# Cell Biology

**Unit 4 · Lesson 1 · Cell cycle and division**

The notes for Lesson 1 of Unit 4: chapters 4.1 to 4.3 of the unit book, with their figures, worked examples, exam traps and quizzes, in one file. The full unit book, with every chapter, the exam question bank and the glossary, is linked at the end.

Lesson 1 of 3 | 3 chapters | Chapters 4.1 to 4.3

## About these notes

These are the notes for **Lesson 1 · Cell cycle and division** of the University free n easy video lessons on Cell Biology Unit 4, Cell Cycle, Division and Cell Death. They are chapters 4.1 to 4.3 of the unit book, unchanged, so a page here is the same page in the full book.

## 4.1 Phases of the cell cycle

The cell cycle is the ordered series of events by which one cell grows, copies its DNA exactly once, and divides into two daughter cells. It exists because a human body of roughly 30 trillion cells has to replace worn-out cells every day, from skin to the lining of the gut to blood, without ever losing or doubling a chromosome. The cycle has four phases, G1, S, G2 and M, and a resting state, G0, outside the cycle. Every later chapter of this unit hangs on these names.

> You need: the nucleus and chromatin (Unit 3, Nucleus, nuclear envelope, nuclear pore and nucleolus) and the idea that DNA is packed into chromosomes.

### The four phases and G0

The cycle is split into **interphase** (G1, S and G2), when the cell grows and prepares, and the **M phase**, when it divides. Interphase is not a "resting" stage, though old books call it that; the cell is busiest then.

- **G1 (gap 1)**: the cell grows, makes proteins and organelles, and checks whether the outside signals (growth factors, nutrients, space) say "divide". This is the most variable phase. Late in G1

the cell passes the **restriction point**; after it, the cell goes on to divide even if growth factors are removed.

- **S (synthesis)**: the cell replicates its DNA. Each chromosome becomes two identical **sister chromatids** held together by a protein ring called **cohesin**. The centrosome is also duplicated in this window.
- **G2 (gap 2)**: the cell checks that replication is complete and the DNA is undamaged, makes the proteins of the spindle, and keeps growing.
- **M (mitosis)**: the nucleus divides (mitosis, Chapter 4.2) and then the cytoplasm divides (**cytokinesis**).
- **G0**: a cell that leaves G1 and stops cycling. Some cells stay in G0 for life (most neurons, cardiac muscle cells); others, such as liver cells (hepatocytes) and resting lymphocytes, can return to G1 when stimulated.

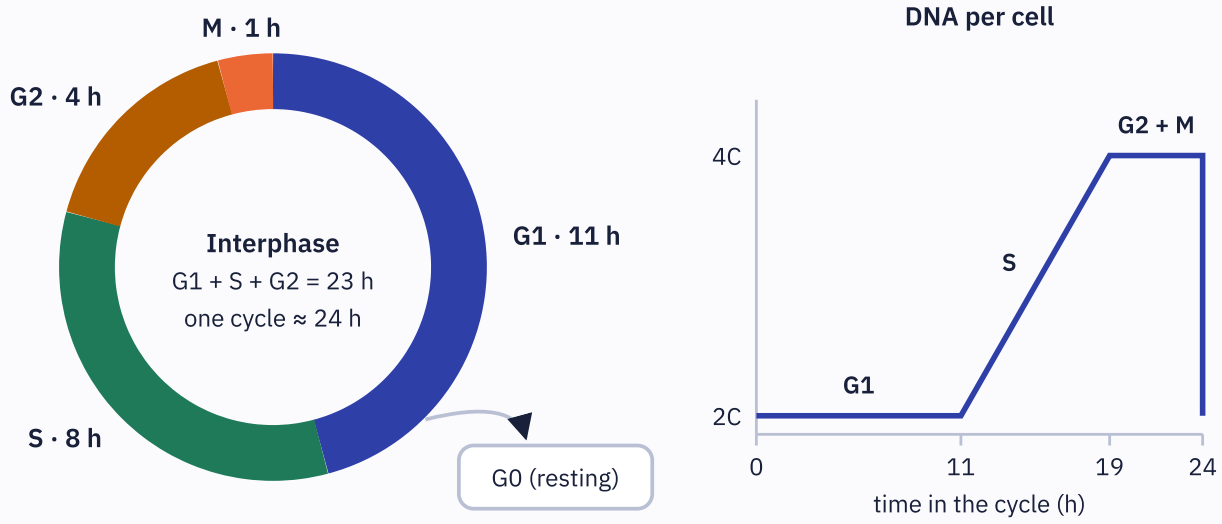



**Figure 4.1.1** Left: the cycle of a typical proliferating human cell in culture drawn as a 24 hour clock; M is the thin slice at the top. Right: DNA per cell stays at 2C through G1, climbs during S, and stays at 4C until the cell divides. Notice that DNA doubles in S, not in mitosis.

## How long each phase takes

A typical proliferating human cell in culture takes about 24 hours per cycle: roughly 11 hours in G1, 8 hours in S, 4 hours in G2 and 1 hour in M (from memory of the standard textbook values; check). Two things matter for the exam. First, M is short, so in any field of view under the microscope most cells are in interphase. Second, the length of the whole cycle is set mainly by G1. Early frog embryo cells skip the gaps and alternate S and M in about 30 minutes, while some adult cells sit in G0 for years.

The **DNA content** per cell is written in units of C, where 1C is the DNA of one haploid set. A diploid human cell in G1 is 2C (46 chromosomes, one chromatid each); after S it is 4C (still 46

chromosomes, now two chromatids each). The chromosome number does not change in S; only the chromatid number and the DNA amount do. Flow cytometry measures this DNA content cell by cell and gives the familiar 2C peak, 4C peak and the S-phase valley between them (see Unit 6, Flow cytometry).

## Measuring the phases in the lab

In an asynchronous culture (cells at every stage, growing steadily), the fraction of cells you see in a phase is close to the fraction of the cycle that phase takes. So if T is the cycle time:

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duration of a phase ≈ (fraction of cells in that phase) × T
mitotic index (MI) = cells in mitosis ÷ total cells counted
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This is an approximation: a dividing culture has slightly more young cells (in G1) than old ones, so the exact formula has a correction factor, but university exams use the simple form. Other methods: labelling with a thymidine analogue such as BrdU or EdU marks cells in S; staining with propidium iodide gives DNA content; and a protein such as Ki-67 marks any cell in the cycle, not in G0.

WORKED EXAMPLE

**Question (6 marks).** A culture of human cells doubles every 20 h. Of 1,000 cells counted, 600 are in G1, 280 have intermediate DNA content (between 2C and 4C), 90 have 4C DNA and are not condensed, and 30 are in mitosis. (a) Find the mitotic index. (b) Estimate the length of each phase. (c) What is the DNA content and chromosome number of a G2 cell?

1. Mitotic index: MI = 30 ÷ 1,000 = 0.03, or 3%.
2. Assign the groups: 2C cells are in G1, intermediate cells are in S, 4C uncondensed cells are in G2, and the 30 condensed cells are in M. Check: 600 + 280 + 90 + 30 = 1,000.
3. G1 ≈ 0.60 × 20 h = 12 h. S ≈ 0.28 × 20 h = 5.6 h. G2 ≈ 0.09 × 20 h = 1.8 h. M ≈ 0.03 × 20 h = 0.6 h (36 min).
4. Check the sum: 12 + 5.6 + 1.8 + 0.6 = 20 h.
5. A G2 cell has finished replication, so it holds 4C DNA but still 46 chromosomes, each made of two sister chromatids (92 chromatids).

**Answer:** MI = 3%; G1 ≈ 12 h, S ≈ 5.6 h, G2 ≈ 1.8 h, M ≈ 0.6 h; a G2 cell is 4C with 46 chromosomes.

## EXAM TRAPS

- "Interphase is the resting phase" is wrong. G0 is the resting state; interphase is when growth and DNA synthesis happen.
- Chromosome number stays 46 through S and G2. DNA content goes from 2C to 4C. Do not write "92 chromosomes" for a G2 cell; write "46 chromosomes, 92 chromatids".
- G0 is outside the cycle, not a fifth phase between G2 and M. Cells enter G0 from G1.
- Cytokinesis is part of the M phase but is not the same as mitosis; mitosis is the division of the nucleus.
- Favourite question: "With a neat diagram, describe the phases of the cell cycle." Draw the circle with all four phases, G0, and mark the restriction point in late G1.

## CHECK YOURSELF

– REMEMBER **Name the four phases of the eukaryotic cell cycle in order.** 2 marks

G1, S, G2 and M (M = mitosis followed by cytokinesis). G1, S and G2 together form interphase.

– REMEMBER **What is G0? Give one example of a cell that stays in it.** 2 marks

A non-dividing state entered from G1, outside the cycle. Mature neurons and cardiac muscle cells stay in G0; hepatocytes can return to G1 after injury.

– UNDERSTAND **Why are most cells in a root-tip squash seen in interphase?** 2 marks

Because interphase takes most of the cycle time (about 23 of 24 hours in a typical human cell) and mitosis is short, so at any moment most cells are in interphase.

– UNDERSTAND **What changes and what stays the same in S phase?** 3 marks

DNA content doubles (2C to 4C) and each chromosome becomes two sister chromatids held by cohesin; the centrosome duplicates. The chromosome number (46 in humans) stays the same.

– APPLY **A culture has T = 18 h and a mitotic index of 5%. How long is M?** 2 marks

M ≈ 0.05 × 18 h = 0.9 h, about 54 minutes.

– APPLY **A flow cytometry plot shows 70% of cells at 2C, 10% at 4C and 20% in between. Which phases are these?** 3 marks

2C = G1 (and any G0 cells); in between = S; 4C = G2 plus M, which DNA content alone cannot separate.

– ANALYZE **Two cell types have the same S, G2 and M times but different cycle times. Which phase differs, and why is that expected?** 4 marks

G1 differs. G1 is the phase where the cell reads growth signals and decides whether to divide, so it absorbs most of the variation between cell types; S, G2 and M are relatively fixed.

BEYOND THE SYLLABUS

Live-cell imaging now follows single cells through many cycles using fluorescent reporters such as FUCCI, which colour cells red in G1 and green in S/G2/M. Single-cell RNA sequencing assigns a cycle phase to every cell in a tissue from its gene expression, and analysis tools routinely "regress out" this cell-cycle signal. Cancer pathologists use Ki-67 staining to grade how fast a tumour grows. None of this is for the exam; search "FUCCI reporter" and "Ki-67 proliferation index" to read further.

## 4.2 Mitosis

Mitosis is the division of a nucleus into two nuclei that each receive one copy of every chromosome. It follows S phase, where every chromosome was copied into two sister chromatids, and its whole job is to pull those sisters apart to opposite ends of the cell before the cytoplasm splits. The result is two daughter cells genetically identical to the parent. Mitosis builds the body from a zygote, heals wounds, and renews skin and blood; when it goes wrong, cells gain or lose chromosomes, which is common in cancer.

You need: 4.1 Phases of the cell cycle (sister chromatids, 2C and 4C) and microtubules (Unit 3, Cytoskeleton: microtubules, actin and intermediate filaments).

### The machinery: chromatids, kinetochores and the spindle

Each replicated chromosome has two **sister chromatids** joined along their length by **cohesin** and most tightly at the **centromere**. On each centromere sits a protein plate, the **kinetochore**, one per chromatid, which grips microtubules. The **mitotic spindle** is built from microtubules that grow out of two **centrosomes** (in animal cells each holds a pair of centrioles). There are three kinds of spindle microtubules: **kinetochore microtubules** that attach to chromosomes, **polar (interpolar) microtubules** that overlap in the middle and push the poles apart, and **astral microtubules** that anchor the poles to the cell cortex.

## The stages, step by step

1. **Prophase.** Chromatin condenses into visible chromosomes, helped by the protein complex **condensin**. The two centrosomes move apart and the spindle begins to form. The nucleolus fades.
2. **Prometaphase.** The nuclear envelope breaks down when CDK1 phosphorylates the nuclear lamins. Spindle microtubules can now reach the chromosomes and capture kinetochores. Chromosomes jerk back and forth as attachments are made and corrected.
3. **Metaphase.** All chromosomes line up on the **metaphase plate**, the plane midway between the poles, with the two sister kinetochores attached to opposite poles (bi-orientation). The cell waits here until every kinetochore is attached (the spindle checkpoint, Chapter 4.5). Chromosomes are most condensed now, which is why karyotypes are made from metaphase cells.
4. **Anaphase.** The enzyme **separase** cuts cohesin, so the sisters separate at once; each chromatid is now called a chromosome. In **anaphase A** the kinetochore microtubules shorten and pull chromosomes to the poles. In **anaphase B** the polar microtubules slide apart and push the poles further away.
5. **Telophase.** The chromosomes reach the poles and decondense. A nuclear envelope re-forms around each set, and the nucleoli reappear. There are now two nuclei in one cell.
6. **Cytokinesis.** In animal cells a **contractile ring** of actin and myosin II pinches the cell in two along a **cleavage furrow**. In plant cells, which have a rigid wall, vesicles from the Golgi gather at the middle on a structure called the **phragmoplast** and fuse into a **cell plate**, which becomes the new wall.

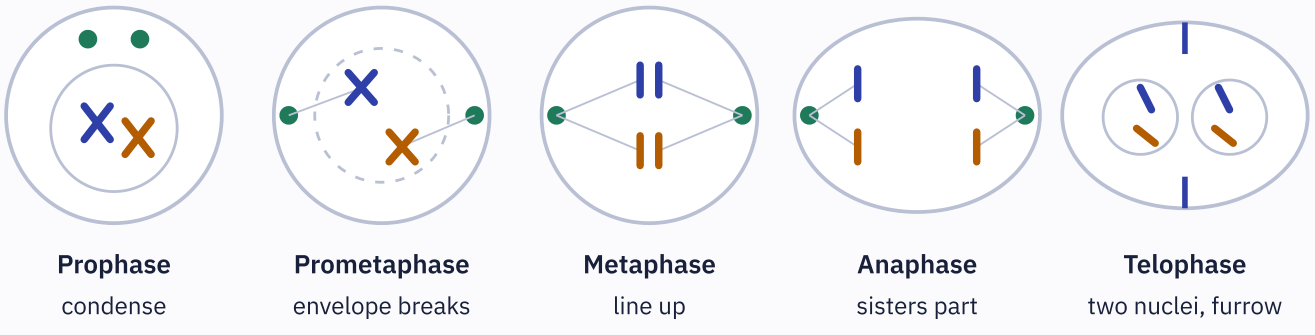



**Figure 4.2.1** Mitosis with two chromosomes (blue and orange); green dots are centrosomes. In metaphase the two sister chromatids of each chromosome face opposite poles; in anaphase they move apart, so each daughter nucleus gets one blue and one orange chromosome. The short bars in telophase mark the cleavage furrow.

## Why mitosis matters, and how it is studied

Mitosis keeps the chromosome number constant (2n → 2n) and the genetic content identical, which is what growth, repair and asexual reproduction need. The classic practical is the **onion root-tip squash**: the tip of an *Allium cepa* root (2n = 16) is fixed, softened in acid, stained (acetocarmine or orcein) and squashed, and cells at each stage are counted. Drugs that bind tubulin, such as **colchicine**, stop spindle formation and trap cells in metaphase; this is used to collect metaphase chromosomes for karyotyping. The anticancer drug **paclitaxel (taxol)** does the opposite, freezing microtubules so they cannot shorten, and it also blocks mitosis.

### WORKED EXAMPLE

**Question (6 marks).** An onion root cell has 2n = 16. (a) Give the number of chromosomes, chromatids and the DNA content (in C) of one cell in G1, metaphase, and anaphase, and of one daughter cell after cytokinesis. (b) In a squash, 52 of 400 cells are in some stage of mitosis. Find the mitotic index.

| STAGE | CHROMOSOMES | CHROMATIDS | DNA |
|---|---|---|---|
| G1 | 16 | 16 | 2C |
| Metaphase | 16 | 32 | 4C |
| Anaphase (whole cell) | 32 | 32 | 4C |
| Daughter cell | 16 | 16 | 2C |

1. After S phase each of the 16 chromosomes has two chromatids, so metaphase has 16 chromosomes, 32 chromatids, 4C.
2. In anaphase the sisters separate and each is counted as a chromosome: 32 chromosomes in one cell, still 4C, until the cell divides.
3. Each daughter receives 16 chromosomes of one chromatid each: 2C, like the parent in G1.
4. Mitotic index = 52 ÷ 400 = 0.13 = 13%.

## EXAM TRAPS

- In anaphase a human cell briefly has 92 chromosomes (an onion cell 32). Examiners love this; count separated chromatids as chromosomes.
- Mitosis is nuclear division; cytokinesis is cytoplasmic division. Some cells (osteoclasts, early insect embryos) do mitosis without cytokinesis and become multinucleate.
- Plant cells have no centrioles and no cleavage furrow; they build a cell plate from the inside out.
- Colchicine arrests cells in metaphase by preventing spindle assembly; it does not "break chromosomes".
- Do not write "chromosomes replicate in prophase". Replication happened earlier, in S phase.

## CHECK YOURSELF

– REMEMBER **List the stages of mitosis in order.** 2 marks

Prophase, prometaphase, metaphase, anaphase, telophase; cytokinesis follows. Some books merge prometaphase into prophase.

– REMEMBER **Which enzyme cuts cohesin at anaphase?** 1 mark

Separase.

– UNDERSTAND **Distinguish anaphase A from anaphase B.** 3 marks

Anaphase A: kinetochore microtubules shorten and pull chromosomes to the poles. Anaphase B: polar microtubules slide apart (and astral microtubules pull) so the poles move further apart.

– UNDERSTAND **How does cytokinesis differ in plant and animal cells?** 4 marks

Animal: an actin–myosin contractile ring forms a cleavage furrow that pinches the cell from outside in. Plant: Golgi vesicles collect at the phragmoplast and fuse into a cell plate that grows from the centre out to the old wall.

– APPLY **A cell with 2n = 8 is in metaphase of mitosis. How many kinetochores does it have?** 2 marks

One kinetochore per chromatid: 8 chromosomes × 2 chromatids = 16 kinetochores.

– APPLY **Why would you treat cells with colchicine before making a karyotype?** 2 marks

Colchicine blocks spindle assembly, so cells pile up in metaphase, when chromosomes are most condensed and easiest to count and band.

– ANALYZE **A drug lets cells enter mitosis but chromosomes never separate, although the spindle looks normal. Suggest two targets.** 4 marks

Separase (cannot cut cohesin) or the APC/C (cannot destroy securin, which keeps separase inactive). A non-cleavable cohesin would give the same result.

BEYOND THE SYLLABUS

Errors in mitosis produce aneuploid cells, and most solid tumours are aneuploid. Live imaging of fluorescent histones and tubulin lets researchers measure how long each cell spends in each stage, and drug screens look for compounds that stop mitosis only in cancer cells, for example inhibitors of the mitotic kinases Aurora and Polo-like kinase 1. This is not for the exam; search "chromosomal instability" and "PLK1 inhibitor" to go further.

## 4.3 Meiosis

Meiosis is the special division that makes gametes (sperm and eggs in animals, spores in plants). One round of DNA replication is followed by two divisions, so one diploid cell (2n) gives four haploid cells (n). Halving the chromosome number keeps it constant from generation to generation when two gametes fuse at fertilization. On the way, meiosis shuffles the parents' chromosomes and swaps pieces between them, so every gamete is genetically unique. This is the cellular basis of Mendel's laws and of most variation in a population.

You need: 4.2 Mitosis (chromatids, kinetochores, the spindle). Meiosis reuses the same machinery with a few key changes.

### Homologues, bivalents and crossing over

A diploid cell has two copies of each chromosome, one from the mother and one from the father. These two are **homologous chromosomes** (homologues): same genes in the same order, possibly different alleles. In mitosis homologues act independently. In meiosis I they find each other and pair along their length (**synapsis**), held by a protein zipper called the **synaptonemal complex**. A paired set is a **bivalent**, also called a **tetrad** because it has four chromatids. Inside the bivalent, non-sister chromatids break and rejoin with each other: this is **crossing over**, and the visible cross-shaped point where they remain linked is a **chiasma** (plural chiasmata).

Chiasmata also hold the homologues together until anaphase I, so they are needed for correct separation.

## Meiosis I: the reductional division

Prophase I is long and is split into five substages, a favourite exam list:

1. **Leptotene**: chromosomes condense into thin threads.
2. **Zygotene**: homologues pair; the synaptonemal complex starts to form (synapsis).
3. **Pachytene**: synapsis is complete; crossing over takes place at recombination nodules.
4. **Diplotene**: the synaptonemal complex dissolves and homologues pull apart except at chiasmata, which become visible. Human oocytes pause here (the dictyotene stage) from before birth until ovulation, years later.
5. **Diakinesis**: chromosomes condense fully, chiasmata move toward the chromosome ends (terminalization), the nucleolus and nuclear envelope disappear.

In **metaphase I** the bivalents, not single chromosomes, line up on the plate. Both sister kinetochores of one homologue face the same pole, and the two homologues face opposite poles. Each bivalent orients independently of the others: this is **independent assortment**. In **anaphase I** the homologues separate and move to opposite poles; the sister chromatids stay joined because the cohesin at the centromere is protected (by a protein called shugoshin). **Telophase I** and cytokinesis give two cells, each with n chromosomes, each chromosome still made of two chromatids. Meiosis I is therefore the division that halves the number.

## Meiosis II: the equational division

After a short pause (**interkinesis**) with **no DNA replication**, each cell divides again. Meiosis II works like mitosis: chromosomes line up singly at metaphase II, the centromeric cohesin is cut, and sister chromatids go to opposite poles at anaphase II. The result is four haploid cells, each with n single-chromatid chromosomes (1C DNA). Because of crossing over, the two sisters were no longer identical, so all four products differ.

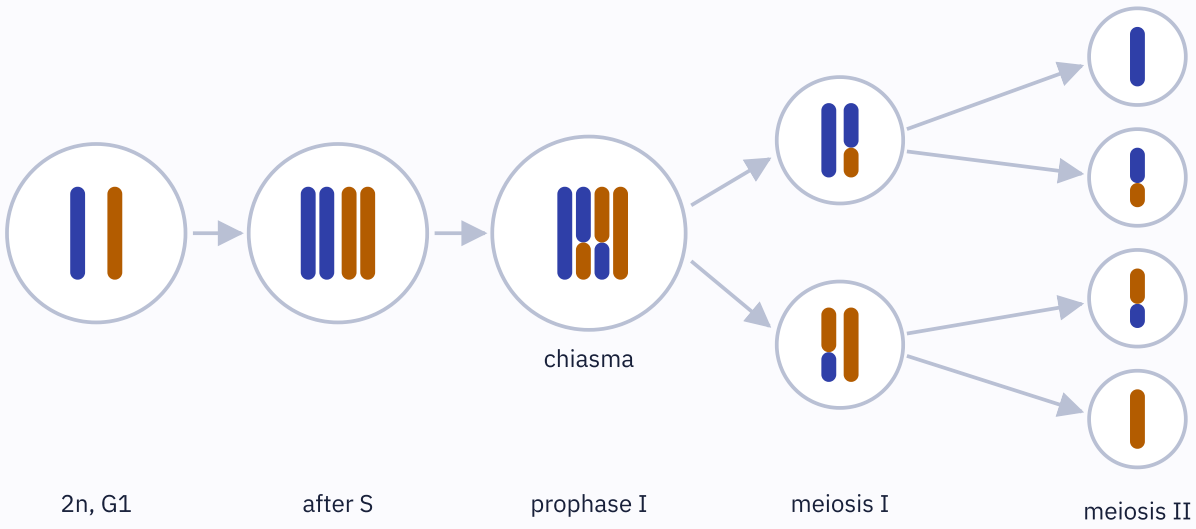



**Figure 4.3.1** One homologous pair (blue from the mother, orange from the father). After S each homologue has two chromatids; in prophase I they pair and two non-sister chromatids exchange their lower ends (the chiasma). Meiosis I separates the homologues; meiosis II separates the sisters. Notice that the four haploid cells are all different.

## Why it matters: variation and errors

Three sources of variation follow from meiosis and fertilization. **Independent assortment**: with n pairs, a parent can make $2^n$ chromosome combinations; for humans (n = 23) that is $2^{23}$ = 8,388,608, before any crossing over. **Crossing over** creates new allele combinations within each chromosome. **Random fertilization** pairs any sperm with any egg: $2^{23} \times 2^{23} \approx 7 \times 10^{13}$ possible zygotes from one couple, still ignoring crossing over.

When homologues (in meiosis I) or sisters (in meiosis II) fail to separate, a gamete gets an extra or missing chromosome. This is **nondisjunction**. A gamete with two copies of chromosome 21 fertilized by a normal one gives trisomy 21 (Down syndrome); the risk rises with maternal age, partly because oocytes stay arrested in prophase I for decades. In males one spermatocyte gives four sperm; in females one oocyte gives one egg and two or three small polar bodies.

| FEATURE | MITOSIS | MEIOSIS |
|---|---|---|
| Divisions after one S phase | one | two |
| Daughter cells | 2, diploid, identical | 4, haploid, all different |
| Pairing of homologues | no | yes (prophase I) |
| Crossing over | no (rare) | yes |
| At metaphase plate | single chromosomes | bivalents (I), single chromosomes (II) |

| FEATURE | MITOSIS | MEIOSIS |
|---|---|---|
| Where | somatic cells | germ cells in gonads, plant sporangia |

### WORKED EXAMPLE

**Question (6 marks).** A cell has 2n = 8. Give the chromosome number, chromatid number and DNA content (C) per cell at: G1, metaphase I, end of telophase I, and end of telophase II. How many chromosome combinations can its gametes have without crossing over?

| STAGE | CHROMOSOMES | CHROMATIDS | DNA |
|---|---|---|---|
| G1 (before S) | 8 | 8 | 2C |
| Metaphase I | 8 (as 4 bivalents) | 16 | 4C |
| After telophase I (each cell) | 4 | 8 | 2C |
| After telophase II (each cell) | 4 | 4 | 1C |

1. S doubles DNA (2C → 4C) and chromatids (8 → 16) but not chromosomes.
2. Meiosis I separates homologues: chromosome number halves to 4; each still has two chromatids, so 8 chromatids and 2C.
3. Meiosis II separates sisters: 4 chromosomes, 4 chromatids, 1C.
4. Combinations: n = 4 pairs, so $2^4 = 16$.

### EXAM TRAPS

- The chromosome number halves in meiosis I, not meiosis II. Meiosis II halves the DNA content (2C → 1C) but not the number.
- There is no S phase between meiosis I and II. Interkinesis is not interphase.
- Crossing over happens in pachytene; chiasmata become visible in diplotene. Do not swap these.
- Crossing over is between non-sister chromatids of homologues, not between sister chromatids.
- $2^n$ uses the haploid number n: humans give $2^{23}$, not $2^{46}$.

## CHECK YOURSELF

- REMEMBER **Name the five substages of prophase I in order.** 2 marks

  Leptotene, zygotene, pachytene, diplotene, diakinesis.

- REMEMBER **What is the synaptonemal complex?** 2 marks

  A protein structure that zips homologous chromosomes together along their length during zygotene and pachytene.

- UNDERSTAND **Why is meiosis I called reductional and meiosis II equational?** 3 marks

  Meiosis I separates homologues, halving the chromosome number (2n → n). Meiosis II separates sister chromatids; the chromosome number stays n in each product, like mitosis.

- UNDERSTAND **Give two roles of chiasmata.** 2 marks

  They are where crossing over has joined non-sister chromatids (recombination), and they hold homologues together so the bivalent orients correctly and separates properly at anaphase I.

- APPLY **A plant has 2n = 24. How many bivalents form, and how many chromosomes are in each pollen grain nucleus?** 2 marks

  12 bivalents; each haploid product has 12 chromosomes.

- APPLY **Nondisjunction of chromosome 21 happens in meiosis I in a mother. What fraction of her gametes from that cell carry two copies?** 3 marks

  In meiosis I both homologues go to one cell; after meiosis II that cell's two products each carry two copies of chromosome 21, and the other two carry none. So 2 of 4 have two copies (though in oogenesis only one becomes the egg).

- ANALYZE **A mutant lacks the protection of centromeric cohesin in meiosis I. What goes wrong?** 4 marks

  Sister chromatids separate too early, at anaphase I, along with the homologues. In meiosis II there are single chromatids with nothing to pair them, so they segregate randomly and many gametes become aneuploid.

BEYOND THE SYLLABUS

Recombination in meiosis starts with deliberate DNA double-strand breaks made by an enzyme called Spo11, which are then repaired using the homologue; this links meiosis to DNA repair biology. Geneticists use crossover frequencies to build linkage maps, and fertility clinics screen embryos for aneuploidy. Not for the exam; search "Spo11 double-strand break" and "maternal age aneuploidy" to read further.

## Key terms of this lesson

| TERM | MEANING OR FORMULA | CHAPTER |
|---|---|---|
| Cell cycle | G1 → S → G2 → M; G0 = resting, entered from G1 | 4.1 |
| Phase length | duration ≈ (fraction of cells in phase) × cycle time T | 4.1 |
| Mitotic index | cells in mitosis ÷ total cells counted | 4.1, 4.2 |
| DNA content | 2C in G1, 4C in G2/M, 1C in a gamete | 4.1, 4.3 |
| Mitosis | prophase, prometaphase, metaphase, anaphase, telophase; 2n → 2n | 4.2 |
| Meiosis | meiosis I separates homologues (2n → n); meiosis II separates sisters | 4.3 |
| Gamete combinations | $2^n$ (n = haploid number); humans $2^{23}$ = 8,388,608 | 4.3 |

## Glossary (terms used in this lesson)

**CDK** Cyclin-dependent kinase: serine/threonine kinase active only with a cyclin partner.

**Checkpoint** Control that halts the cycle until a required step is complete and correct.

**Chiasma** Visible point where non-sister chromatids of homologues remain joined after crossing over.

| | |
|---|---|
| **Cohesin** | Protein ring holding sister chromatids together until separase cuts it at anaphase. |
| **Crossing over** | Exchange of segments between non-sister chromatids of homologues in pachytene. |
| **Cyclin** | Regulatory protein whose level rises and falls in the cycle and which activates a CDK. |
| **G0** | Non-dividing state entered from G1; some cells can return to the cycle. |
| **Kinetochore** | Protein structure on each chromatid's centromere that binds spindle microtubules. |
| **Mitotic index** | Fraction of cells in a population that are in mitosis. |
| **Nondisjunction** | Failure of homologues or sister chromatids to separate, giving aneuploid cells. |
| **Ras** | Small membrane GTPase, on with GTP and off with GDP, relaying growth-factor signals to Raf. |
| **Restriction point** | Point in late G1 after which a cell completes the cycle without further growth factors. |
| **Synaptonemal complex** | Protein zipper that holds homologues together during synapsis. |

## The full unit book

Every chapter of Unit 4, the unit summary, the exam question bank with model answers and the full glossary: Cell Biology · Unit 4 · Cell Cycle, Division and Cell Death (one file, works offline).

## Sources and further reading

### Textbooks


- Bruce Alberts and others, *Molecular Biology of the Cell* (Garland Science / W. W. Norton): the chapters on the cell cycle, cell death, cancer, and stem cells and tissue renewal (from memory; check the edition you are prescribed).
- Harvey Lodish and others, *Molecular Cell Biology* (W. H. Freeman): chapters on regulating the eukaryotic cell cycle and on cancer (from memory; check).
- Geoffrey M. Cooper, *The Cell: A Molecular Approach* (Sinauer / Oxford University Press): chapters on the cell cycle, cell death and cell renewal, and cancer (from memory; check).

- Gerald Karp, *Cell and Molecular Biology: Concepts and Experiments* (Wiley) (from memory; check).
- R. Ian Freshney, *Culture of Animal Cells: A Manual of Basic Technique* (Wiley), for Chapter 4.9 (from memory; check).

## Open resources

- The 2nd edition (2000) of Cooper's *The Cell: A Molecular Approach* is free to read on the NCBI Bookshelf; its cell cycle section: ncbi.nlm.nih.gov/books/NBK9887 (found by search; the page did not load from the writing environment, so check).
- National Cancer Institute, RAS Initiative, frederick.cancer.gov/initiatives/ras-initiative, for current Ras biology and drugs (found by search; not opened).

Values given as typical (phase lengths, the Hayflick range, the $CD34^+$ dose) are standard textbook figures written from memory and marked where they appear; check them against your prescribed book.

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Built for the University free n easy YouTube channel from the universal syllabus of Cell Biology (Oct 2026). Written with top universities' syllabi and standard textbooks; check a formula against your prescribed book before an exam, and report mistakes on the channel.