# Cell and Nuclear Division

There are two different types of cell cycles: mitotic and meiotic. Cell cycles are tightly regulated at various checkpoints. The mitotic cell cycle is necessary for growth and repair while the meiotic cell cycle is necessary to generate gametes. Meiosis gives rise to genetic variation between gametes through crossing over of homologous chromosomes and the independent assortment of bivalents.

## Learning Outcomes

Candidates should be able to:

2(n) describe the events that occur during the mitotic cell cycle and the main stages of mitosis (including the behaviour of chromosomes, nuclear envelope, cell surface membrane and centrioles).

2(o) explain the significance of the mitotic cell cycle (including growth, repair and asexual reproduction) and the need to regulate it tightly (knowledge that dysregulation of checkpoints of cell division can result in uncontrolled cell division and cancer is required, but details of the mechanism are not required)

2(s) describe the events that occur during the meiotic cell cycle and the main stages of meiosis (including the behaviour of chromosomes, nuclear envelope, cell surface membrane and centrioles) (names of the main stages are expected, but not the sub-divisions of prophase).

2(t) explain the significance of the meiotic cell cycle (including how meiosis and random fertilisation can lead to variation)

*Use the knowledge gained in this section in new situations or to solve related problems.*

## Learning Experiences

2.5.4 Different Stages of Mitosis

The behaviour of chromosomes at the different stages of mitosis can be observed through the preparation of microscopy slides of squash root tip cells. The laboratory procedures can be found on OPAL.

2.5.5 Different Stages of Meiosis

The behaviour of chromosomes at the different stages of meiosis can be observed through the preparation of microscopy slides of squashed anther cells.

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## Websites

| S/N | QR Code | What's so interesting? |
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| 1. | | **Mitosis 3D Animation** |
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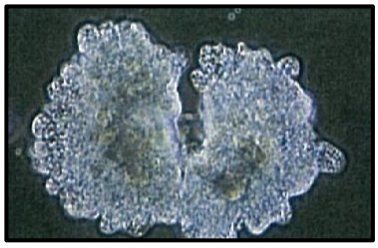
# 1. Cell and Nuclear Division

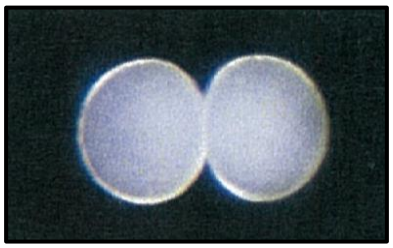
The basic unit of structure and function in living organisms is the **cell**. Cell division hence enables the **continuity of life** based on the production of cells.

In unicellular organisms, the cell division of one cell reproduces an entire organism. This is known as **asexual reproduction**.

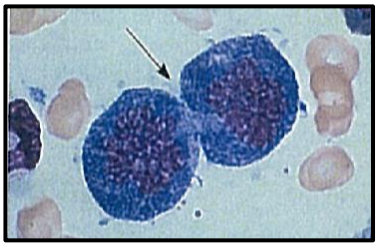
In multicellular organisms, cell division enables **sexually reproducing** organisms to **grow and develop** from a single cell – the fertilised egg or zygote. After an organism is fully grown, cell division continues to function in **renewal and repair**, replacing cells that die from normal wear and tear. (**Fig.1**)



**Reproduction**
An amoeba, a single-celled eukaryote, is dividing into two cells. Each cell will be an individual organism.



**Growth and development**
This micrograph shows a sand dollar embryo shortly after the fertilised egg divided, forming two cells.



**Tissue renewal**
These dividing bone marrow cells (arrow) will give rise to new blood cells.

**Fig. 1: Cell division results in the production of cells.**

**Cell division** consists of:

1. **Nuclear division**
   - The process of separating **nuclear DNA** to daughter cells.
   - There are two types of nuclear division:
     (i) Mitosis which leads to the production of two identical cells
     (ii) Meiosis which leads to the production of gametes e.g. sperm and egg

2. **Cytoplasmic division (cytokinesis)**
   - The process of separating **cytoplasm** and **organelles** to daughter cells.

## 1.1 Chromosome Number

The **chromosome number** is the number of chromosomes in **each cell** of an organism.

- Different species of plants and animals have different chromosome number.
- There is **no** relationship between the size of an organism and the number of chromosomes it possesses, as shown in **Fig. 2**.

| Organism | Chromosome number (2N) |
|---|---|
| **Vertebrates** | |
| human | 46 |
| chimpanzee | 48 |
| gorilla | 48 |
| horse | 64 |
| cattle | 60 |
| dog | 78 |
| cat | 38 |
| rabbit | 44 |
| rat | 42 |
| turkey | 82 |
| goldfish | 94 |

**Fig. 2: Chromosome number in organisms.**

Number of chromosomes is not a measure of the quantity of genetic material.

A karyogram (**Fig. 3**) shows all the chromosomes in a cell (in this case, a human male's somatic cell).

The chromosomes are sorted according to their sizes. We can observe that:

- there are **two sets** of chromosomes (maternal and paternal sets)
- chromosomes arranged in **homologous pairs**
- there are 22 pairs of **autosomes** and 1 pair of **sex chromosomes**

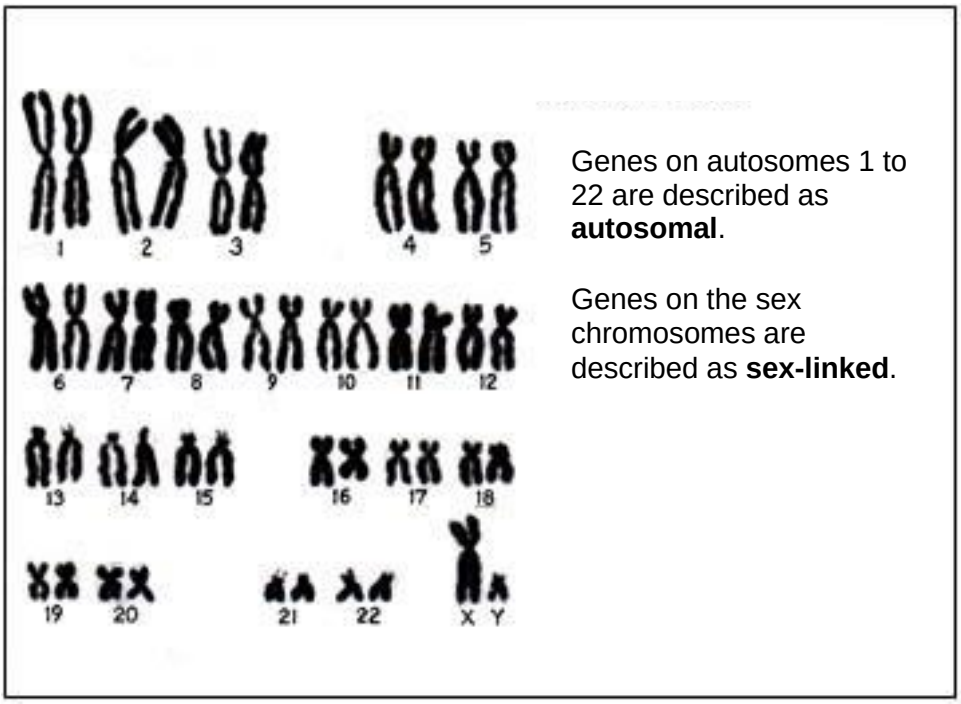



**Fig. 3: Karyogram of a human male.**

In human females, the **two sex chromosomes are alike** and known as **X chromosomes**. In males, there is **one X chromosome and one Y chromosome**.

## 1.2 Ploidy Level

**Ploidy** refers to the **number of sets of chromosomes** within the nucleus of a cell.

**Haploid** cells, such as gametes/sex cells, have only **one** set of chromosomes, abbreviated as **n**.

**Diploid** cells have **two** sets of chromosomes in the nucleus. Human beings, most animals and many plants are diploid organisms since all the cells in the body are diploid except for their gametes.

In human, the common representation is: 2n = 46,
where:

- **n** is the **number of chromosomes in a set** (23 for humans)
- The **number written before n** indicates the **ploidy level** i.e. the number of sets. For humans, there are 2 sets of chromosomes where one set comes from the mother, the other set from the father.

Organisms with more than 2 sets of chromosomes are termed **polyploid**. For example, triploid = 3n and tetraploid = 4n.

**Exercise**

Fill in the table below:

| genetic representation | ploidy level | number of sets of chromosomes | number of chromosomes | |
|---|---|---|---|---|
| | | | per set (n) | total |
| n = 6 | | | | |
| 2n = 4 | | | | |
| 4n = 8 | | | | |
| 2n = 42 | | | | |
| 2n = 38 | | | | |
| 3n = 81 | | | | |

## 1.3 Human Life Cycle

The human life cycle begins when the **haploid sperm** from the father fuses with the **haploid ovum** from the mother. The union of gametes results in fusion of the nuclei called **fertilisation**. The resulting zygote (or fertilised egg) is now **diploid** because it contains two sets of chromosomes, one set from the father and the other set from the mother (**Fig. 4**).

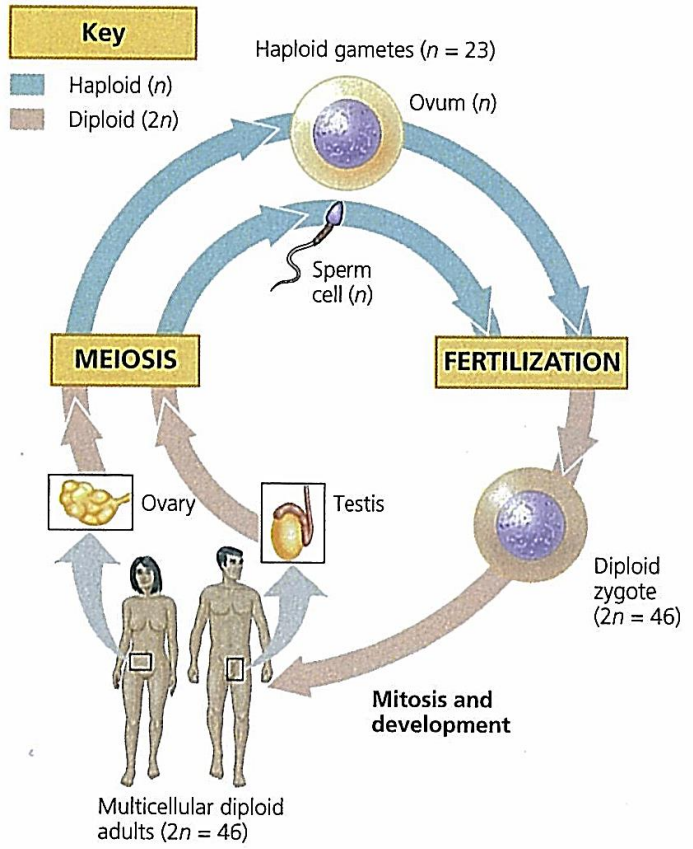



**Fig. 4: The human life cycle.**
In each generation, the doubling of the number of chromosome sets that results from fertilization is offset by the halving of the number of sets that results from meiosis. For humans, the number of chromosomes in a haploid cell is 23, consisting of one set (n = 23); the number of chromosomes in the diploid zygote and all somatic cells arising from it is 46, consisting of two sets (2n = 46).

### 1. Human somatic cells

- **All somatic cells** are generated by **mitosis**.
- Each somatic cell has **2 sets** of chromosomes, one set originating from the father and the other from the mother.
- Hence somatic cells are **diploid (2n)**.
- Each set contains 23 chromosomes (n = 23).
- There will be **46 chromosomes** (2n = 2 x 23 = 46) in **total**.
- Somatic cells will thus have **23 homologous pairs** of chromosomes.

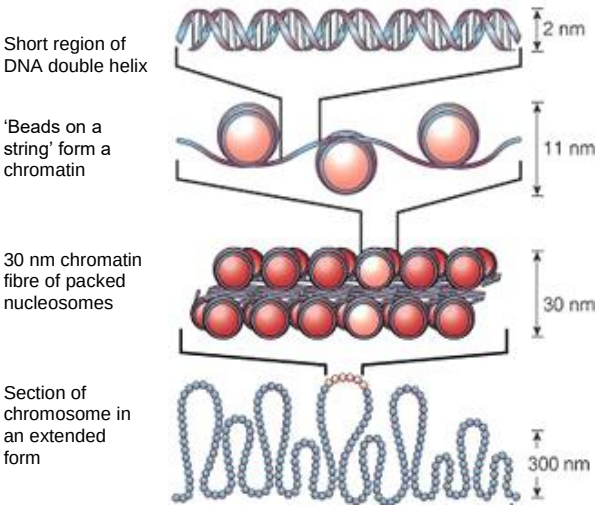
### 2. Human reproductive cells

- **Gametes** (such as spermatozoa or ova) are produced only by **meiosis**.
- Gametes have only **1 set** of chromosomes.
- Hence are **haploid (n)**.
- Each gamete carries 23 chromosomes (n= 23).
- This is to **maintain a constant number of chromosomes and prevent chromosomal doubling** in the next generation.

## 2. Important Terms And Definitions

**1. Chromatin**

- The complex of nucleic acids (DNA) and associated histone and non-histone proteins.
- It is in a **less condensed** state (**Fig. 5**) present during **interphase** of the cell cycle, or in **non-dividing cells**.




**2. Chromosome**

- The **condensed form** of chromatin. Additional proteins known as **scaffolding proteins** are associated with chromosomes and aid in their condensation (**Fig. 5**).
- Chromosomes are **most visible** during **mitosis** and **meiosis**.
- **Genes** are hereditary units located at specific physical locations along each chromosome. This location is known as a **gene locus**.

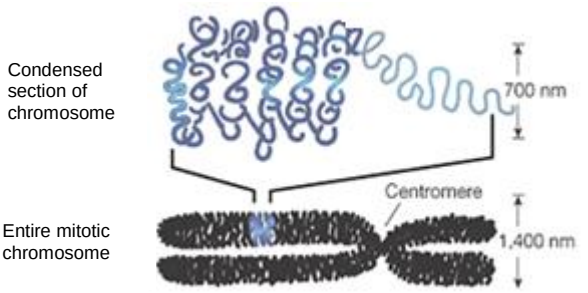



**Fig. 5**: **From chromatin to chromosome.**

**3. Homologous Chromosomes**

- In diploid organisms, homologous chromosomes are
  (a) **structurally similar**: similar **size, shape, centromere position** and **sequence of gene loci**.
  (b) **not genetically identical**: **different alleles** at the same gene loci.
- An allele is an **alternative form of a gene**. (*KIV: Inheritance I*).
- Each chromosome of such a pair is called a **homologue** (**Fig. 6**). They come from separate parents; one homologue comes from the **mother** and the other comes from the **father**.
- Homologous chromosomes **undergo synapsis and pair up** during **meiosis**.

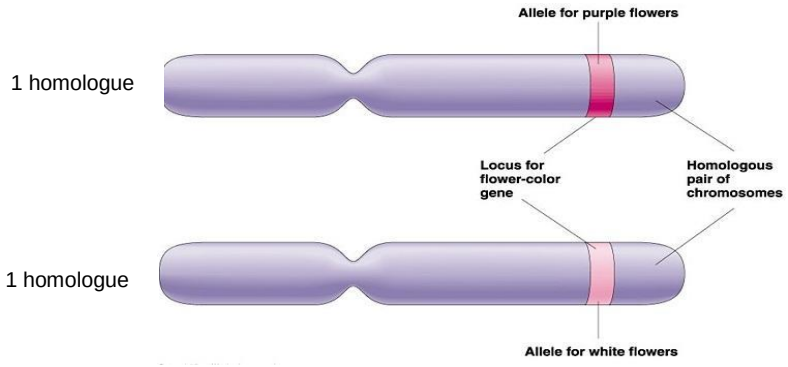



**Fig. 6: A pair of homologous chromosomes in the unreplicated state.**

**4. Sister chromatids**

- Sister chromatids are **replicated forms of a single chromosome** joined together by the **centromere.**
- They are eventually separated during the **anaphase of mitosis** and **anaphase II of meiosis II**.
- The DNA molecules of sister chromatids are identical due to **semi-conservative DNA replication.** Hence, they possesses the same alleles at each gene locus (**Fig. 7**).
- Sister chromatids are hence **structurally identical**: similar size, shape, centromere position, number of genes and sequence of gene loci.
- Sister chromatids can be **genetically identical** or **non-genetically identical** as sister chromatids will no longer possess the same alleles at each gene locus after crossing over occurs in prophase I of meiosis I. (*KIV: Meiosis*)

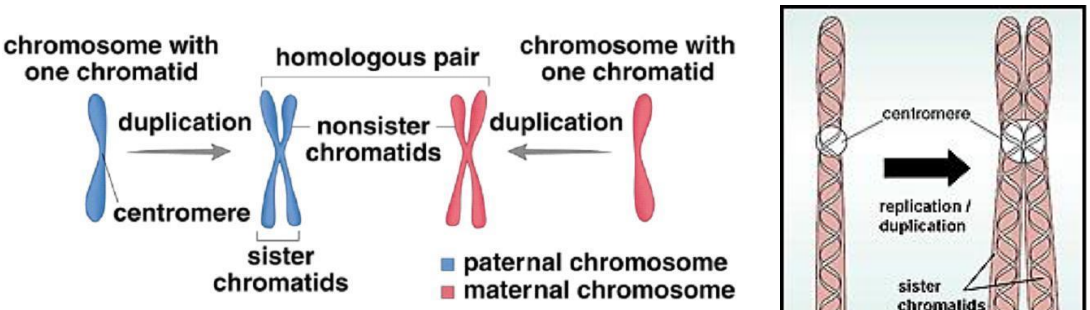



**Fig. 7: The duplication of sister chromatids**

**5. Centromere**

- It is the specialised region of a chromosome where **two sister chromatids** are **joined** after semi-conservative DNA replication.(**Fig. 8)**
- It consists of a short sequence of DNA found in heterochromatin, which are repeated several thousand times in tandem and never transcribed.
- It is associated with protein structures known as **kinetochores** for the attachment of spindle fibers and is the last location to separate during cell division.

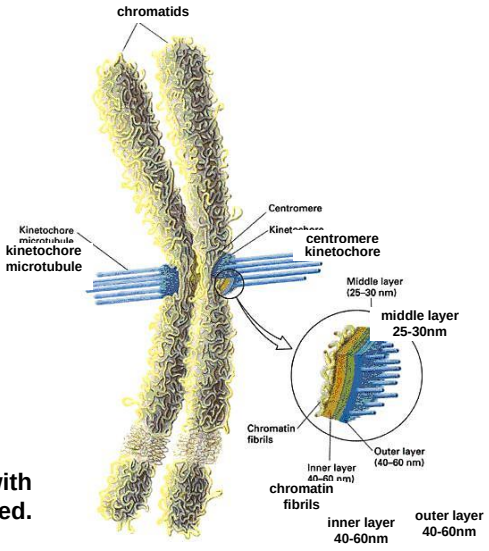



**Fig. 8: The centromere with kinetochore microtubules attached.**

**6. Kinetochore**

- A structure formed by **proteins** associated with specific sections of the chromosome i.e. the **centromere**.
- It is the structure to which the **microtubules of the spindle are attached** during nuclear division.
- The two kinetochores of a replicated chromosome face opposite **poles** of the cell, hence the kinetochore forms part of the structure that plays an **active part** in the **movement of chromosomes** to the opposite poles of the cell.

**7. Centrioles**

- A barrel-shaped organelle which is found **only in animal cells**.
- Centrioles exists as a cylindrical pair in the cytoplasm. Each member of the pair is composed of **nine triplets of microtubules** arranged in a ring.
- The members of the pair are **perpendicular** to each other.
- They are located in a region of the cell known as the **centrosome** (**Fig. 9**).
- At the onset of mitosis, centriole pairs are **duplicated** and each pair moves to the opposite poles of the cell, establishing the two **poles** of the cell.

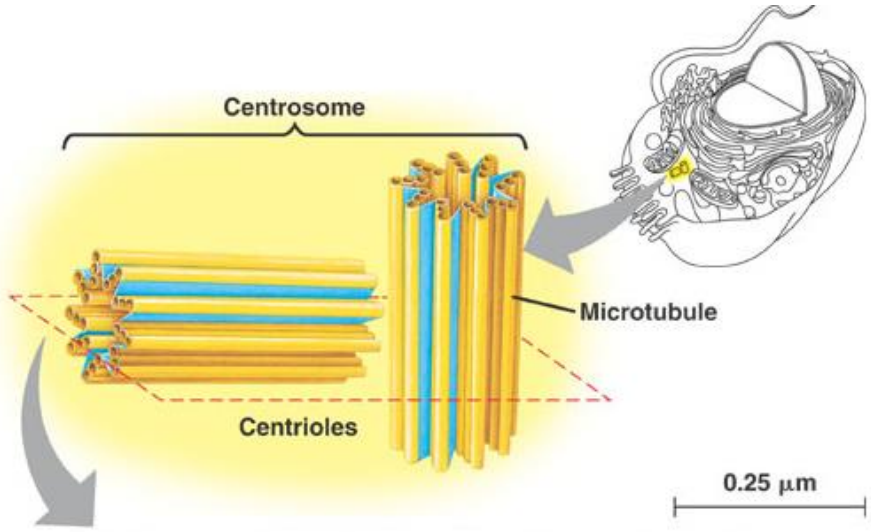



**Fig. 9: The centrosome containing a pair of centrioles.**

**8. Centrosome**

- The centrosome is a specialised region of the cell that includes **a pair of centrioles** (**Fig. 10**) and the **surrounding cytoplasm**, which contains **proteins** that aid in the assembly of spindle microtubules.
- It is the region where the **assembly of spindle microtubules** begins.
- It is also known as the **microtubule organising centre (MTOC).**

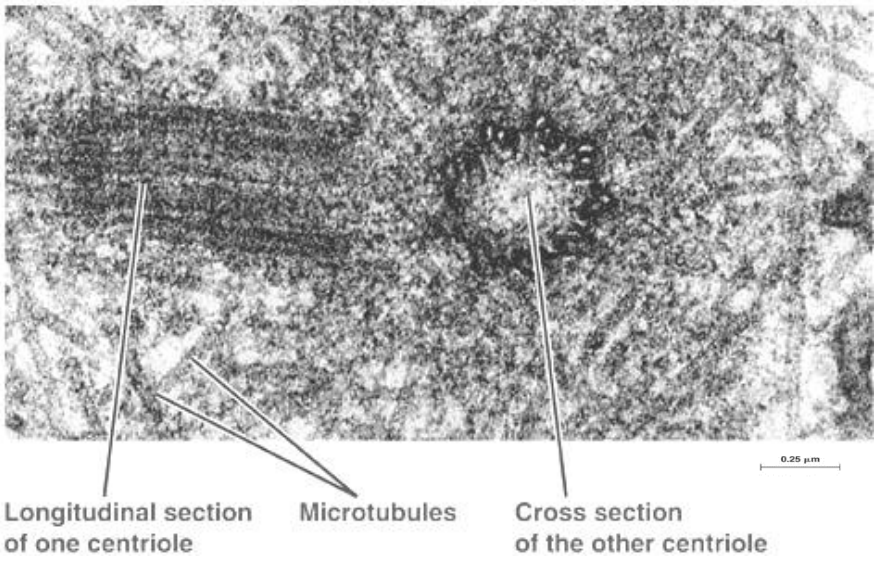



**Fig. 10: Centrosome containing a pair of centrioles.** An animal cell has a pair of centrioles within its centrosome, the region near the nucleus where assembly of the cell's microtubules is initiated.

**9. Microtubules** (also known as spindle fibre)

- Microtubules are **components of the cytoskeleton**. They are rigid hollow rods approximately 25nm in diameter.
- Microtubules are dynamic structures made up of **globular proteins** known as **tubulin**.
- (FYI) Tubulin dimers polymerise to form microtubules, which generally consist of 13 linear protofilaments assembled around a hollow core and continual assembly and disassembly of the tubulins allow for microtubule formation. (Fig. 11)

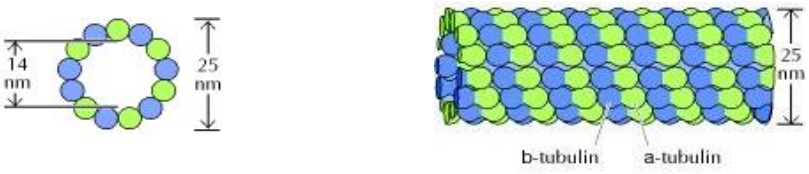



**Fig. 11:** (FYI) Dimers of α- and β-tubulin polymerise to form microtubules, which are composed of 13 protofilaments assembled around a hollow core.

An **organised system of microtubules** that **attaches to the centromeres** of duplicated chromosomes and **pulls them to** opposite **poles** of the cell during eukaryotic cell division (**Fig. 12**).

There are 3 types of microtubules that can be distinguished in mitotic animal cells:

1. **Astral microtubules / asters**
   - Radiate from the centriole towards the peripheral regions of the cells.
   - Only present in cells that contain centrioles.
   - Serve as a support for the functioning of the microtubules.
2. **Kinetochore microtubules**
   - Fibres attached to the **kinetochore**, which forms on the centromere of each chromatid.
   - Serve to attach the chromosomes to the spindle fiber.
   - Pull the sister chromatids towards the opposite poles of the cell during anaphase.
3. **Polar microtubules**
   - Fibres running from pole to pole **overlapping at the equator** of the spindle.
   - Responsible for elongating the whole cell along the polar axis during anaphase.

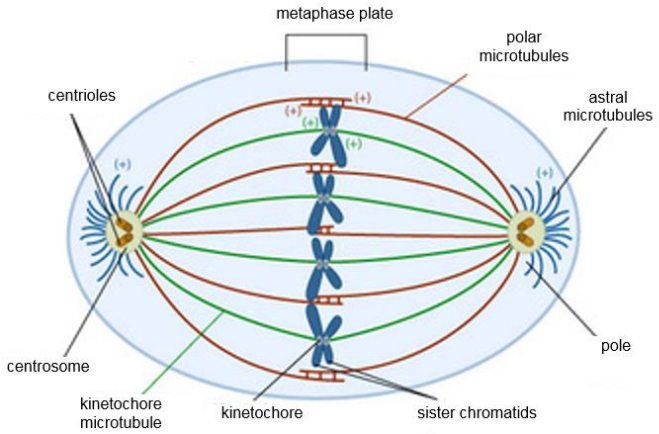



**Fig. 12: The mitotic spindle at metaphase.** The kinetochores of a chromosome's two sister chromatids face in opposite direction. Here, each kinetochore is actually attached to a cluster of kinetochore microtubules extending from the nearest chromosome. Polar microtubules overlap at the metaphase plate.

## 3. The Cell Cycle

During growth, eukaryotic cells continually progress through the four stages of the **cell cycle** (**Fig. 13**), generating new daughter cells. It is the sequence of **growth, DNA replication**, **growth and cell division** that all cells go through in order to form genetically identical cells.

The **cell cycle** consists of:

1. **Interphase** which is divided into **$G_1$**, **S** and **$G_2$**.
2. **Mitosis** which is subdivided into **prophase**, **metaphase**, **anaphase** and **telophase**.
3. **Cytokinesis** which is the division of the cytoplasm to form two daughter cells, which usually occurs simultaneously with telophase.

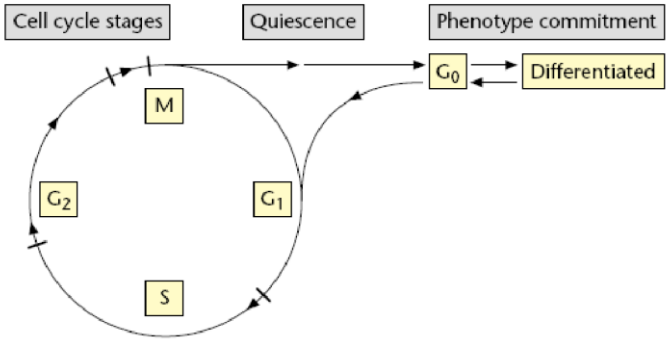



**Fig.13: Cell cycle regulation.** The four stages of the somatic cell cycle ($G_1$, $G_2$, and M) support duplication of the genome and subsequent segregation of a diploid set of chromosomes into two progeny cells. Cells can exit the cell cycle into a quiescent non-dividing state ($G_0$) with the option to re-enter the cell cycle or to differentiate into a committed cell expressing phenotypic markers characteristic of discrete tissue-specific lineages.

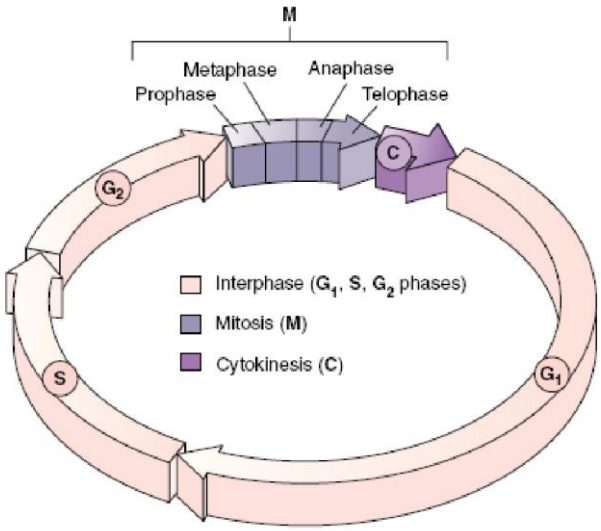
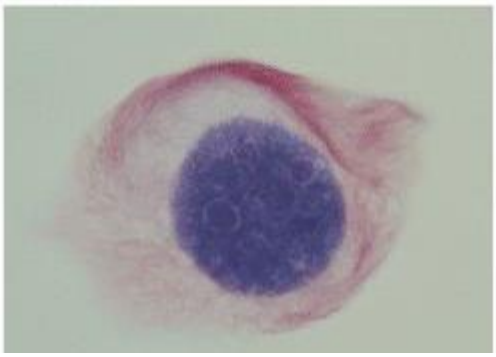



**Fig.14: The cell cycle.**
$G_1$ represents the primary growth phase of the cell cycle.
S the phase during which a replica of the genome is synthesised.
$G_2$ the second growth phase.

When cells are non-dividing or quiescent, they are said to be in the **$G_0$ phase** of the cell cycle. The cell cycle is very tightly controlled and is regulated by proteins known as **cyclins** (*KIV: Molecular Basis of Cancer*).

### 3.1 Interphase

Interphase often accounts for about 90% of the length of the cell cycle. It is the **longest** phase of the cell cycle and hence most cells observed are in interphase (**Fig. 14**). Interphase is divided into three sub-phases, **$G_1$**, **S** and **$G_2$** and is a period of **intense metabolic activity** of the nucleus.



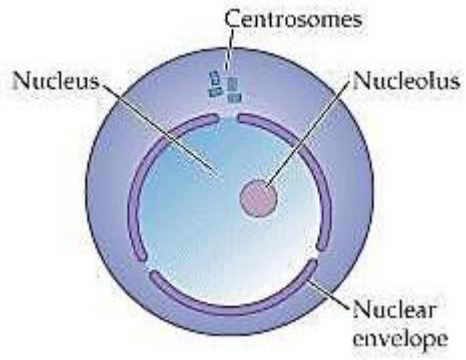
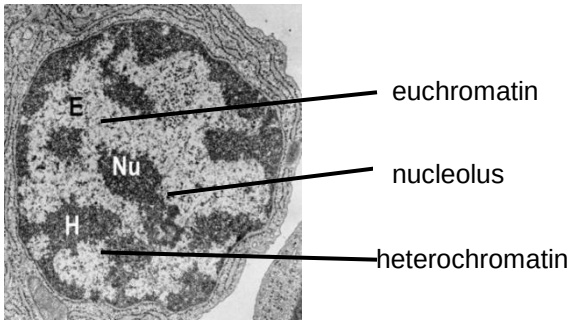
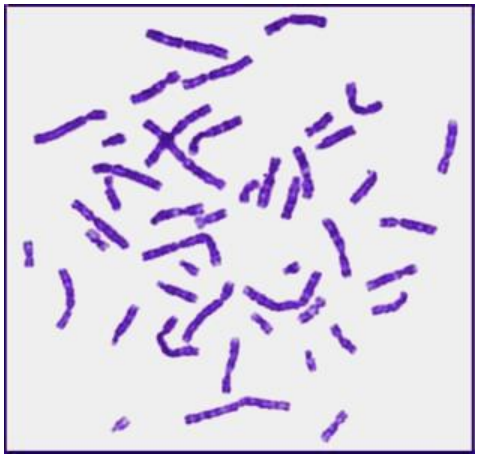



**Fig. 14: The process of interphase.** It is the longest stage of the cell cycle and occurs prior to mitosis.

During all three sub-phases, the cell grows by replicating DNA, producing proteins and cytoplasmic organelles such as mitochondria and endoplasmic reticulum. There is a clear purpose for each phase:

| | |
|---|---|
| **$G_1$ PHASE** (Gap 1) | • Begins after cytokinesis of the previous cell division - cells are thus small in size and low in ATP.<br>• Hence, cells **increase in size** and **acquire ATP** during this phase.<br>• Intensive cellular **gene expression** and **synthesis of appropriate organelles and proteins**. |
| **S PHASE** (Synthesis) | • Each DNA molecule undergoes **semi-conservative DNA replication**, resulting in the production of two identical DNA molecules.<br>• **Histone proteins** are synthesised and associate with each DNA molecule.<br>• After the DNA have replicated in S phase, they remain fully extended and uncoiled. |
| **$G_2$ PHASE** (Gap 2) | • Since the formation of new DNA is an energy-consuming process, the cell undergoes a **second growth** and **energy acquisition** stage.<br>• Cells **increase in size** and **acquire ATP** during this phase.<br>• Further synthesis of appropriate organelles and proteins occurs.<br>• **Centrioles** replicate and the **mitotic spindle** begins to form. |

**Characteristics of cells in non-dividing and dividing forms**

| Non-dividing cells (Interphase) | Dividing cells (Mitosis) |
|---|---|
| • DNA exists in the form of very **loosely-coiled** and **decondensed** threads called **chromatin** (**Fig. 15a**).<br>• Chromatin exists in two forms:<br>**1. Euchromatin**<br>- Decondensed/less condensed chromatin<br>- transcriptionally **active**<br>**2. Heterochromatin**<br>- highly condensed chromatin<br>- transcriptionally **inactive**<br>  <br>**Fig. 15a: Euchromatin and heterochromatin.** | • DNA exists in a **highly condensed** form.<br>• Chromatin condenses with the aid of specific proteins into discrete **chromosomes**. (**Fig. 15b**).<br>  <br>**Fig. 15b: Diagram of chromosomes.** |
| • **Nuclear envelope still intact** and **nucleolus present.** | • **Nuclear envelope has disintegrated** and chromosomes are released into the cytoplasm. The **nucleolus no longer present**. |
| • Cell is **transcriptionally active**; gene expression occurs. | • The cell is now **transcriptionally inactive**. Protein synthesis is temporarily suspended as the cell prepares for nuclear division. |

## 4. Nuclear Division – Mitosis

Mitosis involves the **nuclear division** of **one nucleus into two genetically identical nuclei**. Following cytokinesis, it produces **two daughter cells** that are **genetically identical** to each other and to the original parent cell.

The main stages of mitosis are: **prophase**, **metaphase**, **anaphase** and **telophase**.

Mitosis occurs in **somatic cells**. It allows daughter nuclei to receive precisely the **same number of chromosomes** as the parental nucleus. Hence, the **diploid (2n)** condition is maintained from one generation of cells to the next.

Passing **identical genetic material** to daughter cells is **a crucial function of cell division**. Changes in the genetic material of the daughter cells, such as having a different number of chromosomes from their parent cell, may lead to cancerous cells.

### 4.1 Stages of Mitosis

#### Prophase

This is the **longest stage** of mitosis. During prophase, changes occur in both the nucleus and cytoplasm.

**In the nucleus**

- **Nuclear envelope disintegrates** into small vesicles, which disperse.
- **Nucleolus** gradually **disappears**.
- Chromatin **become more tightly coiled** (i.e. shorten and thicken) and **condense into discrete chromosomes** observable under a light microscope (**Fig. 16**).

**In the cytoplasm**

- In **animal cells, centriole pairs migrate to** opposite **poles of the cell**.
  (Note that **plant cells do not possess centrioles** but are able to assemble the spindle apparatus nonetheless.)

- The spindle fibre that began to form in G2 phase of interphase **continues to develop**.

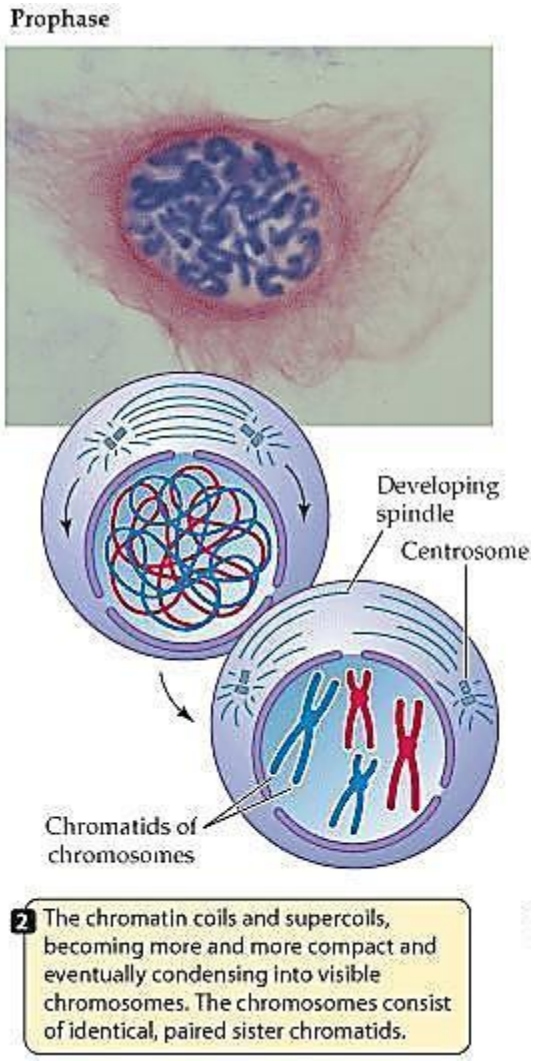



**Fig. 16: Cell undergoing prophase**

## Metaphase

- **Centriole pairs** are positioned at opposite **poles** of the cell.
- **Shortening and thickening** of the **chromosomes is at its maximum.**
- **Two sister chromatids** joined at the **centromeres** of each chromosome.
- **Each** of the two sister chromatids of a replicated chromosome has a **kinetochore** at the centromere.
- **Kinetochore microtubules** attach to the kinetochores at the centromeres of chromosomes (**Fig. 18**).

- Chromosomes **migrate** and **align singly** at the **metaphase plate** (also known as the **equatorial plate**) which is the plane equidistant from the spindle poles (**Fig. 17**). They are pulled to the metaphase plate by the action of kinetochore microtubules (**Fig. 19, Fig. 20**).
- There is **no pairing** of homologous chromosomes at the metaphase plate during mitosis.
- Certain drugs like **colchicine** interfere with spindle function and can be used to arrest cells at metaphase.

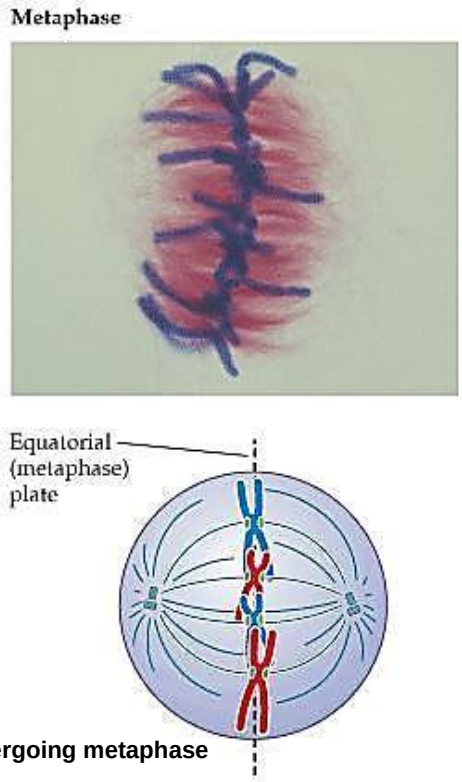



**Fig.17: Cell undergoing metaphase**

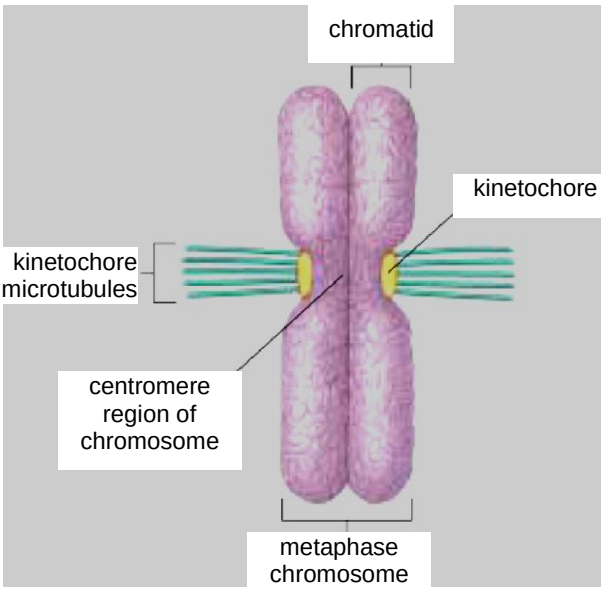



**Fig. 18: Kinetochores.** In a metaphase chromosome, kinetochore microtubules are anchored to proteins at the centromere.

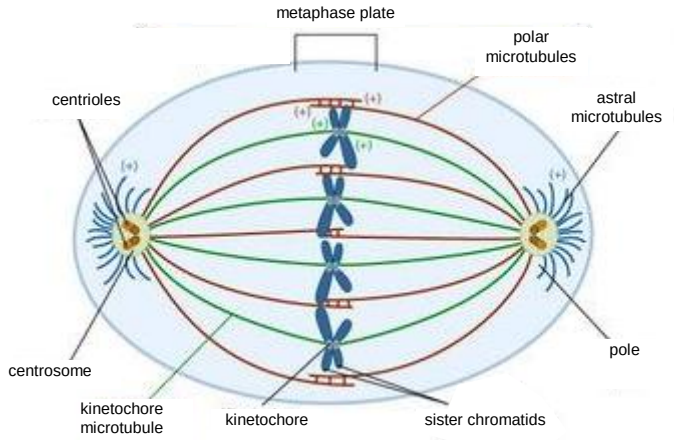



**Fig. 19. Chromosomes align singly at the metaphase plate.**


**Fig. 20: The three types of microtubules during metaphase.**

## Anaphase

- Anaphase is the **shortest stage** of mitosis. (**Fig. 21**)
- **Centromeres divide** and sister chromatids are separated.
- Once the centromeres of the **sister chromatids** are **separated**, the chromatids are known as **daughter chromosomes**.
- Daughter chromosomes are pulled to the opposite **poles of the cell** as their **kinetochore microtubules shorten** (**Fig. 22a**).
- As these kinetochore microtubules are attached at the kinetochore/centromere, the chromosomes move with **centromere leading towards the poles** of the cell. (**Fig. 22b**).

- Separated daughter chromosomes are hence pulled along **behind the centromeres**, producing a **characteristic 'V' shape pattern**.

- At the same time, the poles of the cell move farther apart as the **polar microtubules slide past each other**, hence **elongating the cell** (**Fig. 22b**).
- Special **motor proteins** are involved in the rapid and abrupt movement of chromosomes towards the poles of the cell during anaphase.
- At the **end of anaphase**, the two poles of the cell have **equal** and **complete sets of chromosomes**.

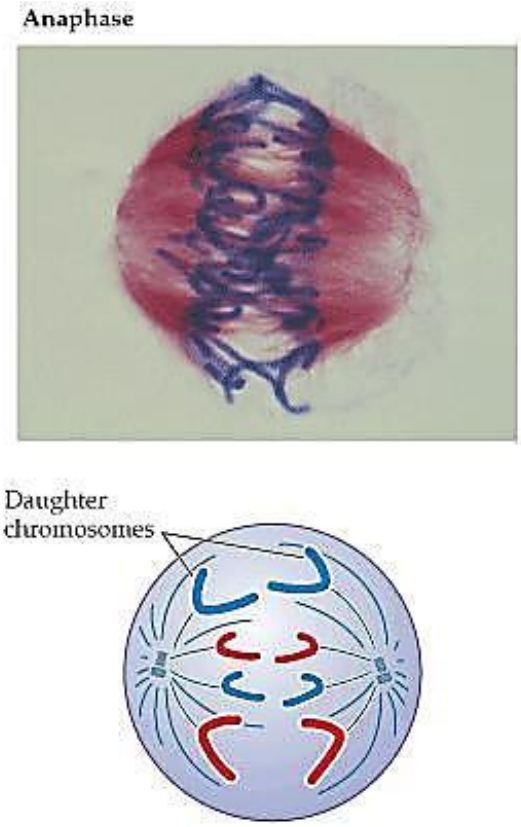



**Fig. 21: Cell at anaphase.**

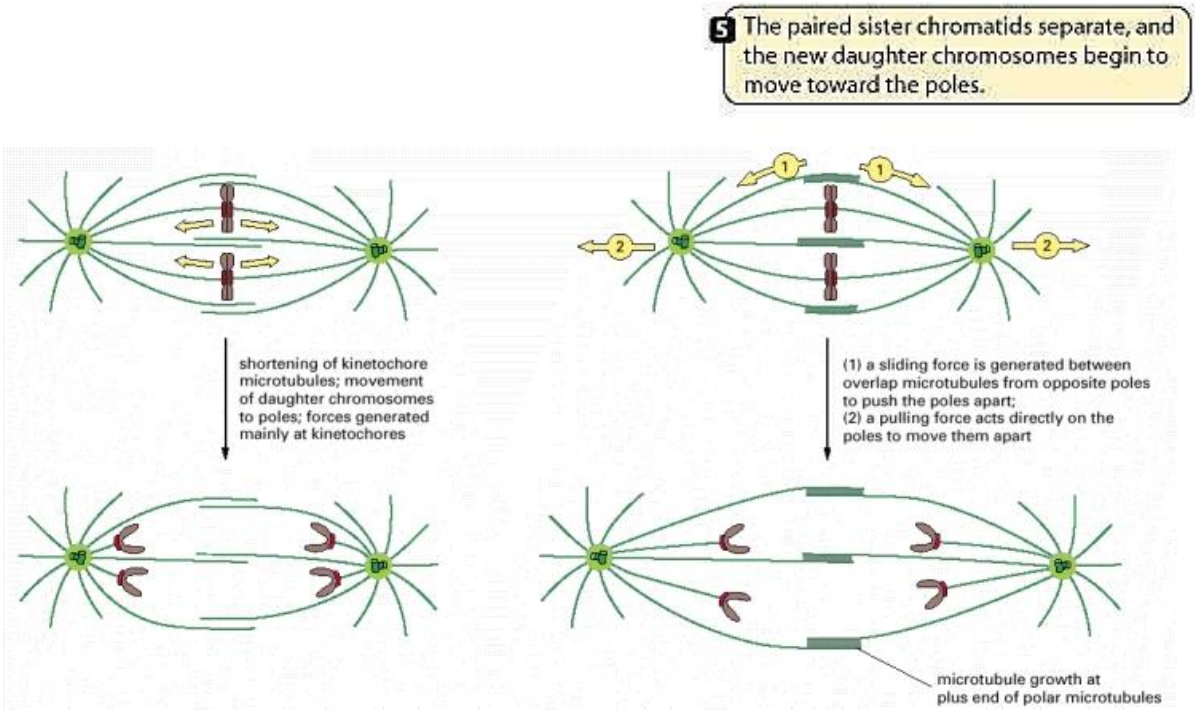



**Fig. 22a: Action of kinetochore microtubules during anaphase moving the daughter chromosomes to the poles.**

**Fig. 22b: Action of polar microtubules during anaphase pushing the poles apart.**

**Telophase**

- It begins when the daughter chromosomes reach their respective poles.
- The chromosomes **decondense** into the **chromatin** form by uncoiling. (**Fig. 23**).
- The **nucleolus** and the **nuclear envelope re-form**.
- This results in the two nuclei taking on the granular appearance of interphase.
- **Microtubules disassemble**. A pair of centrioles ends up in each daughter cell.

**Mitosis, the equal division of one nucleus into two genetically identical nuclei, is now complete.**

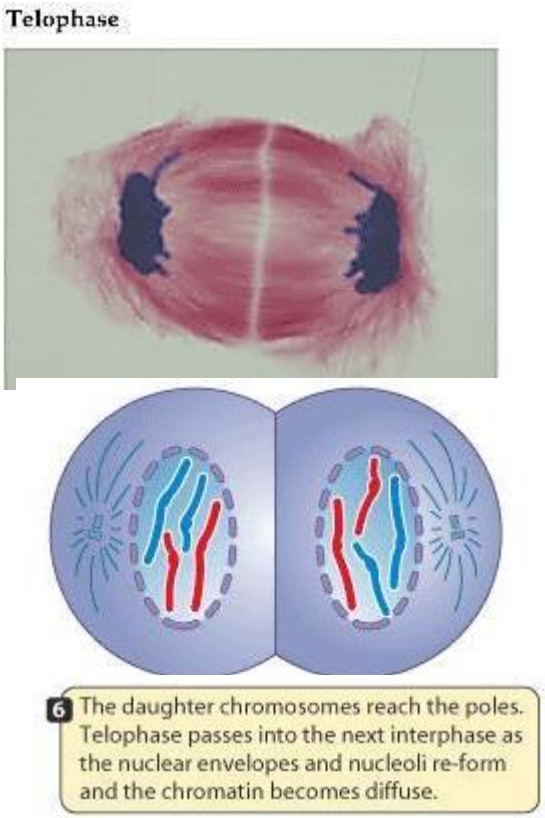



**Fig. 23: Cells at telophase**.

## 4.2 Significance of Stages in Mitosis

| Stage | Chromosomal behaviour | Significance |
|---|---|---|
| **1. To ensure integrity of genetic information in daughter cells** | | |
| **Interphase** | **Semi-conservative DNA replication** during S phase of interphase. | ● **Semi-conservative replication** of DNA requires the parental DNA molecule to serve as the template for making genetically identical copies of daughter DNA molecule.<br>● Semi-conservative DNA replication occurs **before the disintegration of the** protective **nuclear membrane.**<br>● Semi-conservative DNA replication occurs **prior to the distribution of genetic material to the two daughter cells**. |
| **2. To ensure equal distribution of nuclear DNA to daughter cells** | | |
| **Prophase** | Coiling of long, thin chromatin into **condensed, thick and discrete chromosomes**. | To **prevent entanglement** of chromatin and DNA breakage during the separation of genetic material. |
| **Metaphase** | **Chromosomes align singly** at the **metaphase plate/equatorial plate** of cell. **No pairing** of homologous chromosomes. | To ensure that each daughter cell will have the **complete diploid set** of DNA. |
| **Anaphase** | **Separation of sister chromatids** towards opposite **poles** of the cell by shortening of kinetochore microtubules. | |
| **Telophase** | Daughter chromosomes **reach the** opposite **poles of the cell** before cytokinesis. | |

## 4.3 Cytoplasmic Division – Cytokinesis

- **Cytokinesis** is the **division of the cytoplasm** to produce **two daughter cells**.
- In preparation for cytoplasmic division, the **cell organelles** become **evenly distributed** towards the two poles of the parent cell, along with the chromosomes, during telophase. This allows for the equal allocation of the cell organelles e.g. Golgi apparatus, mitochondria and cytoplasm to each daughter cell.
- **Two smaller**, **genetically identical cells** result. These cells may then grow and develop into different forms via differentiation and developmental processes.
- It generally begins **simultaneously with telophase**.
  Note that cytokinesis in animal cells differs from that in plant cells.

### Cytokinesis in Animals

- Cytokinesis involves the formation of a **cleavage furrow**, which pinches the cell in two. (**Fig. 24**)
- It first forms as a shallow groove in the cell surface near the metaphase plate.
- On the cytoplasmic side of the furrow is a **contractile ring of microfilaments**. As the ring of microfilaments contracts, the cleavage furrow deepens until the parent cell pinches into two daughter cells, each with a complete nucleus and share of cytosol, organelles and other subcellular structures (**Fig. 25**).

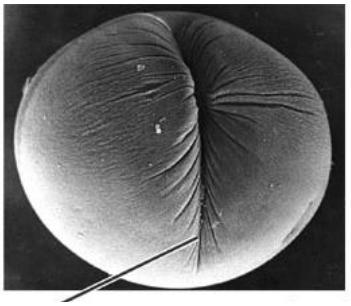
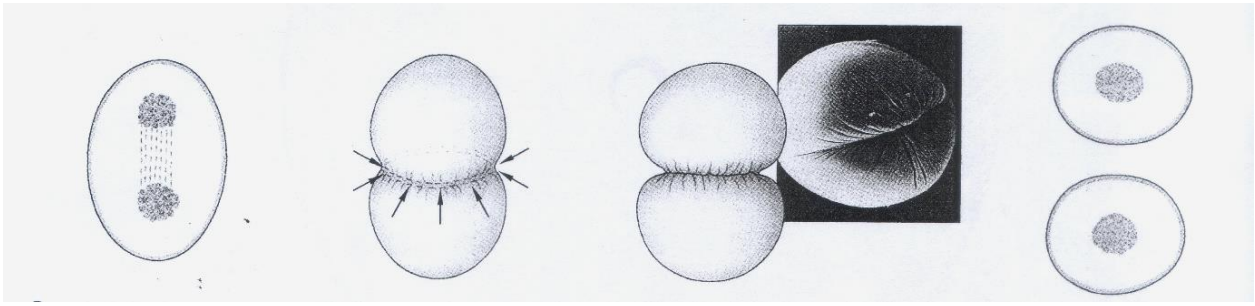


**Fig. 24: Cleavage furrow**.



Mitosis is completed, and the bipolar spindle is starting to dissemble.

At the former spindle equator, a ring of actin filaments attached to the plasma membrane contracts.

The diameter of the contractile ring continues to shrink and pull the cell surface inward.

The contractile mechanism continues to operate until the cytoplasm is partitioned.

**Fig. 25: Following completion of mitosis, a contractile ring consisting of microfilaments divides the cell in two.**

## Cytokinesis in Plants

- Cytokinesis in plant cells is different from that in animal cells due to the presence of the **cell wall**. **No cleavage furrow** is formed.

- The process occurs by the growth of a **cell plate** during telophase across the **metaphase plate** of the plant cell.

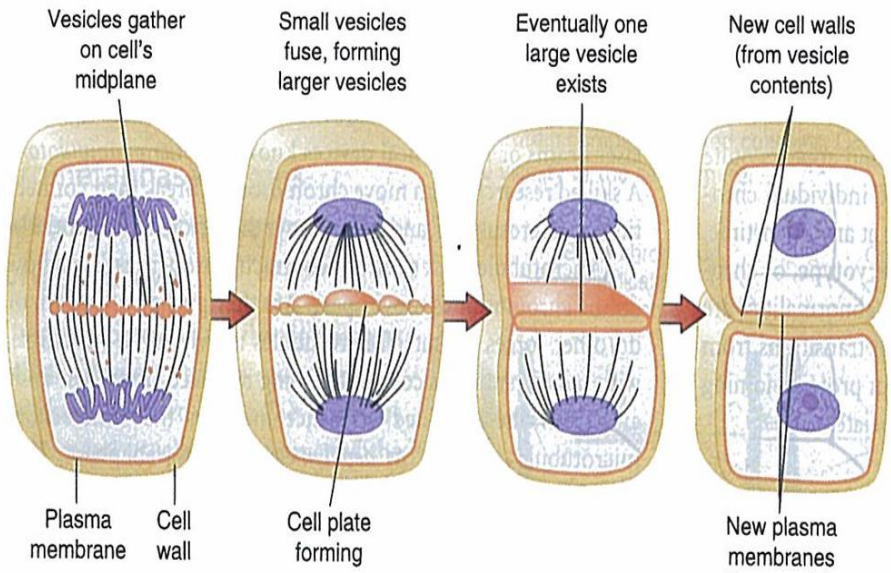
- Vesicles derived from the **Golgi apparatus** move to the middle of the cell where they **fuse**, producing a cell plate.

- The vesicles contain materials to construct both a **primary cell wall** for each daughter cell and a **middle lamella** that cements the primary cell walls of adjacent cells together. These materials carried in the vesicles collect in the cell plate as it grows.

- The cell plate enlarges until its surrounding membrane, formed by the fusion of the vesicle membranes, fuses with the plasma membrane along the perimeter of the parent cell.

- This results in the formation of two daughter cells, each with its own plasma membrane.

- **Cellulose** is laid down between the two membranes of the cell plate to form the **cell wall** (**Fig. 26**).



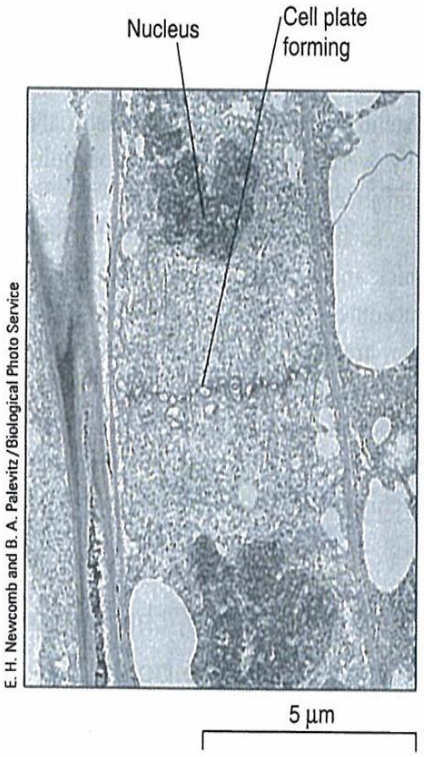




**Fig. 26: Cell plate formation during cytokinesis in a plant cell.** The TEM shows a maple leaf cell (*Acer saccharinum*) undergoing cytokinesis.

## 4.4 Significance of Mitosis

### 1. Genetic stability

- Mitosis produces two daughter cells which have the **same number of chromosomes**.
- **Semi-conservative DNA replication** during S phase of interphase gives rise to **genetically identical** daughter DNA molecules.
- **Daughter chromosomes** are subsequently **distributed equally** to the daughter cells.
- There is **no variation** in genetic information during mitosis.
- Hence daughter cells are **genetically identical** to the parent cell.
- The production of genetically identical cells ensures the **preservation of genetic stability** across generations of cells and hence, in the organism.

### 2. Growth, repair, and regeneration

**Growth**

- If a tissue is to **grow**, it is important that the new cells formed are **genetically identical** to the existing cells in order to carry out the **same functions**.

**Repair**

- Damaged cells are **replaced** by exact copies of the original, thus allowing for a tissue to be restored to its former condition.

**Regeneration**

- Mitosis also allows for the **regeneration** of missing parts, such as legs in crustacean, and cell replacement occurs, to varying degree, in multicellular organisms.

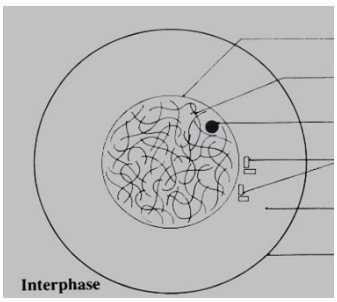
### 3. Asexual reproduction

- Many animal and plant series are propagated by **asexual reproduction** involving the mitotic division of cells. The offspring is **identical** to i.e. a clone, of their parents.
- Unicellular eukaryotic organism e.g. amoeba divides and forms duplicate offspring, the division of one cell **reproduces an entire organism**. This form of asexual reproduction involves mitotic cell division.
- The offspring cells are **genetically identical** to the original parent organism, thus ensuring the **preservation of favourable traits from generation to generation**.
- Another example of asexual reproduction is **vegetative propagation** of plants.

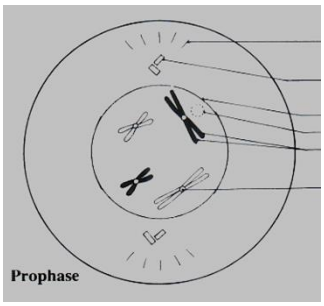
## CONCEPT CHECK I

1. The diagram below shows the different stages of mitosis and cytokinesis.
   Label the different parts of the cell at each stage and fill in the blanks.

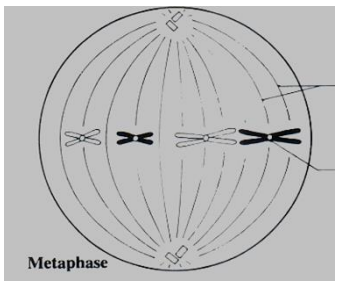
   The DNA content **in a cell** is represented by **x**.



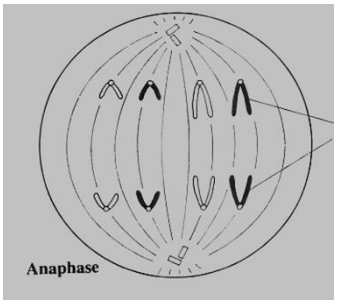

Chromosome number: ___
DNA content: ____



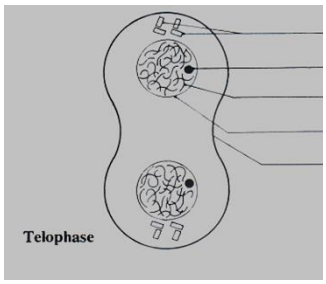

Chromosome number: ___
DNA content: ____



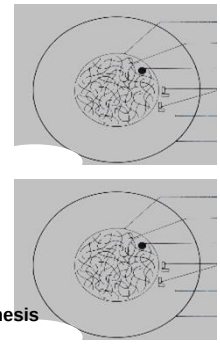

Chromosome number: ___
DNA content: ____




Chromosome number: ___
DNA content: ____

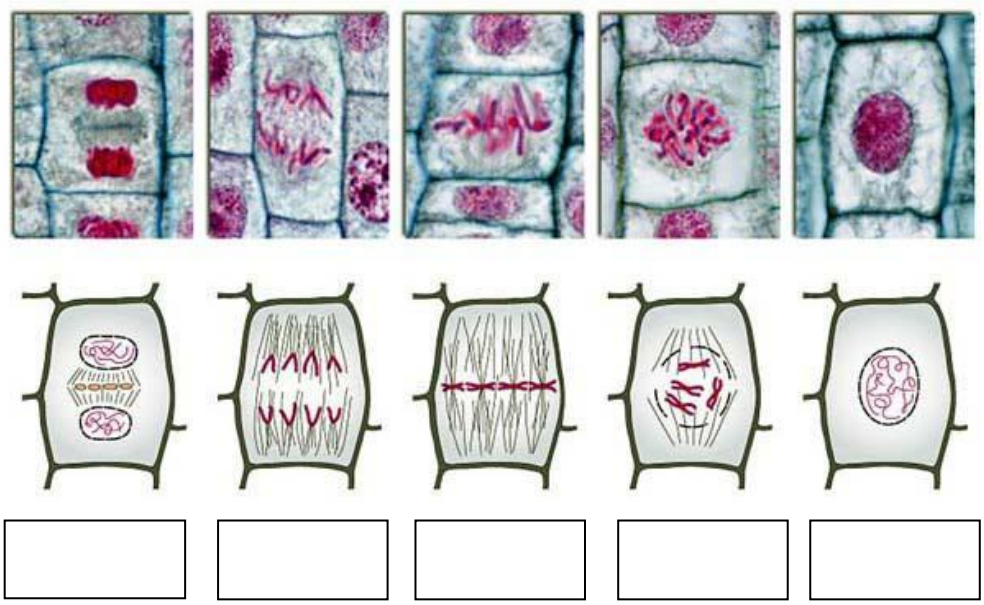



Chromosome number: ___
DNA content: ____




Chromosome number: ___
DNA content: ____

2. Match the correct stages of mitosis to the diagrams below.



## 5. Nuclear Division – Meiosis

Meiosis occurs only in specialized cells within the gonads or sex organs of sexually reproducing organisms. In humans and most animals, the male gonads are the testes, while the female gonads are the ovaries. During meiosis, specialised reproductive or sex cells called **gametes** are produced, as shown in **Fig. 27 and Fig. 28**.

Gametes are **haploid cells (n)** and cannot be generated from **diploid (2n)** precursor cells by mitosis.

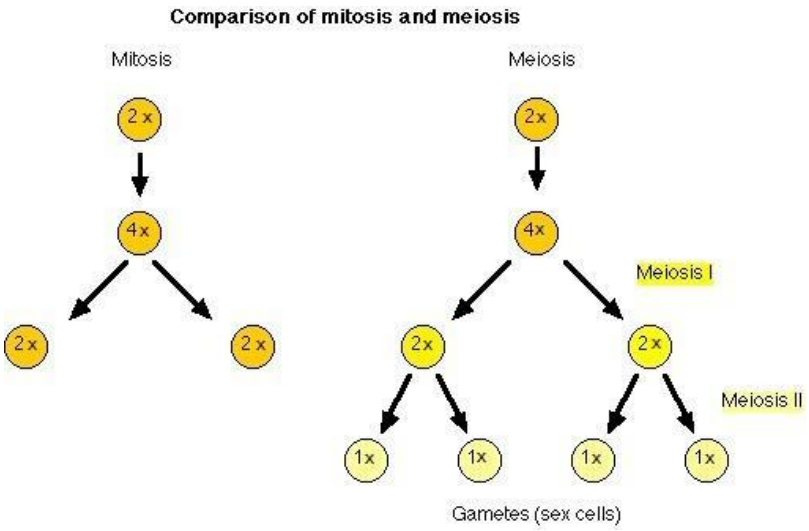



**Fig. 27: Comparison of mitosis and meiosis**.

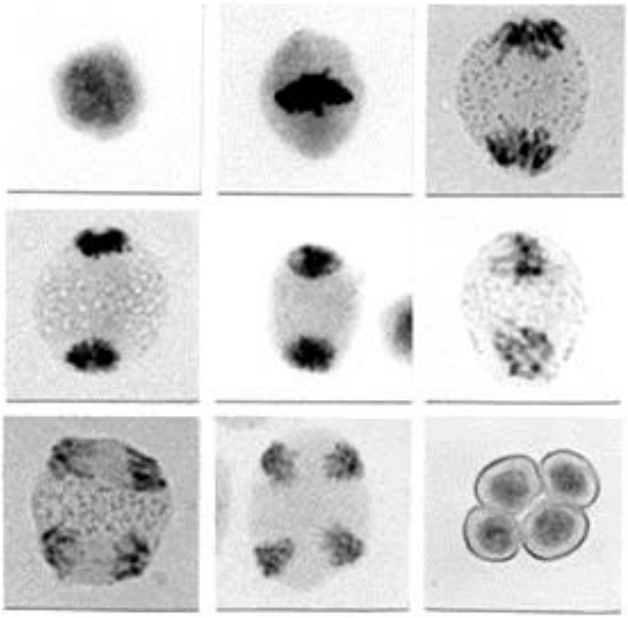


**Fig. 28: Micrographs of a cell undergoing meiosis.**

Meiosis is preceded by an interphase where **semi-conservative DNA replication** occurs.

- This process of replication is similar to the semi-conservative DNA replication preceding mitosis. For each chromosome, the result is two **genetically identical** sister chromatids, which remain attached at their centromeres.

- The chromosomes **only replicate once**.

The pair of **centrioles also replicates** during interphase.

Meiosis involves **two successive** nuclear divisions, named **meiosis I** and **meiosis II**.

The two nuclear divisions result in the production **four** haploid daughter cells. This is to ensure that at the end of meiosis, each daughter cell contains only **half the original complement of chromosomes** of the original parent cell.

## 5.1 Stages of Meiosis I

### Prophase I

Prophase I of meiosis lasts longer and is more complex than prophase of mitosis.

Prophase I of meiosis is similar to prophase of mitosis. The following events are also observed in prophase I of meiosis (**Fig. 29**).

- The **nucleolus disappears** and the **nuclear membrane** disintegrates.
- The **chromatin condenses** (i.e. shortens and thickens) until the chromosomes become **discrete**.

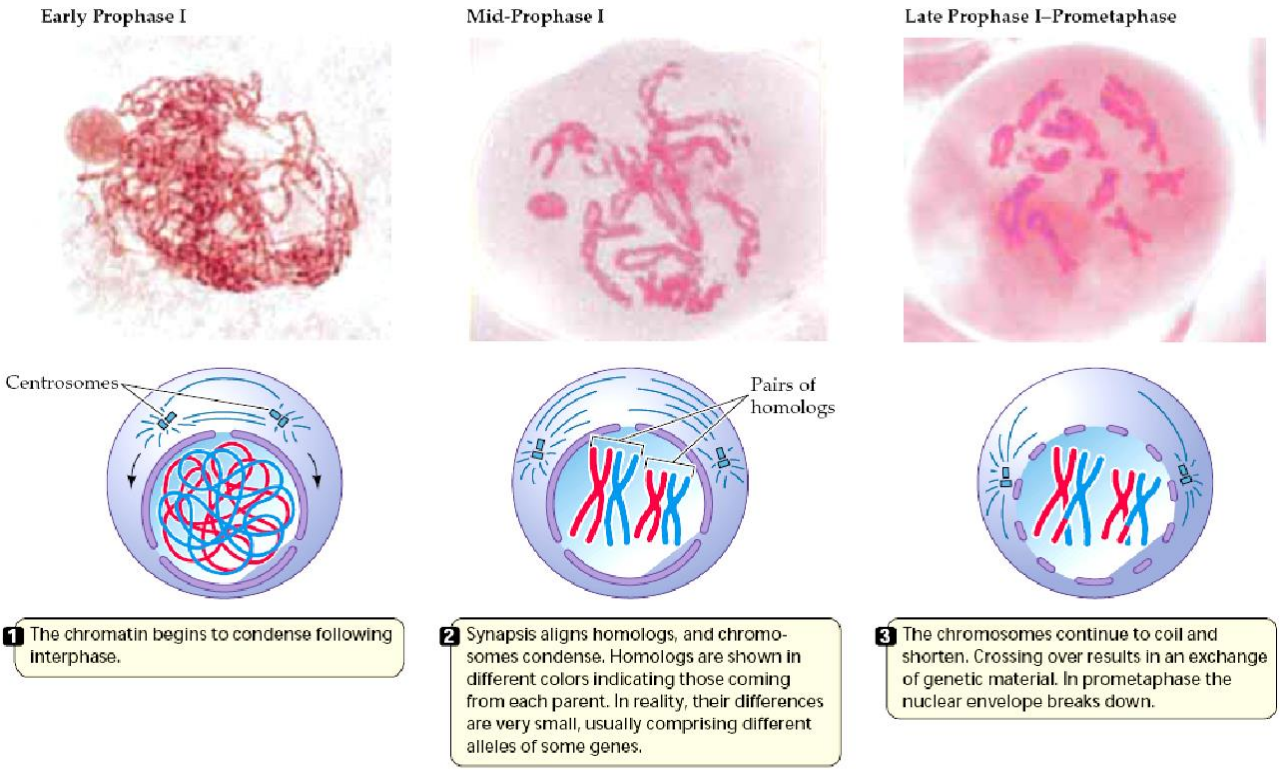



**Fig. 29: The stages of prophase I of meiosis.**

However, there are events that are **unique** to prophase I of meiosis.

- Homologous chromosomes **pair up** to form a **bivalent**. The four chromatids in each bivalent are collectively known as a **tetrad**.

- This physical pairing process is known as **synapsis** (unique to prophase I of meiosis), where the homologues are bridged by the **synaptonemal complex** consisting of proteins and RNA (**Fig. 30**). The process is precise and brings the genes on each chromosome into **precise alignment**.

- The pairing of homologous chromosomes is essential for the **exchange of alleles** during crossing over in prophase I of meiosis.

- **Crossing over occurs during prophase I of meiosis**, where **non-sister chromatids** of homologous chromosomes undergo **exchange of alleles**. As a result, sister chromatids are now **genetically non-identical** and are known as **recombinant chromatids**.

- **Chiasma** (plural: **chiasmata**) refers to the **X-shaped microscopic visible region** where **crossing over** has **occurred** earlier in prophase I of meiosis between **non-sister chromatids of homologous chromosomes.** (**Fig. 31a** and **Fig. 31b**).

- **Chiasmata** may be formed **at one or more points** between **non-sister chromatids** of homologous chromosomes.

- Chiasmata become visible after synapsis ends, with the **two homologues** remaining associated due to sister chromatid cohesion**.**

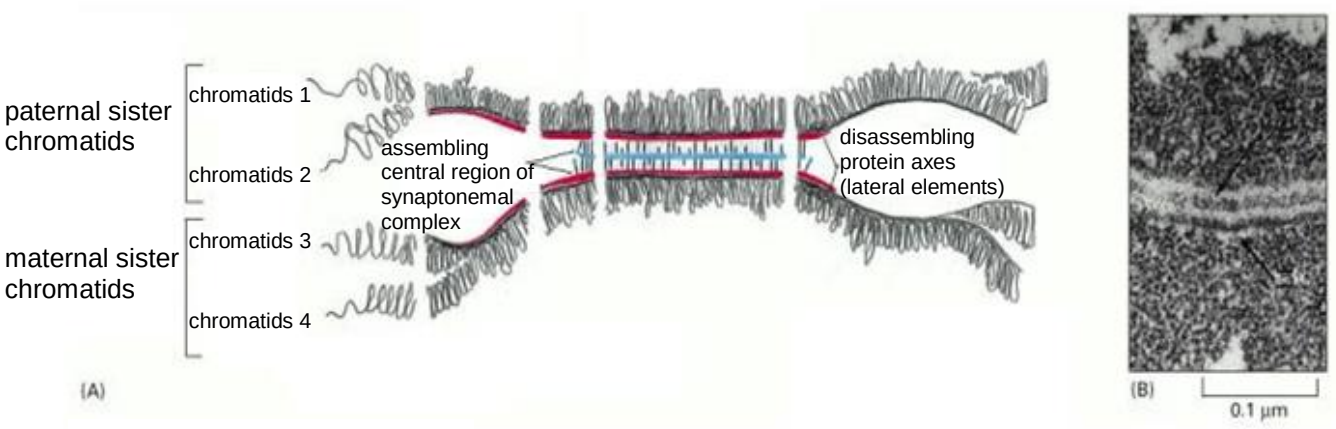



**Fig.30: Synaptonemal complex.**

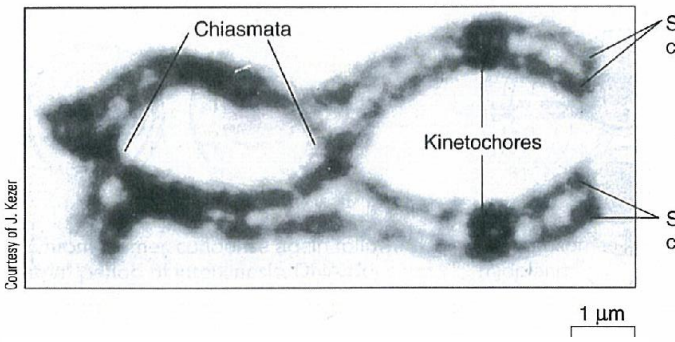



**Fig. 31a: A tetrad during late prophase I of meiosis of a male meiotic cell (spermatocyte) from a salamander.**

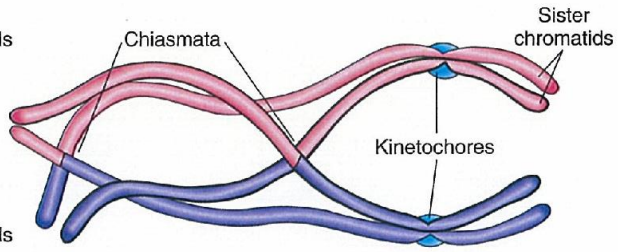



**Fig. 31b: A drawing showing the structure of the tetrad. The paternal chromatids are blue and the maternal chromatids are red.**

## Metaphase I

- **Kinetochore microtubules** attach to the **kinetochore** at the centromere of one chromosome (homologue) of each bivalent, while kinetochore microtubules from the opposite pole attach to the other homologue.

- Homologous chromosomes or bivalents **randomly align** at the **metaphase plate or equatorial plate** (**Fig. 32**).

- **Independent assortment** of homologous chromosomes occurs at this stage. It refers to the fact that when a bivalent lines up on the metaphase plate, the **orientation** of homologues towards the poles in any one bivalent is **random**, and is **independent of that of any other bivalent**.

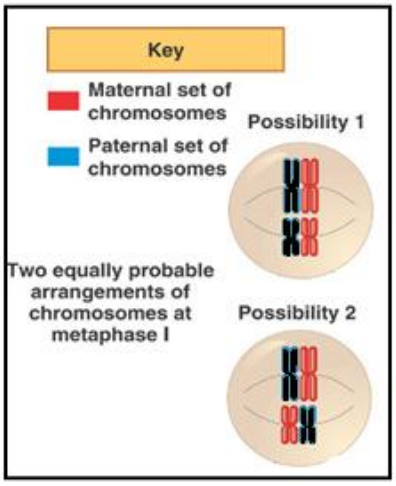



**Fig.32a: A single bivalent is shown.**

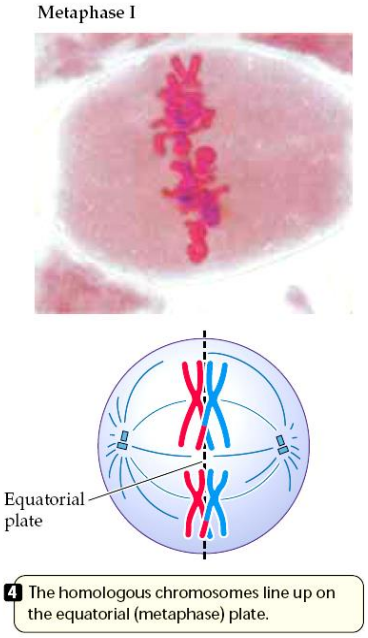



**Fig.32b: Cells at metaphase I of meiosis I.**

## Anaphase I

- The two **homologous chromosomes** of each bivalent **separate** and move towards the opposite poles of the cell.
- **Homologous chromosomes** are **pulled** to opposite **poles** with **centromeres leading**, producing a **characteristic 'V' shape pattern** (**Fig. 33**).

- **The centromeres** in anaphase I of meiosis **remain intact** and the **sister chromatids remain attached to each other**.

- This physical segregation is referred to as **disjunction**, meaning the separation of chromosomes from one another.

- Note that **non-disjunction**, which is the failure of chromosome to separate results in mutation.

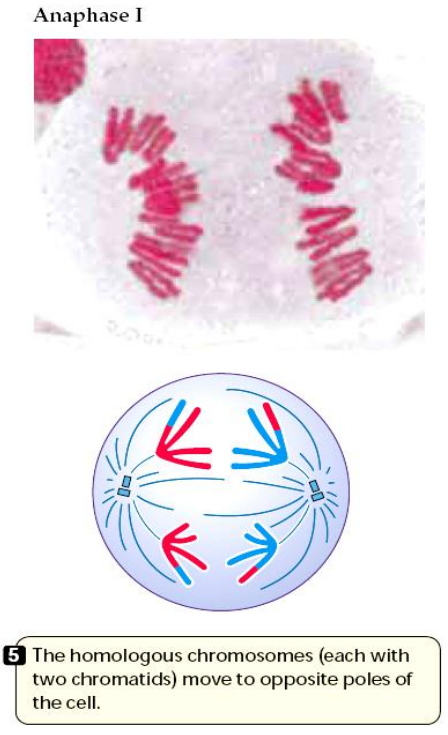



**Fig. 33: Cells at anaphase I of meiosis I.**

**Telophase I**

- Chromosomes arrive at opposite poles of the cell.
- Microtubules usually **disassemble**.
- In animals and some plants, chromatids usually **decondense** and a nuclear envelope **reforms** around each set of chromosomes.

- Nuclei formed are **haploid (n)** because the **chromosome number and ploidy level have been halved** (**Fig. 34**). Each of the chromosomes still exists as **two chromatids** joined at the centromeres, which may not be genetically identical due to crossing over.

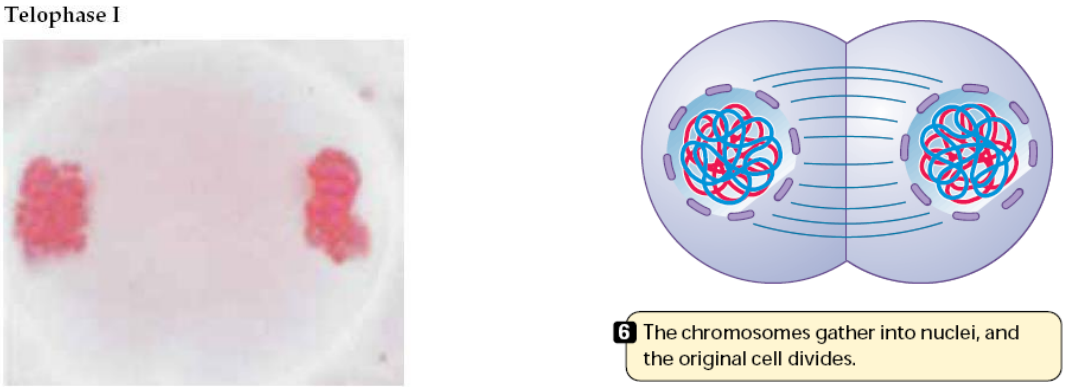



**Fig. 34: Cells at telophase I of meiosis I.**

## 5.2 Cytokinesis I

- **Cytokinesis I occurs simultaneously** with telophase I of meiosis, forming **two haploid (n) daughter cells**.
- Note that cytokinesis I does not occur in all species.

**Meiosis I – Key Concepts**

**Meiosis I** is also known as **reduction division**.

- The **homologous chromosomes separate** into two cells (the sister chromatids do not separate).
- Each daughter cell receives only one homologue of each pair homologous of chromosomes.
- **Chromosome number** and **ploidy level** is reduced by **half**. Daughter cells formed are **haploid (n)**.
- The **amount of DNA** is the **same** as that of the parent cell prior to replication.

The events unique to meiosis occur in meiosis I. These include:

**(a) synapsis and crossing over of homologous chromosomes**, and

**(b)** their **subsequent segregation** to different daughter cells.

## 5.3 Stages of Meiosis II

The second meiotic division usually follows **almost immediately after meiosis I**. Depending on the species, the interphase between the two divisions is either very short or non-existent. Even if interphase is present, note that **no further semi-conservative DNA replication occurs during the interphase between meiosis I and II**.

**Meiosis II** consists of four stages, namely **prophase II**, **metaphase II**, **anaphase II** and **telophase II**.

### Prophase II

- **Nucleoli disperse** and **nuclear envelopes disintegrate** (if formed during telophase I of meiosis).
- **Chromatin undergoes condensation** (i.e. shorten and thicken) to re-form discrete chromosomes (**Fig. 35**).
- In animal cells, centrioles move to opposite **poles** of the cells at the end of prophase II of meiosis.
- New spindle fibres appear and are arranged at **right angles** to the spindle of meiosis I.

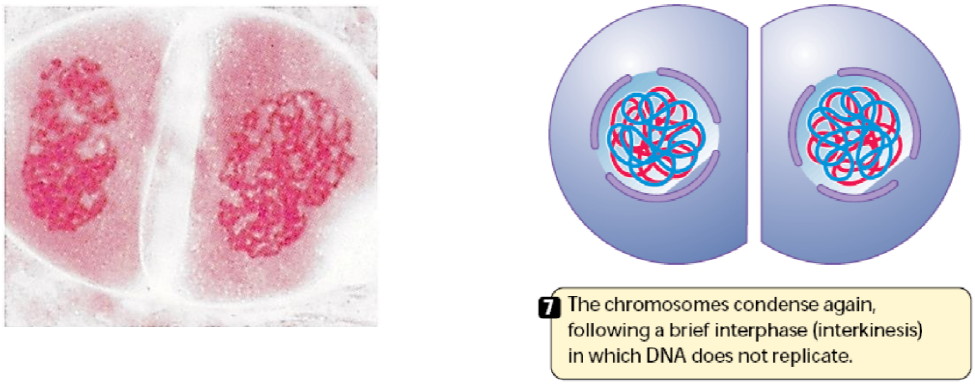



**Fig. 35: Cells at prophase II of meiosis.**

### Metaphase II

- **Kinetochore microtubules attach** to the **kinetochores at the centromeres** of the chromosomes.
- Chromosomes **migrate** and **align singly** at the **metaphase plate / equatorial plate** of the cell (**Fig. 36**).
- Note that the metaphase plate of meiosis II is **perpendicular** to that of meiosis I.

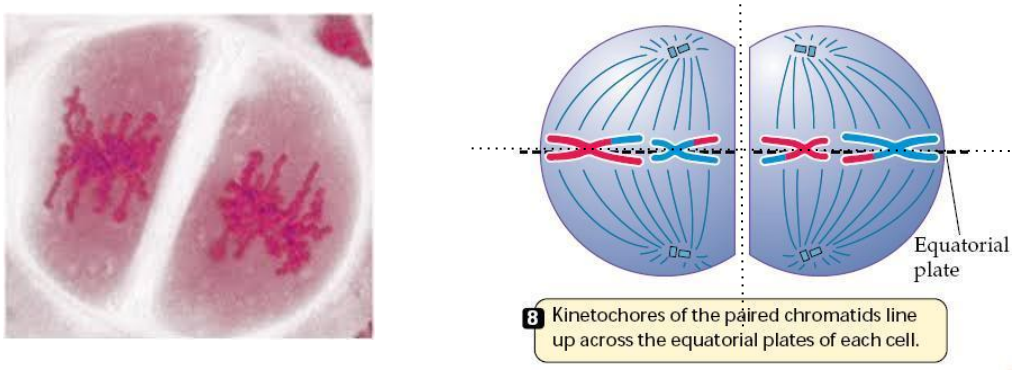


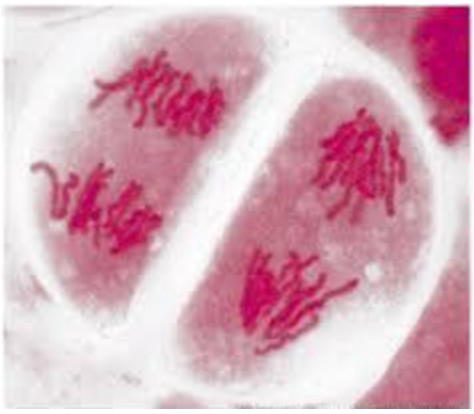

**Fig. 36: Cells at metaphase II of meiosis.**

## Anaphase II

- **Centromeres divide** and the **two chromatids separate and are called daughter chromosomes** (**Fig. 37a**).

- **Daughter chromosomes are pulled** to opposite poles of the cell, **centromeres first/leading** as shown in **Fig. 37b**, as their kinetochore microtubules shorten.

- The poles of the cell move further apart as the **polar microtubules slide past each other,** hence **elongating the cell.**



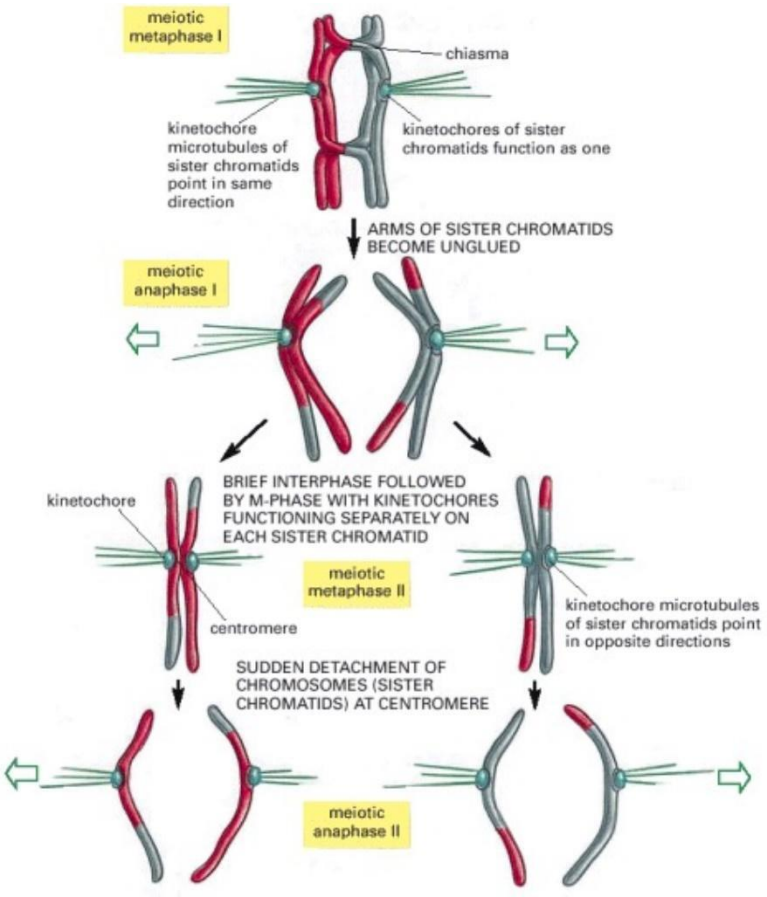
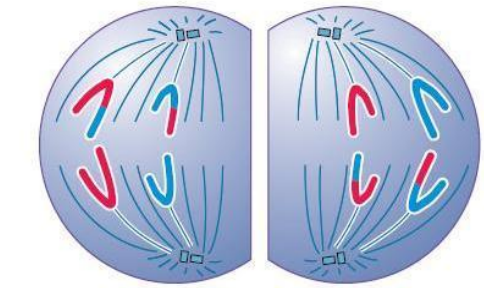



**Fig. 37a: Comparison of the mechanisms of chromosome alignment (at metaphase) and separation (at anaphase) in meiotic division I and meiotic division II.**



9 The chromatids finally separate, becoming chromosomes in their own right, and are pulled to opposite poles. Because of crossing over in prophase I, each new cell will have a different genetic makeup.

**Fig. 37b: Cells at Anaphase II.**

**Telophase II**

- The chromosomes **decondense** into the **chromatin form** by uncoiling.
- Microtubules **disassemble** and a pair of centrioles end up in each daughter cell.
- **Nuclear envelopes reform** around each nucleus (**Fig. 38**).

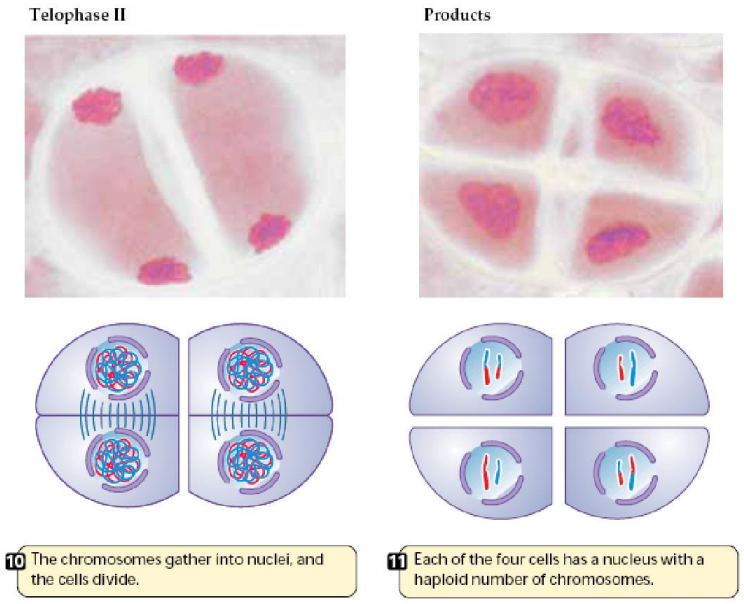



**Fig. 38: Cells at telophase II of meiosis.**

## 5.4 Cytokinesis II

- Cytokinesis produces **four haploid genetically non-identical** daughter cells from the original single diploid parent cell, each with half the chromosome number and ploidy level of a normal somatic cell.

**Meiosis II – Key Concepts**

Due to the **crossing over** that may have occurred during prophase I of meiosis, the **sister chromatids in meiosis II may not be genetically identical to each other.**

Meiosis II is known as **equational division** (equal in chromosomal number).

- The **chromosome number does not change** in this nuclear division.
- However, as a consequence of reduction division in meiosis I, **haploid gamete cells** have **half** the **chromosome number** and **ploidy level** compared to the parent cell.
- The **amount of DNA** in the **daughter cell** is **half** of that of the parent cell before replication.
- This ensures that subsequent fertilisation results in a diploid zygote with a **constant number of chromosomes** characteristic of every somatic cell in the sexually reproducing species.

A summary of the differences between Meiosis I and II is illustrated in **Fig. 39**.

## Summary of Meiosis I and Meiosis II

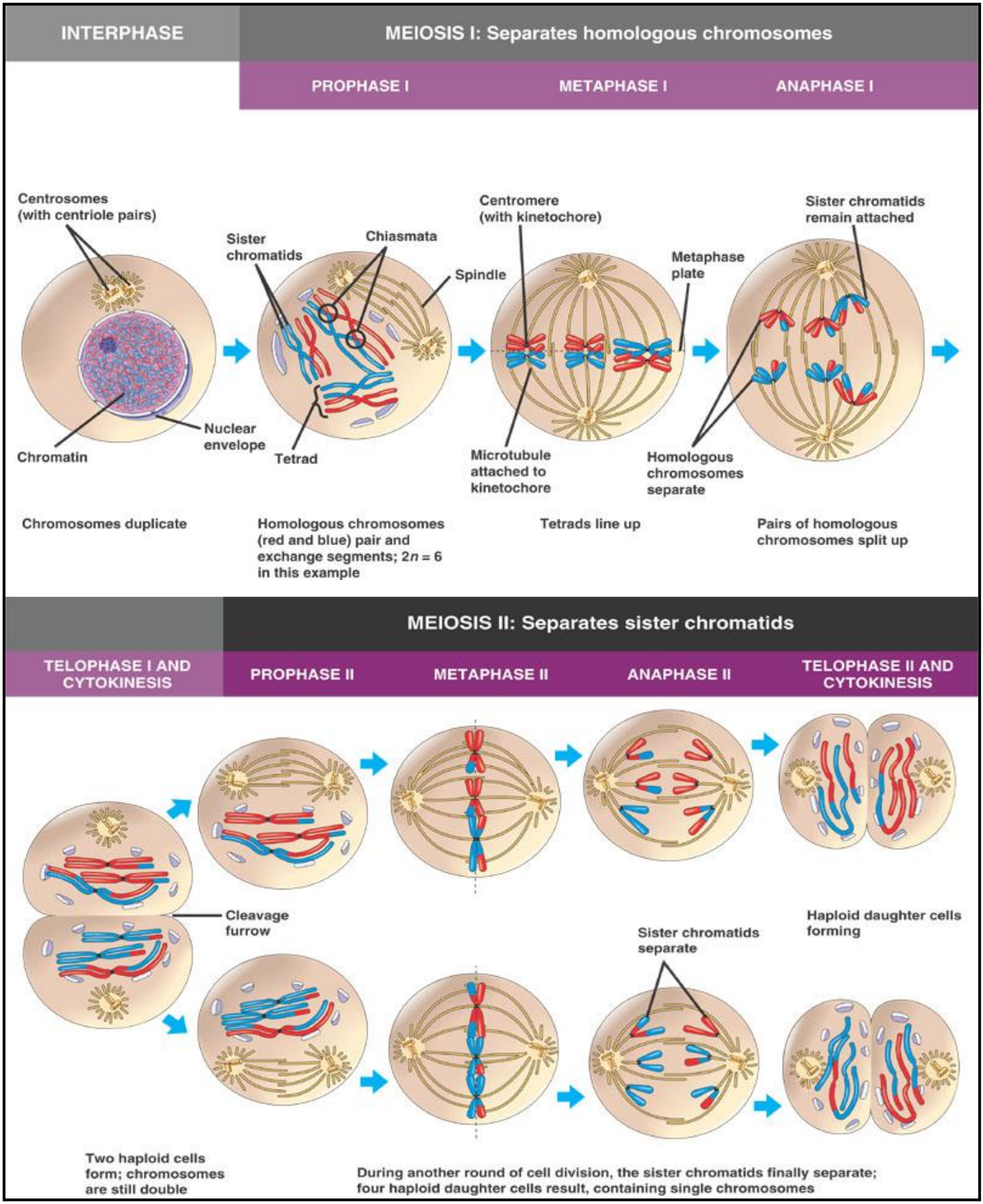



**Fig. 39: Comparison between meiosis I and meiosis II.**

## 5.5 Significance of Stages in Meiosis

| Stage | Chromosomal behaviour | Significance |
|---|---|---|
| **1. To increase genetic variation in gametes** | | |
| **Prophase I** | Formation of bivalents to allow for **crossing over** to occur between the non-sister chromatids of homologous chromosomes. | Gives rise to **new combinations of paternal and maternal alleles** in each chromatid. Homologous chromosome pairs are segregated into different daughter cells. |
| **Metaphase I** | **Independent assortment** of paired homologous chromosomes at the metaphase plate. | **Random distribution** of paternal and maternal chromosomes in each gamete. |
| **2. To distribute half the nuclear DNA to each gamete** | | |
| **Interphase I** | DNA replicates only **once.** | Semi-conservative DNA replication is immediately followed by **two** successive nuclear divisions to produce **haploid cells**. |
| **Metaphase I** | **Alignment** of paired homologous chromosomes at the **metaphase plate.** | To ensure **equal distribution** of chromosomes to each daughter cell in subsequent anaphase I of meiosis. |
| **Anaphase I** | **Segregation** of homologous chromosomes. | ● **Equal distribution** of chromosomes to each daughter cell.<br>● Chromosome number in each of the **two resultant daughter cells** is **halved**.<br>● Ploidy level in each of the two **resultant daughter cells** is **haploid**. |
| **Metaphase II** | Chromosomes align **singly** at the metaphase plate. | ● To ensure **equal distribution** of chromosomes to each gamete.<br>● Ploidy level of each gamete is **haploid**. |

## 5.6 Significance of Meiosis

### 1. Sexual reproduction (production of gametes)

- Meiosis results in the production of gametes with **half the number of chromosomes** in the parent cell in all organisms carrying out sexual reproduction (**Fig. 40**).
- If this does not occur, the fusion of gametes during subsequent fertilisation will result in a **doubling of chromosome number** for each successive generation.
- Meiosis, therefore, **stabilises** and **maintains a constant chromosome number** in every generation of a species.

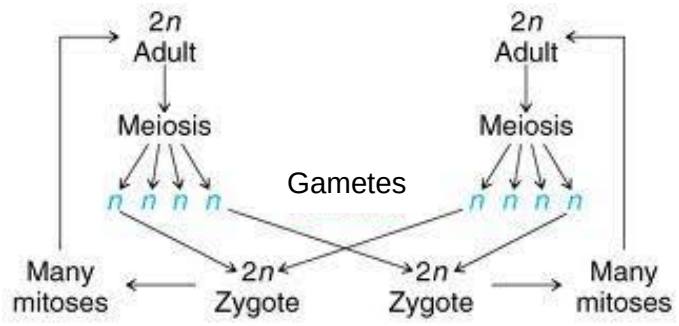



**Fig. 40: Meiosis and ploidy.**

### 2. Genetic variation

Meiosis also allows for **new combinations of alleles** in gametes. This leads to **genetic variation** in the **genotype** and **phenotype** of the offspring produced by the fusion of gametes.

**(a) Crossing over** at prophase I of meiosis

- During **prophase I of meiosis I**, **synapsis** occurs and homologues pairs up along their lengths to form **bivalents**.
- This facilitates **chiasmata formation** and **crossing over** between non-sister chromatids of homologous chromosomes, resulting in **recombination** of segments of non-sister chromatids between homologous chromosomes (**Fig. 41**).

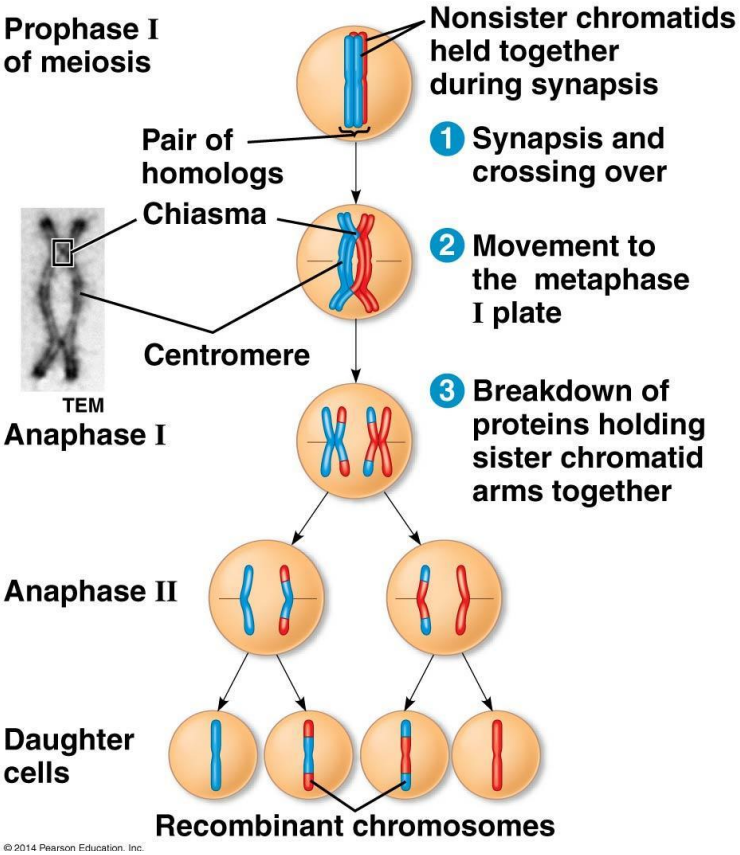



**Fig. 41: Stages of meiosis I and II.**

- This leads to the formation of **new combinations of alleles** on the chromosomes of gametes. The resultant **recombinant sister chromatids** will then carry alleles different from those carried on the non-recombinant sister chromatids.

- Gamete cells that contain the recombinant chromosomes are called **recombinant gametes**, while those that contain the non-recombinant chromosomes are called parental gametes.

**(b) Independent assortment** of homologous chromosomes at metaphase I of meiosis and metaphase II of meiosis II

- At **metaphase I of meiosis**, each pair of homologous chromosomes aligns at the metaphase plate.
- The orientation of the bivalents with respect to the poles is **random**. There is hence a 50% chance that a daughter cell gets a paternal chromosome or a maternal chromosome.

- As the **orientation of one bivalent is independent of another**, the first meiotic division results in random assortment of paternal and maternal chromosomes between nuclei of daughter cells. This is termed **independent assortment**, which is illustrated in **Fig. 42** below.
- Likewise, at metaphase II of meiosis, chromosomes randomly align singly at the metaphase plate. The orientation of one non-sister chromatid (due to crossing over) is independent of the other.

Number of possible combinations of chromosomes in gametes due to independent assortment
= $\underline{\mathbf{2^n}}$ for a diploid organism,
where n = number of pairs of homologous chromosomes.

In humans, the possible number of combinations of chromosomes in gametes produced by one person would then be $\mathbf{2^{23}}$ or about **8 million**!

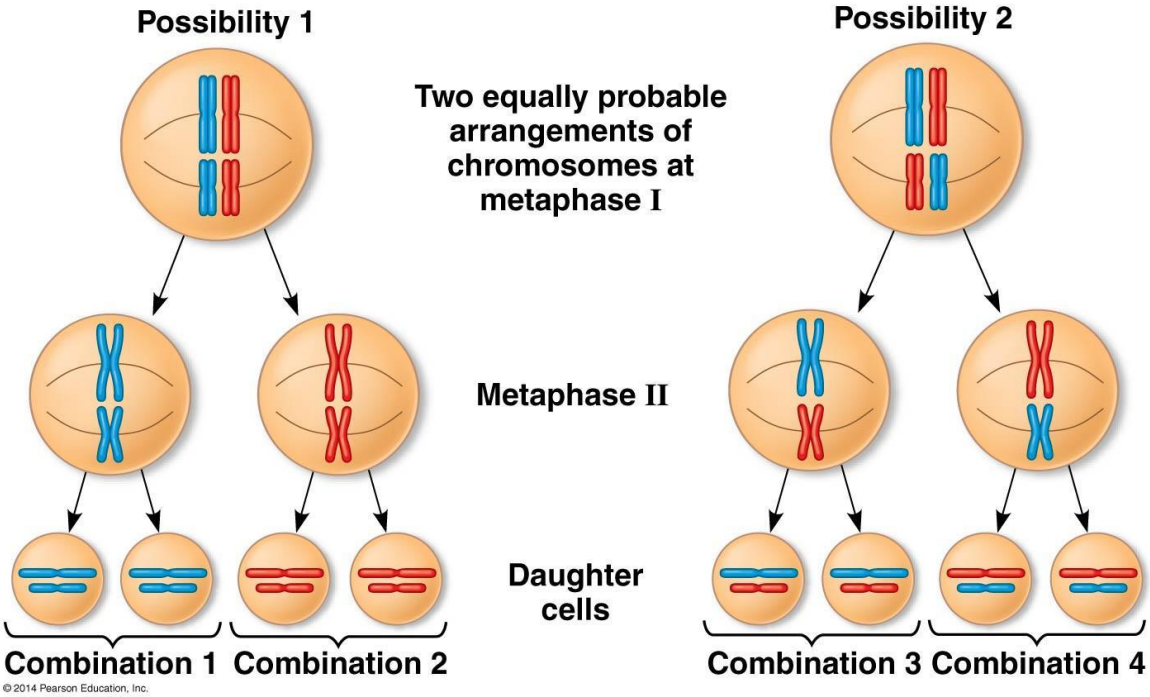



**Fig. 42: Independent assortment.**

**(c) Random fertilisation**

Random fertilisation of gametes carrying **different combinations of chromosomes** adds to genetic variation of the zygote formed.

## 4. Comparing Mitosis and Meiosis

**Similarities**

1. **Interphase** and **semi-conservative DNA replication** precedes both processes.
2. In both processes, **microtubules attach to the kinetochore** to **separate chromosomes**.
3. At the end of both processes, **cytokinesis** takes place.

**Differences (as illustrated in Fig. 43)**

| | Mitosis | Meiosis |
|---|---|---|
| **Prophase** | ● Homologous chromosomes **remain separate.**<br>● **No formation of chiasmata.**<br>● **No crossing over.** | ● Homologous chromosomes **pair up.**<br>● **Chiasmata** form.<br>● **Crossing over** may occur. |
| **Metaphase** | ● Pairs of **sister chromatids** line up on the equatorial plate.<br>OR **Chromosomes** line up **singly** on the equatorial plate.<br>● **No independent assortment** of **homologous chromosomes.** | ● Pairs of **chromosomes** line up on the equatorial plate.<br>● **Independent assortment** between homologous chromosomes. |
| **Anaphase** | ● **Centromeres** divide.<br>● **Sister chromatids** separate.<br>● Separating chromatids are **genetically identical.** | ● **Centromeres** do not divide.<br>● **Homologous chromosomes** separate. Each of the chromosomes that separate consists of two chromatids.<br>● **Separating chromosomes** and their **chromatids may not be genetically identical** due to crossing over. |
| **Telophase & cytokinesis** | ● Daughter cells contain the **same number** of chromosomes as parent cells.<br>● **Both homologues of each pair of homologous chromosomes present** in daughter cells. | ● Daughter cells contain **half the number** of chromosomes present in parent cells.<br>● **Only one homologue of each pair of homologous chromosomes present** in daughter cells. |
| **Occurrence** | ● May occur in haploid, diploid or polyploid cells.<br>● Occurs during the formation of **somatic cells.** | ● Only occurs in diploid or polyploid cells.<br>● Occurs during the **formation of gametes.** |

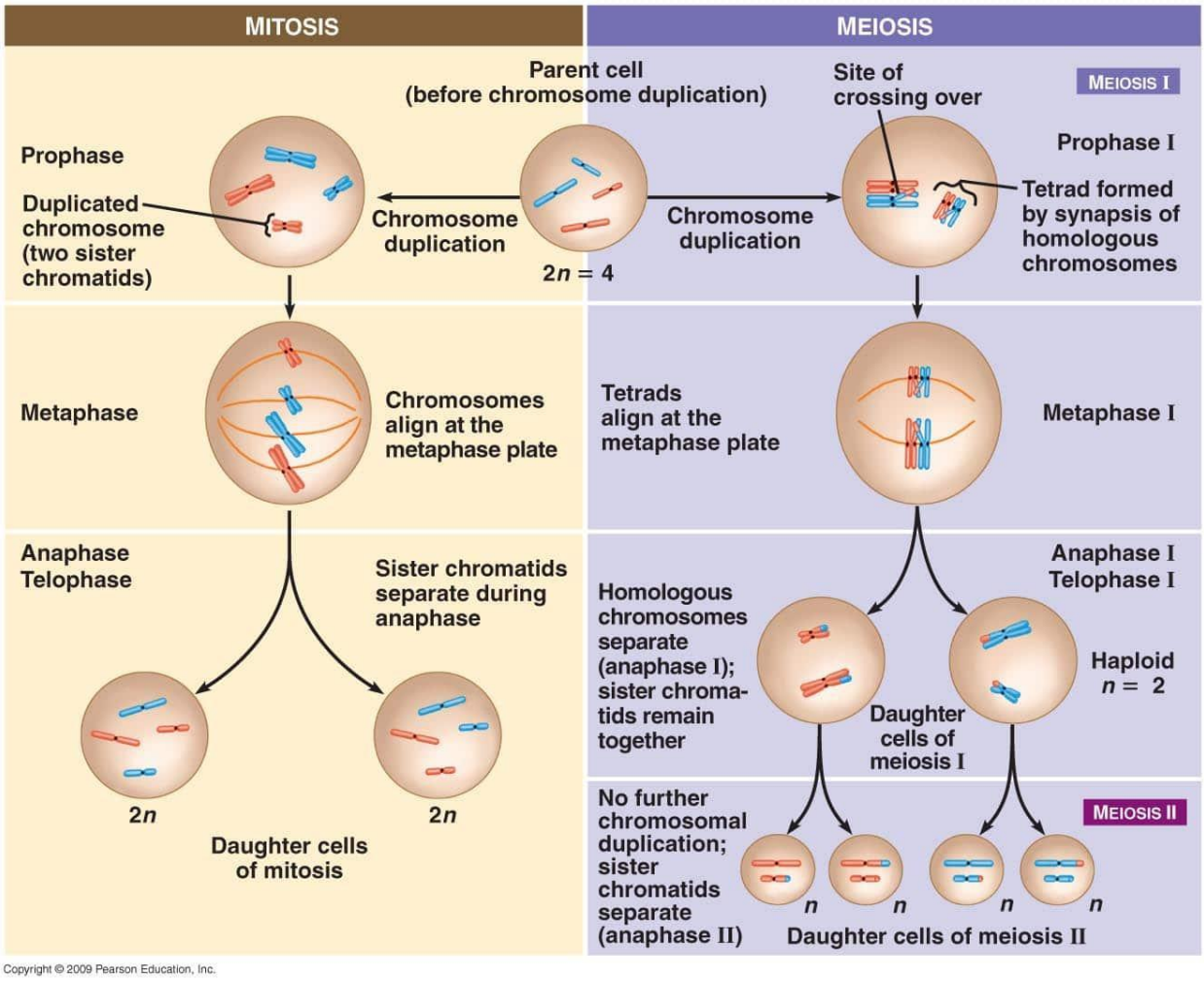



**Fig. 43 Comparison between mitosis and meiosis.**