Pr. G. Giménez-Martin/Photo Researchers, Inc./Science Source

12 The Cell Cycle

This cell, from a hyacinth plant, is undergoing a type of nuclear division called mitosis. Understanding how mitosis occurs is a major focus of this chapter.

In this chapter you will learn how

The life cycle of a cell culminates in division

starting with
The four phases of the cell cycle 12.1

asking
How does cell division take place? 12.2
via Mitosis
and Cytokinesis

by examining
Control of the cell cycle 12.3
and applying
Cancer: out-of-control cell division 12.4

The cell theory maintains that all organisms are made of cells and that all cells arise from preexisting cells (Chapter 1). Although the cell theory was widely accepted among biologists by the 1860s, most thought that new cells arose within preexisting cells by a process that resembled the growth of mineral crystals. But Rudolf Virchow proposed that new cells are formed by the splitting of preexisting

Virchow's hypothesis. Plants and animals start life as single-celled embryos and grow through a series of cell divisions.

Early studies revealed two fundamentally different ways that nuclei divide before cell division: meiosis and mitosis. In animals, **meiosis** leads to the production of sperm and eggs, which are the male and female reproductive cells termed **gametes.** Meiosis is equally important in other eukaryotes, but the cells produced are not gametes. In plants, for example, the products of meiosis are **spores. Mitosis** leads to the production of the other cell types, referred to as **somatic** (literally, "body-belonging") **cells.** (You can see how meiosis and mitosis are related to each other and to the transmission of genetic information in the Big Picture on pages 408–409.)

BIG PICTURE

This chapter is part of the Big Picture. See how on pages 408–409.

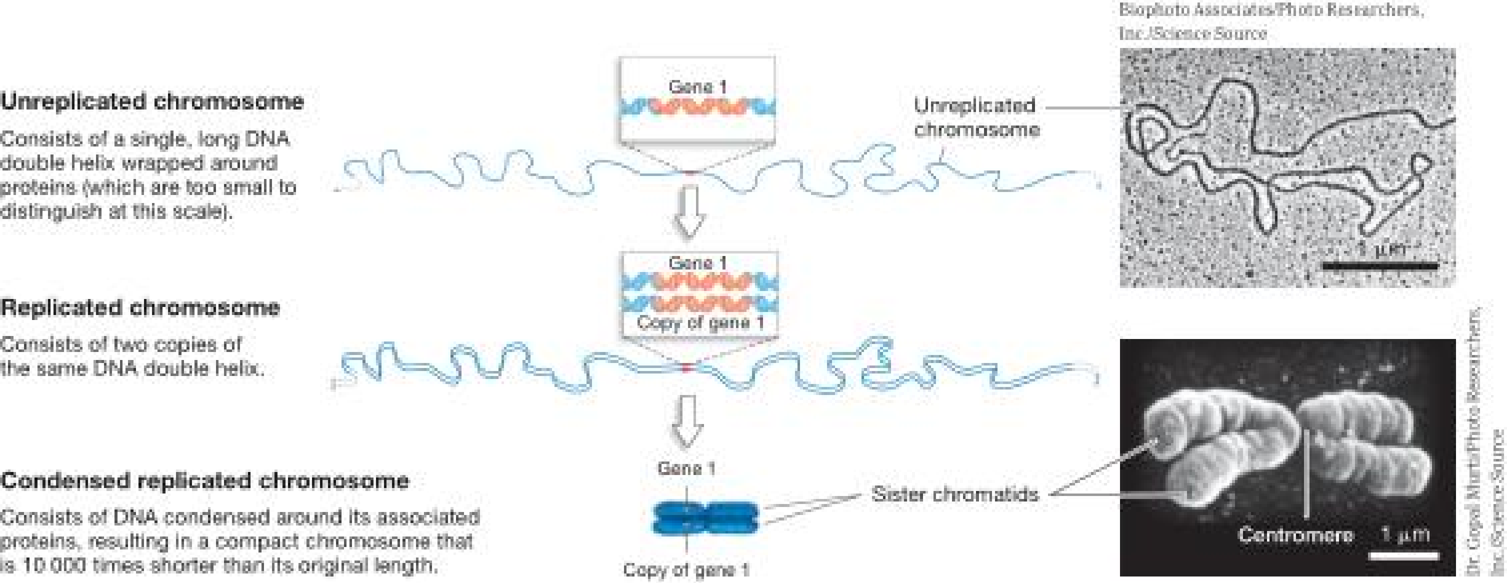
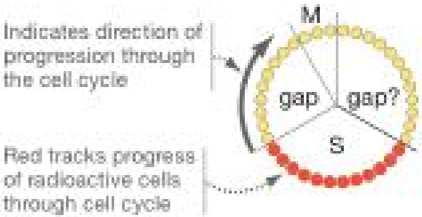
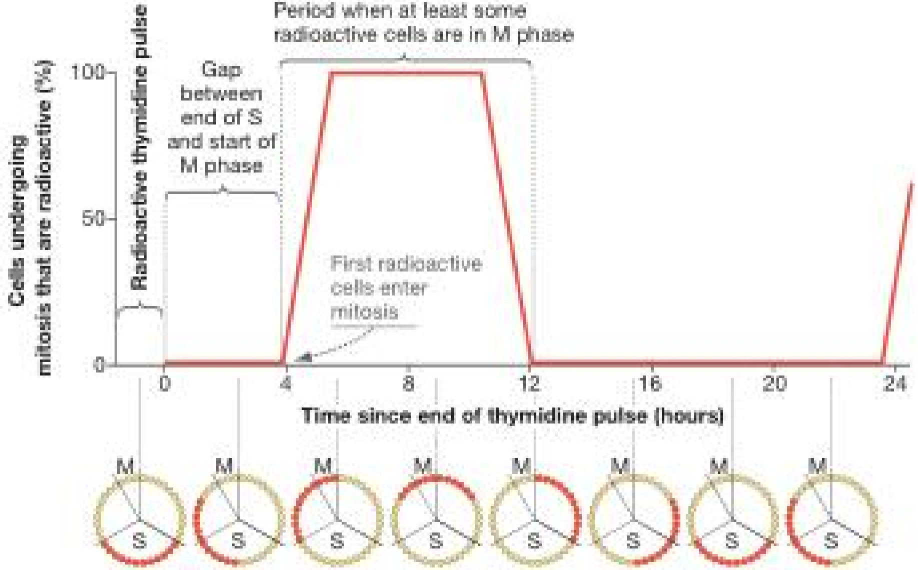


Figure 12.1 Changes in Chromosome Morphology. After chromosomes replicate, the two identical copies of the double-stranded DNA are attached to each other along their entire length. Early in mitosis, replicated chromosomes condense and sister chromatids remain attached at a region called the centromere.

Figure 12.2 A Pulse–Chase Experiment Reveals a Gap Phase. Cells labelled with radioactive thymidine during the pulse were tracked during the chase. The period between the end of the pulse and the appearance of the first radioactive mitotic cells represents a gap between the end of S phase and start of M phase.





One striking result emerged early on: None of the radioactive cells started mitosis immediately. Because the cultures were asynchronous, at least some of the cells must have been at the very end of their S phase when they were exposed to the pulse. If S phase were immediately followed by M phase, then some of these radioactive cells would have entered M phase just as the chase began. Instead, it took several hours before any of the radioactive cells began mitosis.

The time between the end of the pulse and the appearance of the first radioactive mitotic nuclei corresponds to a gap between the end of S phase and the beginning of M phase. This gap is a period when chromosome replication is complete but mitosis has not yet begun. The graph in Figure 12.2 shows how cells labelled with radioactive thymidine can be tracked as they progress through M phase.

and an interphase consisting of the G_1, S, and G_2 phases. In the cycle diagrammed here, G_1 phase is about twice as long as G_2 phase, but their actual durations vary depending on the cell type and growth conditions.

Why do the gap phases exist? In multicellular organisms, cells perform their functional roles mostly during G_1 phase. G_1 is also the period when the cell "decides" to begin replication and transitions to S phase (as will be explained in Section 12.3). Before mitosis can take place, a cell uses G_2 phase to prepare for M phase. The time spent in both G_1 and G_2 allows the cell to grow and replicate organelles so it will be able to divide into two cells that can function normally.

Now let's turn to M phase. Once the genetic material has been copied in S phase, how is it divided between daughter cells?

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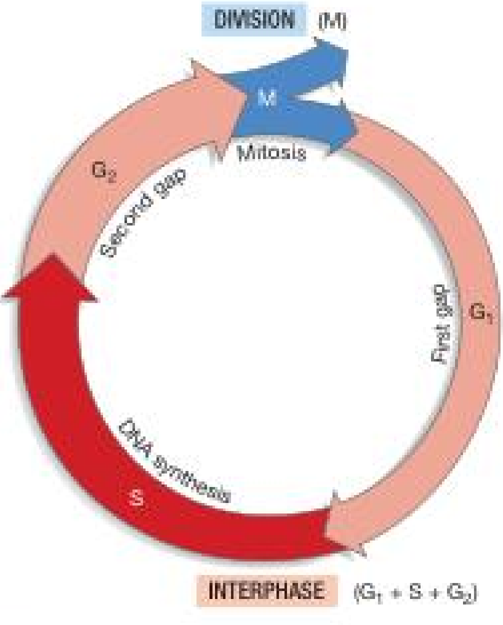

Figure 12.3 The Cell Cycle Has Four Phases. The duration of the G_1 and G_2 phases varies dramatically among cells and organisms.

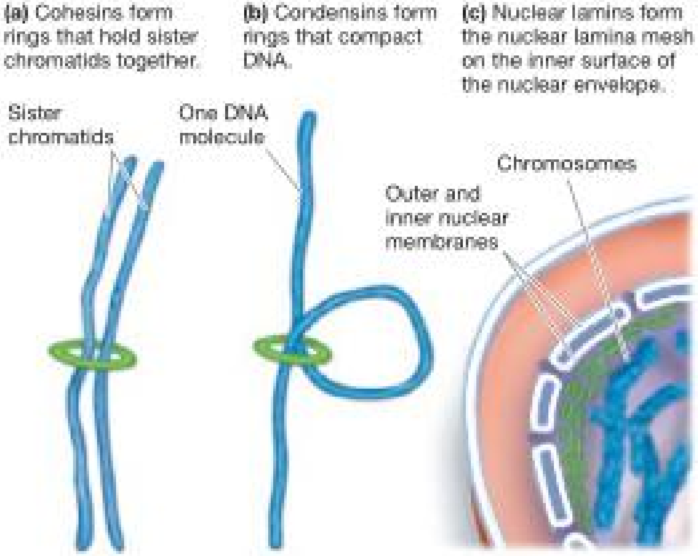

Figure 12.4 Cohesins, Condensins, and Nuclear Lamins Each Play an Important Role during Mitosis. Because cohesin and condensin proteins are tiny in comparison with entire chromosomes, it takes thousands of cohesins to hold the sister chromatids together and thousands of condensins to compact each chromosome in preparation for cell division.

Condensins The other difference between our hypothetical cell and an actual cell is the length of the chromosomes. An average human chromosome contains a piece of DNA 75 mm long! Even when wrapped around histone proteins, the chromosome is 2 mm long. While this is acceptable in the interphase nucleus, it would be impossible during cell division to move 46 chromosomes to each pole if each was several times longer than the cell was wide.

The solution to this third problem is that, at the beginning of cell division, the chromosomes must become more condensed. This is done with proteins called **condensins.** As seen in Figure 12.4b, they, like cohesins, are ring-shaped; like cohesins, they are also made of three subunits. They also encircle DNA, but instead of holding two different pieces together, they stabilize loops in the same piece of DNA. Condensin proteins allow our chromosomes to be about 5 μm long during mitosis (Figure 12.1).

There are other proteins involved in mitosis, some of which will be introduced later in this chapter. However, at its simplest level, mitosis is a story of DNA working together with five proteins: cohesins, microtubules, kinetochore proteins, nuclear lamins, and condensins.

Events in Mitosis

Although mitosis is a continuous process, biologists identify five subphases within M phase on the basis of distinctive events