metaphase I: The bivalent chromosomes align on the equatorial plate (Figure 10.3). The microtubules from the opposite poles of the spindle attach to the pair of homologous chromosomes.

Anaphase I: The homologous chromosomes separate, while sister chromatids remain associated at their centromeres (Figure 10.3).

Telophase I: The nuclear membrane and nucleolus reappear, cytokinesis follows and this is called the dyad of cells (Figure 10.3). Although in many cases the chromosomes do undergo some dispersion, they do not reach the extremely extended state of the interphase nucleus. The stage between the two meiotic divisions is called interkinesis and is generally short lived. Interkinesis is followed by prophase II, a much simpler prophase than prophase I.

Meiosis II

Prophase II: Meiosis II is initiated immediately after cytokinesis, usually before the chromosomes have fully elongated. In contrast to meiosis I, meiosis II resembles a normal mitosis. The nuclear membrane disappears by the end of prophase II (Figure 10.4). The chromosomes again become compact.

Metaphase II: At this stage the chromosomes align at the equator and the microtubules from opposite poles of the spindle get attached to the kinetochores (Figure 10.4) of sister chromatids.

Anaphase II: It begins with the simultaneous splitting of the centromere of each chromosome (which was holding the sister chromatids together), allowing them to move toward opposite poles of the cell (Figure 10.4).

Telophase II: Meiosis ends with telophase II, in which the two groups of chromosomes once again get enclosed by a nuclear envelope; cytokinesis follows resulting in the formation of tetrad of cells i.e., four haploid daughter cells (Figure 10.4).

Significance Of Meiosis

Meiosis is the mechanism by which conservation of specific chromosome number of each species is achieved across generations in sexually reproducing organisms, even though the process, per se, paradoxically, results in reduction of chromosome number by half. It also increases the genetic variability in the population of organisms from one generation to the next. Variations are very important for the process of evolution.

Meiosis I

Meiosis I segregates homologous chromosomes, which are joined as tetrads ($2n$, $4c$), producing two haploid cells (n chromosomes, 23 in humans) which each contain chromatid pairs ($1n$, $2c$). Because the ploidy is reduced from diploid to haploid, meiosis I is referred to as a *reductional division*. Meiosis II is an *equational division* analogous to mitosis, in which the sister chromatids are segregated, creating four haploid daughter cells ($1n$, $1c$).

Prophase I

Prophase I is typically the longest phase of meiosis. During prophase I, homologous chromosomes pair and exchange DNA (homologous recombination). This often results in chromosomal crossover. This process is critical for pairing between homologous chromosomes and hence for accurate segregation of the chromosomes at the first meiosis division. The new combinations of DNA created during crossover are a significant source of genetic 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 has historically been divided into a series of substages which are named according to the appearance of chromosomes.

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 fibers takes 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 assembly of central element of the synaptonemal complex. Pairing is brought about in a zipper-like fashion and may start at the centromere (pro centric), at the chromosome ends (proterminal), or at any other portion (intermediate). Individuals of a pair are equal in length and in 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 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. Non-sister chromatids of homologous chromosomes may exchange segments over regions of homology. Sex chromosomes, however, are not wholly identical, and only exchange information over a small region of homology. 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.

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 are severed at the transition to anaphase I.

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 *dictyotene 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 actually visible. Sites of crossing over entangle together, effectively overlapping, making chiasmata clearly visible. Other than this observation, the rest of the stage closely resembles prometaphase of mitosis; the nucleoli disappear, the nuclear membrane disintegrates into vesicles, and the meiotic spindle begins to form.

Synchronous processes

During these stages, two centrosomes, containing a pair of centrioles in animal cells, migrate to the two poles of the cell. These centrosomes, which were duplicated during S-phase, function as microtubule organizing centers nucleating microtubules, which are essentially cellular ropes and poles. The microtubules invade the nuclear region after the nuclear envelope disintegrates, attaching to the chromosomes at the kinetochore. The kinetochore functions as a motor, pulling the chromosome along the attached microtubule toward the

originating centrosome, like a train on a track. There are four kinetochores on each tetrad, but the pair of kinetochores on each sister chromatid fuses and functions as a unit during meiosis I.

Microtubules that attach to the kinetochores are known as *kinetochore microtubules*. Other microtubules will interact with microtubules from the opposite centrosome: these are called *nonkinetochore microtubules* or *polar microtubules*. A third type of microtubules, the aster microtubules, radiates from the centrosome into the cytoplasm or contacts components of the membrane skeleton.

Metaphase I

Homologous pairs move together along the metaphase plate: As *kinetochore microtubules* from both centrosomes 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 the metaphase plate, with respect to the orientation of the other bivalents along the same equatorial line. The protein complex cohesin 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 requires at least one crossover per chromosome pair in addition to cohesion between sister chromatids.

Anaphase I

Kinetochore microtubules shorten, pulling homologous chromosomes (which consist of a pair of sister chromatids) to opposite poles. Nonkinetochore microtubules lengthen, pushing the centrosomes farther apart. The cell elongates in preparation for division down the center. Unlike in mitosis, only the cohesin from the chromosome arms is degraded while the cohesin surrounding the centromere remains protected. This allows the sister chromatids to remain together while homologs 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.

Summary

According to the cell theory, cells arise from preexisting cells. The process by which this occurs is called cell division. Any sexually reproducing organism starts its life cycle from a single-celled zygote. Cell division does not stop with the formation of the mature organism but continues throughout its life cycle.

The stages through which a cell passes from one division to the next is called the cell cycle. Cell cycle is divided into two phases called (i) Interphase – a period of preparation for cell division, and (ii) Mitosis (M phase) – the actual period of cell division. Interphase is further subdivided into G₁, S and G₂. G₁ Phase is the period when the cell grows and carries out normal metabolism.

Most of the organelle duplication also occurs during this phase. S phase marks the phase of DNA replication and chromosome duplication. G₂ phase is the period of cytoplasmic growth. Mitosis is also divided into four stages namely prophase, metaphase, anaphase and telophase. Chromosome condensation occurs during prophase. Simultaneously, the centrioles move to the opposite poles. The nuclear envelope and the nucleolus disappear and the spindle fibers start appearing. Metaphase is marked by the alignment of chromosomes at the equatorial plate. During anaphase the centromeres divide and the chromatids start moving towards the two opposite poles. Once the chromatids reach the two poles, the chromosomal elongation starts, nucleolus and the nuclear membrane reappear. This stage is called the telophase. Nuclear division is then followed by the cytoplasmic division and is called cytokinesis.

Mitosis thus, is the equational division in which the chromosome number of the parent is conserved in the daughter cell.

In contrast to mitosis, meiosis occurs in the diploid cells, which are destined to form gametes. It is called the reduction division since it reduces the chromosome number by half while

making the gametes. In sexual reproduction when the two gametes fuse the chromosome number is restored to the value in the parent.

Meiosis is divided into two phases – meiosis I and meiosis II. In the first meiotic division the homologous chromosomes pair to form bivalents, and undergo crossing over. Meiosis I has a long prophase, which is divided further into five phases. These are leptotene, zygotene, pachytene, diplotene and diakinesis. During metaphase I the bivalents arrange on the equatorial plate. This is followed by anaphase I in which homologous chromosomes move to the opposite poles with both their chromatids. Each pole receives half the chromosome number of the parent cell. In telophase I, the nuclear membrane and nucleolus reappear. Meiosis II is similar to mitosis. During anaphase II the sister chromatids separate. Thus, at the end of meiosis four haploid cells are formed.