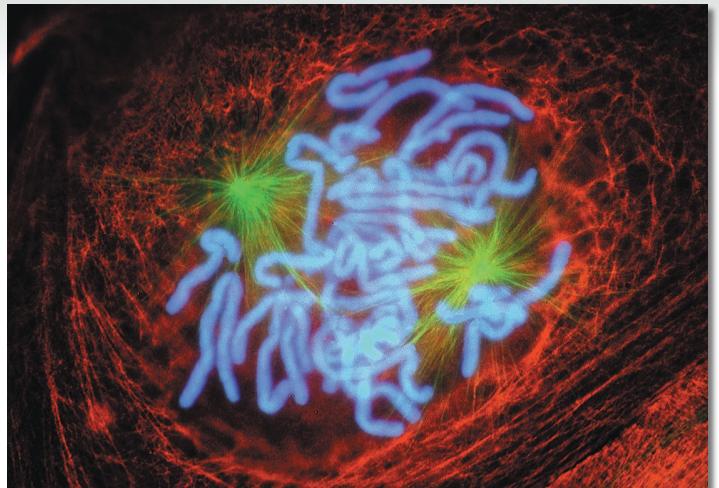


## UNIT II. PATTERNS OF INHERITANCE

### CHAPTER OUTLINE

- 2.1 General Features of Chromosomes
- 2.2 Cell Division
- 2.3 Mitosis and Cytokinesis
- 2.4 Meiosis
- 2.5 Sexual Reproduction
- 2.6 Sex Chromosomes and Sex Determination



**Chromosome sorting during cell division.** When eukaryotic cells divide, their chromosomes (shown in blue) are replicated and sorted, so that each cell receives the correct number.

Photomicrograph by Dr. Conly L. Rieder, Wadsworth Center, Albany, New York 12201-0509

# 2

## CHROMOSOME TRANSMISSION DURING CELL DIVISION AND SEXUAL REPRODUCTION

In this chapter, we will begin by considering the general features of chromosomes and how they are observed under the microscope. We then examine how bacterial and eukaryotic cells divide. During cell division, eukaryotic cells can sort their chromosomes in two different ways. One process, called mitosis, sorts chromosomes so that each daughter cell receives the same number and types of chromosomes as the original mother cell had. A second process, called meiosis, results in daughter cells with half the number of chromosomes that the mother cell had. Meiosis is necessary for sexual reproduction in eukaryotic species, such as animals and plants. During sexual reproduction, gametes with half the number of chromosomes unite at fertilization. We will also explore how chromosomes and environmental factors can determine whether individuals develop into males or females.

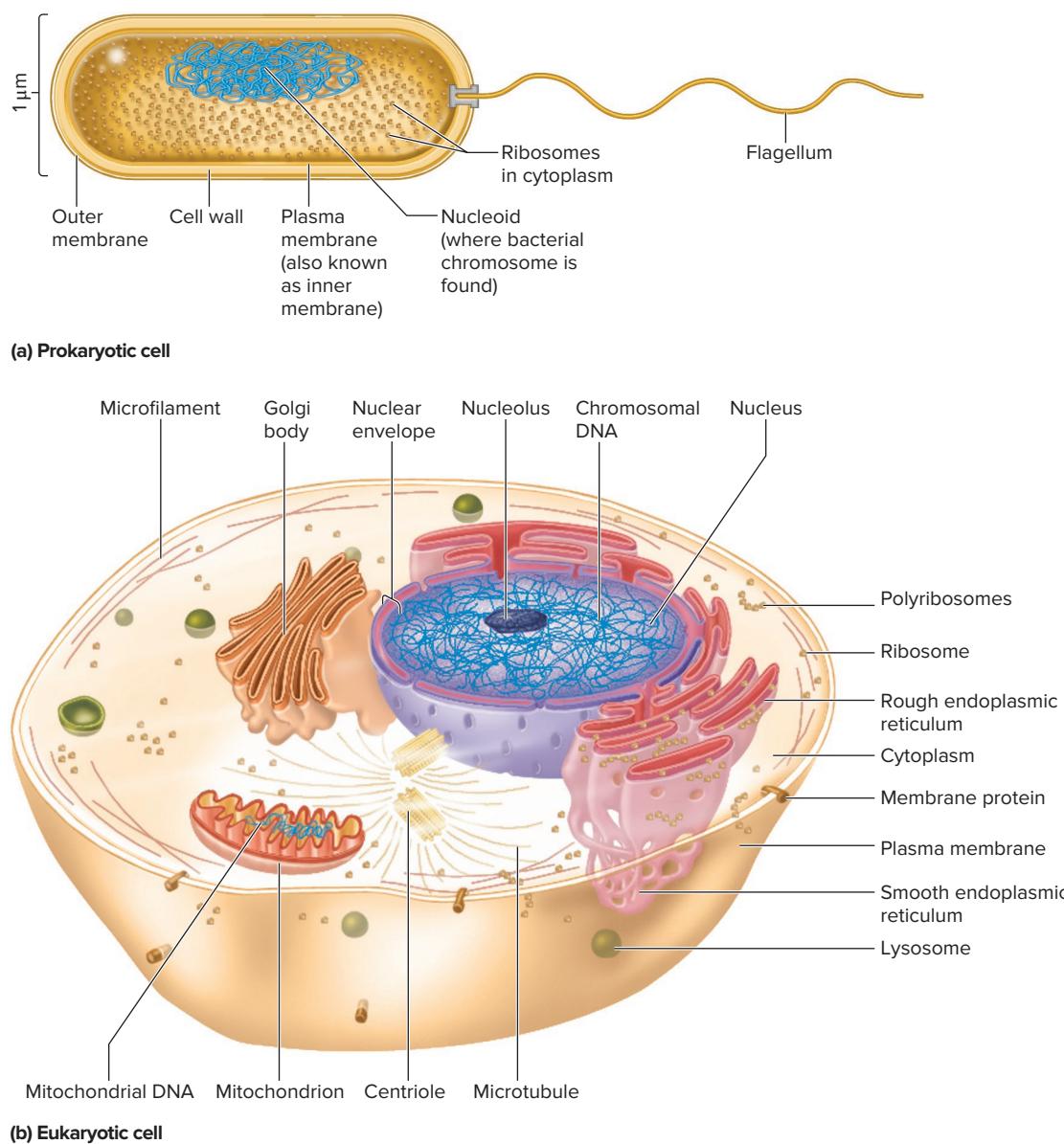
### 2.1 GENERAL FEATURES OF CHROMOSOMES

#### Learning Outcomes:

1. Define the term *chromosome*.
2. Outline the key differences between prokaryotic and eukaryotic cells.
3. Describe the procedure for making a karyotype.
4. Summarize the similarities and differences between homologous chromosomes.

The **chromosomes** are structures within living cells that contain the genetic material. The term *chromosome*—meaning “colored body”—refers to the microscopic observation of chromosomes after they have been stained with dyes. Genes are physically located within chromosomes. Biochemically, each chromosome





**FIGURE 2.1** The basic organization of cells. (a) A prokaryotic cell. The example shown here represents a typical bacterium, such as *Escherichia coli*, which has an outer membrane. (b) A eukaryotic cell. The example shown here is a typical animal cell.

**CONCEPT CHECK:** Eukaryotic cells exhibit compartmentalization. Define *compartmentalization*.

contains a very long segment of DNA, which is the genetic material, and proteins, which are bound to the DNA and provide it with an organized structure. In eukaryotic cells, this complex between DNA and proteins is called **chromatin**. In this chapter, we will focus on the cellular mechanics of chromosome transmission during cell division to better understand the patterns of gene transmission that we will consider in Chapters 3 and 4. In particular, we will examine how chromosomes are copied and sorted into newly made cells.

Before we begin a description of chromosome transmission, we need to consider the distinctive cellular differences between prokaryotic and eukaryotic species. Bacteria and archaea are referred to as **prokaryotes**, from the Greek meaning

“prenucleus,” because their chromosomes are not contained within a membrane-bound nucleus in the cell. Prokaryotes usually have a single type of circular chromosome in a region of the cytoplasm called the **nucleoid** (Figure 2.1a). The cytoplasm is enclosed by a plasma membrane that regulates the uptake of nutrients and the excretion of waste products. Outside the plasma membrane is a rigid cell wall that protects the cell from breakage. Certain species of bacteria also have an outer membrane on the exterior side of the cell wall.

**Eukaryotes**, from the Greek meaning “true nucleus,” include some simple species, such as single-celled protists and some fungi (such as yeast), and more complex multicellular species, such as plants, animals, and other fungi. The cells of eukaryotic

species have internal membranes that enclose highly specialized compartments (**Figure 2.1b**). These compartments form membrane-bound **organelles** with specific functions. For example, the lysosomes play a role in the degradation of macromolecules. The endoplasmic reticulum and Golgi body play a role in protein modification and trafficking. A particularly conspicuous organelle is the **nucleus**, which is bounded by two membranes that constitute the nuclear envelope.

Most of the genetic material in a eukaryotic cell is found within chromosomes, which are located in the nucleus. In addition to the nucleus, certain organelles in eukaryotic cells contain a small amount of their own DNA. These include the mitochondrion, which functions in ATP synthesis, and the chloroplast, in plant and algal cells, which functions in photosynthesis. The DNA found in these organelles is referred to as extranuclear, or extra-chromosomal, DNA to distinguish it from the DNA that is found in the cell nucleus. We will examine the role of mitochondrial and chloroplast DNA in Chapter 5.

In this section, we will focus on the composition of chromosomes found in the nucleus of eukaryotic cells. As you will learn, eukaryotic species contain genetic material that comes in sets of linear chromosomes.

## Eukaryotic Chromosomes Are Examined Cytologically to Prepare a Karyotype

Insights into inheritance patterns have been gained by observing chromosomes under the microscope. **Cytogenetics** is the field of genetics that involves the microscopic examination of chromosomes. The most basic observation that a **cytogeneticist** can make is the examination of the chromosomal composition of a particular cell. For eukaryotic species, this is usually accomplished by observing the chromosomes as they are found in actively dividing cells. When a cell is preparing to divide, the chromosomes become more tightly coiled, which shortens them and increases their diameter. The consequence of this shortening is that distinctive shapes and numbers of chromosomes become visible with a light microscope.

Each species has a particular chromosome composition. For example, most human cells contain 23 pairs of chromosomes, for a total of 46. On rare occasions, some individuals may inherit an abnormal number of chromosomes or a chromosome with an abnormal structure. Such abnormalities can often be detected by a microscopic examination of the chromosomes within actively dividing cells. In addition, a cytogeneticist may examine chromosomes as a way to distinguish between two closely related species.

**Figure 2.2a** shows the general procedure for preparing human chromosomes to be viewed by microscopy. In this example, the cells were obtained from a sample of human blood; more specifically, the chromosomes within leukocytes (also called white blood cells) were examined. Blood cells are a type of **somatic cell**. This term refers to any cell of the body that is not a gamete or a precursor to a gamete. The **gametes** (sperm and egg cells or their precursors) are also called **germ cells**.

After the blood cells have been removed from the body, they are treated with one chemical that stimulates them to begin cell

division and another chemical that halts cell division during mitosis, which is described later in this chapter. As shown in Figure 2.2a, these actively dividing cells are subjected to centrifugation to concentrate them. The concentrated preparation is then mixed with a hypotonic solution that makes the cells swell. This swelling causes the chromosomes to spread out within the cell, thereby making it easier to see each individual chromosome. Next, the cells are treated with a fixative that chemically freezes them so that the chromosomes will no longer move around. The cells are then treated with a chemical dye that binds to the chromosomes and stains them. As discussed in greater detail in Chapter 8, this gives chromosomes a distinctive banding pattern that greatly enhances the ability to visualize and to uniquely identify them (look ahead to Figure 8.1c, d). The cells are then placed on a slide and viewed with a light microscope.

In a cytogenetics laboratory, the microscopes are equipped with a camera that can photograph the chromosomes. In recent years, advances in technology have allowed cytogeneticists to view microscopic images on a computer screen (**Figure 2.2b**). On the screen, the chromosomes can be arranged in a standard way, usually from largest to smallest. As seen in **Figure 2.2c**, the human chromosomes are lined up, and a number is used to designate each type of chromosome. An exception is the sex chromosomes, which are designated with the letters X and Y. An organized representation of the chromosomes within a cell is called a **karyotype**. A karyotype reveals how many chromosomes are found within an actively dividing somatic cell.

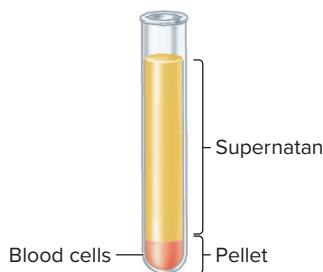
## Eukaryotic Chromosomes Are Inherited in Sets

Most eukaryotic species are **diploid** or have a diploid phase in their life cycle, which means that each type of chromosome is a member of a pair. A diploid cell has two sets of chromosomes. In humans, most somatic cells have 46 chromosomes—two sets of 23 each. Other diploid species, however, have different numbers of chromosomes in their somatic cells. For example, the dog has 39 chromosomes per set (78 total), the fruit fly has 4 chromosomes per set (8 total), and the tomato plant has 12 per set (24 total).

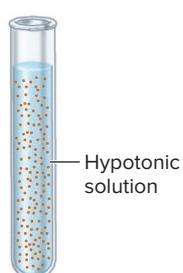
When a species is diploid, the members of a pair of chromosomes are called **homologs**; each type of chromosome is found in a homologous pair. As shown in Figure 2.2c, for example, a human somatic cell has two copies of chromosome 1, two copies of chromosome 2, and so forth. Within each pair, the chromosome on the left is a homolog to the one on the right, and vice versa. In each pair, one chromosome was inherited from the female parent, and its homolog was inherited from the male parent.

The two chromosomes in a homologous pair are usually identical in size, have the same banding pattern, and contain a similar composition of genetic material. If a particular gene is found on one copy of a chromosome, it is also found on the other homolog. However, the two homologs may carry different versions of a given gene, which are called **alleles**. As discussed in Chapter 3, some alleles are dominant, meaning that they mask the expression of recessive alleles. As an example, let's consider a gene in humans, called *Herc2*, which is one of a few different genes that affect eye color. The *Herc2* gene is located on

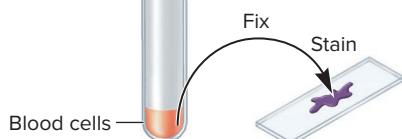
A sample of blood is collected and treated with chemicals that stimulate the cells to divide. Colchicine is added because it disrupts spindle formation and stops cells in mitosis when the chromosomes are highly compacted. The cells are then subjected to centrifugation.



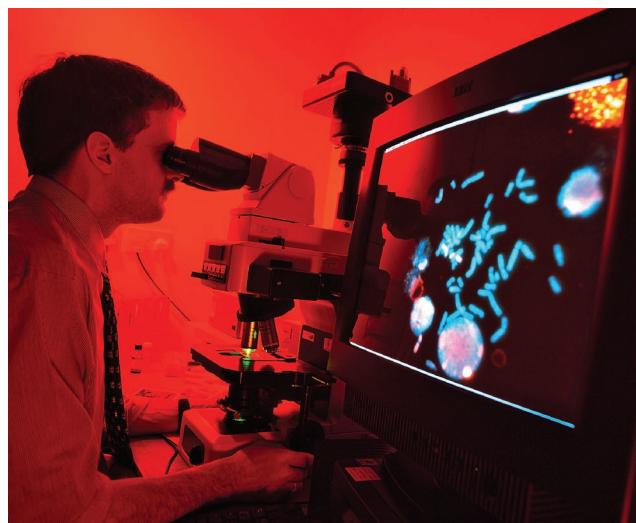
The supernatant is discarded, and the cell pellet is suspended in a hypotonic solution. This causes the cells to swell.



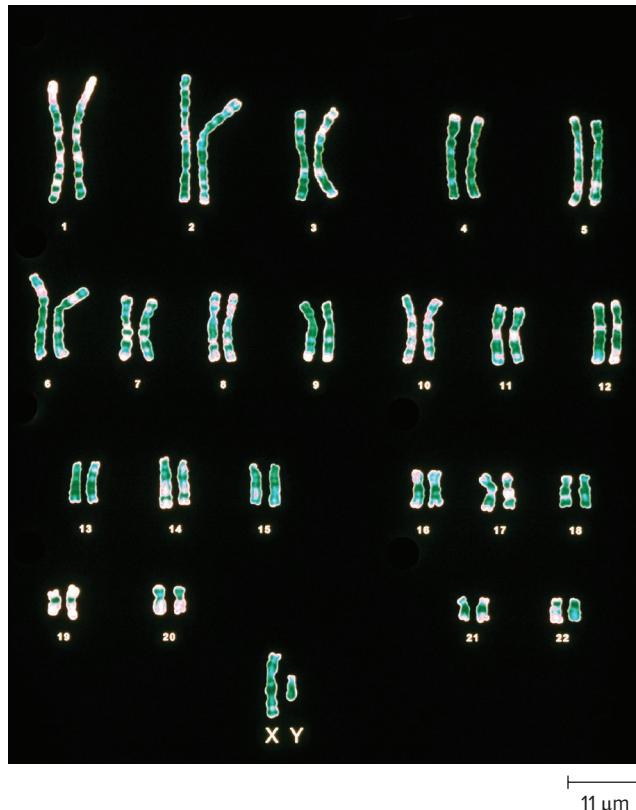
The sample is subjected to centrifugation a second time to concentrate the cells. The cells are suspended in a fixative, stained, and placed on a slide. As shown in part (b), the chromosomes within leukocytes (white blood cells) are observed under a microscope.



**(a) Preparing cells for a karyotype**



**(b) The slide is viewed by a light microscope; the sample is seen on a computer screen. The chromosomes can be arranged electronically on the screen.**



**(c) For a diploid human cell, two complete sets of chromosomes from that cell constitute a karyotype of the cell.**

## FIGURE 2.2 The procedure for making a human karyotype.

(b): David Parker/Science Source; (c): Leonard Lessin/Science Source

**CONCEPT CHECK:** How do you think the end results of karyotype preparation would be affected if the blood cells were not treated with a hypotonic solution?

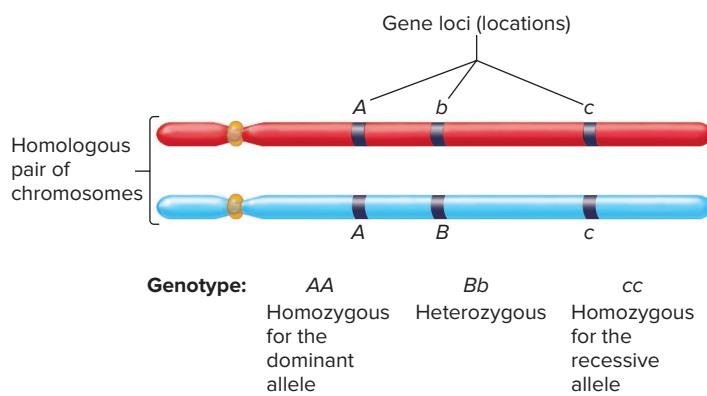
chromosome 15 and comes in variants that result in brown or blue eyes. In a person with brown eyes, one copy of chromosome 15 may carry a dominant brown allele, whereas its homolog may carry a recessive blue allele.

At the molecular level, how similar are homologous chromosomes? The answer is that the sequence of bases of one homolog usually differs from the sequence of the other homolog by less than 1%. For example, the DNA sequence of chromosome 1 that you inherited from your female parent is more than 99% identical to the sequence of chromosome 1 that you inherited from your male parent.

It is worth emphasizing that the DNA sequences on homologous chromosomes are not completely identical. The slight differences in DNA sequences provide the allelic differences in genes. Again, if we use the eye color gene as an example, a slight difference in DNA sequence distinguishes the brown and blue alleles.

However, the striking similarities between homologous chromosomes do not apply to the pair of sex chromosomes—X and Y. These chromosomes differ in size and genetic composition. Certain genes that are found on the X chromosome are not found on the Y chromosome, and vice versa. The X and Y chromosomes are not considered homologous chromosomes even though they do have short regions of homology.

**Figure 2.3** shows two homologous chromosomes with three different genes labeled. Dominant alleles are denoted with an uppercase letter, whereas recessive alleles are denoted with a lowercase letter. An individual having these two chromosomes is **homozygous** for the dominant allele of gene A, which means that both homologs carry the same allele. The individual is **heterozygous**, *Bb*, for the second gene, meaning that the homologs carry different alleles. For the third gene, the individual is homozygous for a recessive allele, *c*. The physical location of a gene is called its **locus** (plural: **loci**). As seen in Figure 2.3, for example, the locus of gene C is toward one end of this chromosome, whereas the locus of gene B is more in the middle.



**FIGURE 2.3** A comparison of homologous chromosomes.

Each of the homologous chromosomes in a pair carries the same types of genes, but, as shown here, the alleles may or may not be different.

**CONCEPT CHECK:** How are homologs similar to each other, and how are they different?

## 2.1 COMPREHENSION QUESTIONS

- Which of the following is *not* found in a prokaryotic cell?
  - Plasma membrane
  - Ribosome
  - Cell nucleus
  - Cytoplasm
- When a karyotype is prepared, which of the following steps is carried out?
  - Treat the cells with a chemical that causes them to begin cell division.
  - Treat the cells with a hypotonic solution that causes them to swell.
  - Expose the cells to chemical dyes that bind to the chromosomes and stain them.
  - All of the above steps are carried out.
- How many sets of chromosomes are found in a human somatic cell, and how many chromosomes are within one set?
  - 2 sets, with 23 in each set
  - 23 sets, with 2 in each set
  - 1 set, with 23 in each set
  - 23 sets, with 1 in each set

## 2.2 CELL DIVISION

### Learning Outcomes:

- Describe the process of binary fission in bacteria.
- Outline the phases of the eukaryotic cell cycle.

Now that we have an appreciation for the chromosomal composition of living cells, we can consider how chromosomes are copied and transmitted when cells divide. One purpose of cell division is **asexual reproduction**. In this process, a preexisting cell divides to produce two new cells. By convention, the original cell is usually called the mother cell, and the two new cells are the daughter cells. In unicellular species, the mother cell is judged to be one organism, and the two daughter cells are two new separate organisms. Asexual reproduction is how bacterial cells proliferate. In addition, certain unicellular eukaryotes, such as the amoeba and baker's yeast (*Saccharomyces cerevisiae*), can reproduce asexually.

Another purpose of cell division is to achieve **multicellularity**. Species such as plants, animals, most fungi, and some protists are derived from a single cell that has undergone repeated cellular divisions. Humans, for example, begin as a single fertilized egg; repeated cell divisions produce an adult with trillions of cells. The precise transmission of chromosomes during every cell division is critical so that all cells of the body receive the correct amount of genetic material.

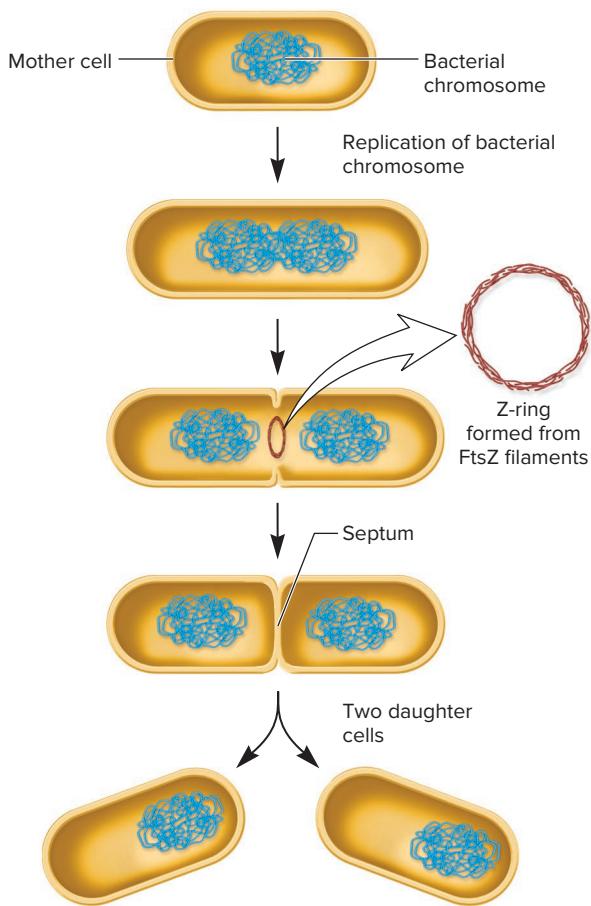
In this section, we will consider how the duplication, organization, and distribution of the chromosomes are critical to the process of cell division. In bacteria, which have a single circular chromosome, the division process is relatively simple. Prior to cell division, bacteria duplicate their circular chromosome; they then

distribute a copy into each of the two daughter cells. This process, known as binary fission, is described first. Eukaryotes have multiple chromosomes that occur as sets. This added complexity in eukaryotic cells requires a more complicated sorting process, called mitosis, so that each newly made cell receives the correct number and types of chromosomes.

### Bacteria Reproduce Asexually by Binary Fission

As discussed earlier in this chapter (see Figure 2.1a), bacterial species are typically unicellular, although individual bacteria may associate with each other to form pairs, chains, or clumps. Unlike eukaryotes, which have their chromosomes in a separate nucleus, the circular chromosome of a bacterium is in direct contact with the cytoplasm.

The capacity of bacteria to divide is really quite astounding. Some species, such as *Escherichia coli* (*E. coli*), a common species in the intestine, can divide every 20 to 30 minutes. Prior to cell division, bacterial cells copy, or replicate, their chromosomal DNA. This produces two identical copies of the genetic material, as shown at the top of **Figure 2.4**. Following DNA replication, a



**FIGURE 2.4** **Binary fission: the process by which bacterial cells divide.** Prior to division, the chromosome replicates to produce two identical copies. These two copies segregate from each other, with one copy going to each daughter cell.



**CONCEPT CHECK:** What is the function of the FtsZ protein during binary fission?

bacterial cell divides into two daughter cells by a process known as **binary fission**.

- Prior to cell division, bacterial cells copy, or replicate, their chromosomal DNA. This produces two identical copies of the genetic material, as shown at the top of Figure 2.4.
- A protein called FtsZ is the first protein to move to the division site that will separate the two daughter cells. Filaments composed of FtsZ protein assemble into a structure called a Z-ring (see inset in Figure 2.4).
- FtsZ recruits other proteins to produce a septum, which is a new cell wall between the daughter cells. The filaments within the Z-ring are thought to pull on each other and tighten to promote the formation of a septum. FtsZ is evolutionarily related to a eukaryotic protein called tubulin. As discussed later in this chapter, tubulin is the main component of microtubules, which play a key role in chromosome sorting in eukaryotes. Both FtsZ and tubulin form structures that provide cells with organization and play key roles in cell division.
- As a result of binary fission, a bacterial cell called the mother cell has divided into two daughter cells. Each daughter cell receives a copy of the chromosomal genetic material. Except when rare mutations occur, the daughter cells are usually genetically identical because they contain exact copies of the genetic material from the mother cell.

Binary fission is an asexual form of reproduction because it does not involve genetic contributions from two different gametes. On occasion, bacteria can transfer small pieces of genetic material to each other, which is described in Chapter 7.

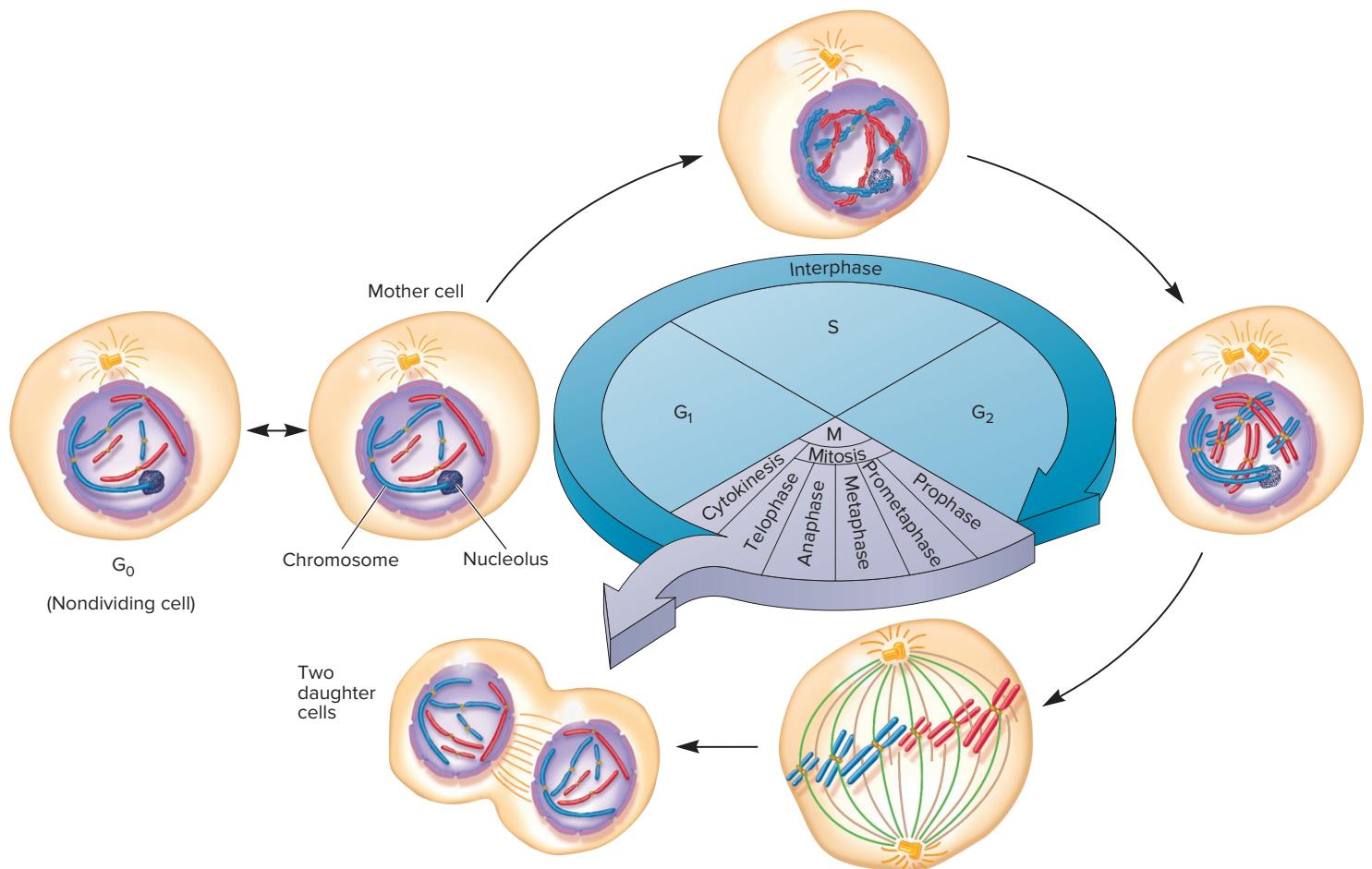
### Eukaryotic Cells Advance Through a Cell Cycle to Produce Genetically Identical Daughter Cells

The common outcome of eukaryotic cell division is the production of two daughter cells that have the same number and types of chromosomes as the original mother cell. This requires a replication and division process that is more complicated than simple binary fission. Eukaryotic cells that are destined to divide advance through a series of phases known as the **cell cycle** (Figure 2.5). These phases are named G for gap, S for synthesis (of the genetic material), and M for mitosis. There are two G phases: G<sub>1</sub> and G<sub>2</sub>. The term *gap* originally described the gaps between S phase and mitosis in which it was not microscopically apparent that significant changes were occurring in the cell. However, we now know that both gap phases are critical periods in the cell cycle that involve many molecular changes. In actively dividing cells, the G<sub>1</sub>, S, and G<sub>2</sub> phases are collectively known as **interphase**.

In addition, cells may remain permanently, or for long periods of time, in a phase of the cell cycle called G<sub>0</sub>. A cell in the G<sub>0</sub> phase is either temporarily not advancing through the cell cycle or, in the case of terminally differentiated cells such as most nerve cells in an adult mammal, never dividing again. In other words, the G<sub>0</sub> phase is a nondividing stage.

Let's consider the key steps in these four phases.

- During the **G<sub>1</sub> phase**, a cell may prepare to divide. Depending on the cell type and the conditions the cell



**FIGURE 2.5** The eukaryotic cell cycle. Dividing cells advance through a series of phases, denoted G<sub>1</sub>, S, G<sub>2</sub>, and M. This diagram shows the advancement of a cell through mitosis to produce two daughter cells. The original diploid cell had three pairs of chromosomes, for a total of six individual chromosomes. During S phase, these have replicated to yield 12 chromatids found in six pairs of sister chromatids. After mitosis and cytokinesis are completed, each of the two daughter cells contains six individual chromosomes, just like the mother cell. Note: The chromosomes in G<sub>0</sub>, G<sub>1</sub>, S, and G<sub>2</sub> phases are not actually condensed as shown here. In this drawing, they are shown partially condensed so they can be easily counted.

**CONCEPT CHECK:** What is the difference between the G<sub>0</sub> and G<sub>1</sub> phases?

encounters, a cell in the G<sub>1</sub> phase may accumulate molecular changes (e.g., produce new proteins) that cause it to advance through the rest of the cell cycle. When this occurs, cell biologists say that a cell has reached a **restriction point** and is committed to a pathway that leads to cell division.

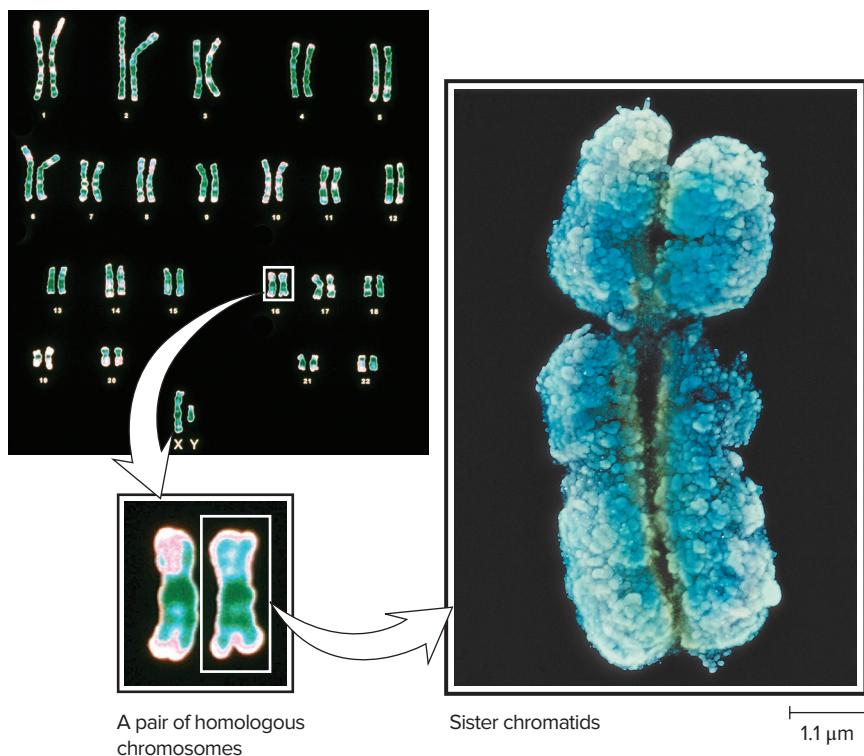
- Once past the restriction point, the cell then advances to the **S phase**, during which the chromosomes are replicated. After replication, the two copies of a chromosome are called **chromatids**. They are joined to each other at a region of DNA called the **centromere** to form a unit known as a pair of **sister chromatids**, or a **dyad** (Figure 2.6). A single chromatid within a dyad is called a **monad**. An unreplicated chromosome can also be called a monad. The **kinetochore** is a group of proteins that are bound to the centromere. These proteins help to hold the sister chromatids together and also play a role in chromosome sorting, as discussed later in this chapter.

When S phase is completed, a cell has twice as many chromatids as it had chromosomes in the G<sub>1</sub> phase. For example, a human cell in the G<sub>1</sub> phase has 46 distinct

chromosomes, whereas in G<sub>2</sub>, it has 46 pairs of sister chromatids, for a total of 92 chromatids. The term *chromosome* can be a bit confusing because it originally meant a distinct structure that is observable with the microscope. Therefore, *chromosome* can refer either to a pair of sister chromatids (a dyad) during G<sub>2</sub> and early stages of M phase or to a structure that is observed at the end of M phase and during G<sub>1</sub>, which is a monad and contains the equivalent of one chromatid (refer back to Figure 2.5).

- During the **G<sub>2</sub> phase**, the cell accumulates the materials necessary for nuclear and cell division.
- Next, the cell advances into the **M phase** of the cell cycle, when **mitosis** occurs.
- In most cases, two daughter cells are formed by a process called cytokinesis.

The primary purpose of mitosis is to distribute the replicated chromosomes, dividing one cell nucleus into two nuclei, so that each daughter cell receives the same complement of



(a) Homologous chromosomes and sister chromatids

(b) Schematic drawing of sister chromatids

**FIGURE 2.6 Chromosomes following DNA replication.** (a) The photomicrograph on the upper left shows a human karyotype. The large photomicrograph on the right shows a chromosome in the form called a dyad, or pair of sister chromatids. This chromosome is in the metaphase stage of mitosis, which is described later in this chapter. Note: Each of the 46 chromosomes that are viewed in a human karyotype (upper left) is actually a pair of sister chromatids. Look closely at the two insets. (b) A schematic drawing of sister chromatids. This structure has two chromatids that lie side by side. As seen here, each chromatid is a distinct unit, called a monad. The two chromatids are held together by kinetochore proteins that bind to each other and to the centromere of each chromatid.

(a): (top left & bottom inset) Leonard Lessin/Science Source; (right): Biophoto Associates/Science Source

**CONCEPT CHECK:** What is the difference between homologs and sister chromatids?

chromosomes. For example, a human cell in the G<sub>2</sub> phase has 92 chromatids, which are found in 46 pairs. During mitosis, these pairs of chromatids are separated and sorted in such a way that each daughter cell receives 46 chromosomes.

Mitosis was first observed microscopically in the 1870s by German biologist Walther Flemming, who coined the term *mitosis* (from the Greek *mitos*, meaning “thread”). He studied the dividing epithelial cells of salamander larvae and noticed that chromosomes were constructed of two parallel “threads.” These threads separated and moved apart, one going to each of the two daughter nuclei. We will examine the steps of mitosis in the next section.

- c. begins with a single mother cell and produces two genetically identical daughter cells.

- d. All of the above are true of binary fission.

- 2. Which of the following is the correct order of phases of the eukaryotic cell cycle?

- a. G<sub>1</sub>, G<sub>2</sub>, S, M
- b. G<sub>1</sub>, S, G<sub>2</sub>, M
- c. G<sub>1</sub>, G<sub>2</sub>, M, S
- d. G<sub>1</sub>, S, M, G<sub>2</sub>

- 3. What critical event occurs during the S phase of the eukaryotic cell cycle?

- a. The cell either prepares to divide or commits to not dividing.
- b. DNA replication produces pairs of sister chromatids.
- c. The chromosomes condense.
- d. The single nucleus is divided into two nuclei.

## 2.2 COMPREHENSION QUESTIONS

1. Binary fission
  - a. is a form of asexual reproduction.
  - b. is a way for bacteria to reproduce.

## 2.3 MITOSIS AND CYTOKINESIS

### Learning Outcomes:

1. Describe the structure and function of the mitotic spindle apparatus.
2. List and describe the phases of mitosis.
3. Outline the key differences between animal and plant cells with regard to cytokinesis.

As we have seen, eukaryotic cell division involves a cell cycle in which the chromosomes are replicated and then sorted so that each daughter cell receives the same amount of genetic material. This process ensures genetic consistency from one generation of cells to the next. In this section, we will examine the stages of mitosis and cytokinesis in greater detail.

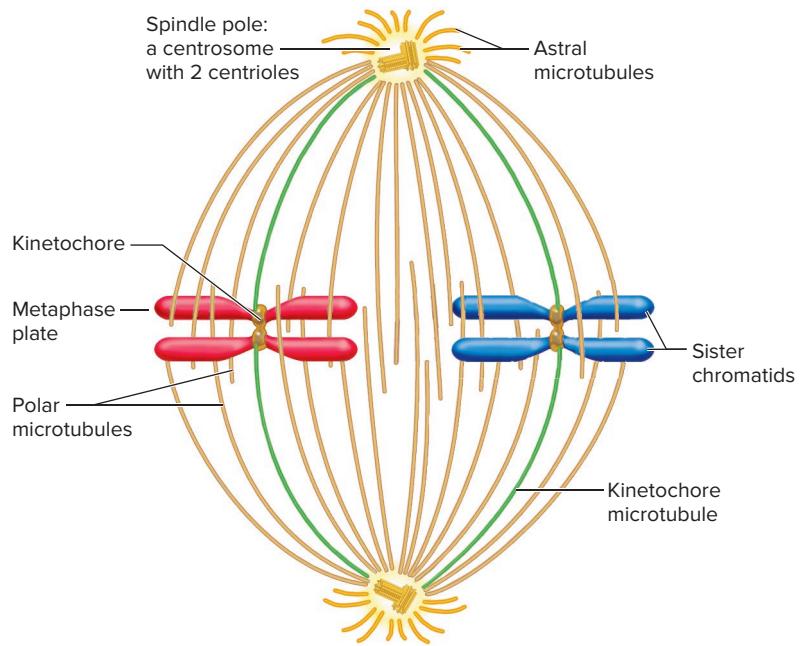
### The Mitotic Spindle Apparatus Organizes and Sorts Eukaryotic Chromosomes

Before we discuss the events of mitosis, let's first consider the structure of the **mitotic spindle apparatus** (also known simply as the **spindle apparatus** or the **mitotic spindle**), which is involved in the organization and sorting of chromosomes (Figure 2.7). The spindle apparatus is formed from **microtubule-organizing centers** (MTOCs), which are structures found in eukaryotic cells from which microtubules grow. Microtubules are produced from the rapid polymerization of tubulin proteins. In animal cells, the spindle apparatus is formed from two MTOCs called **centrosomes**. Each centrosome is located at a **spindle pole**. A pair of **centrioles** at right angles to each other is found within each centrosome. Centrosomes and centrioles are found in animal cells but not in all eukaryotic species. For example, plant cells do not have centrosomes. Instead, the nuclear envelope functions as an MTOC for the formation of the spindle apparatus in plant cells.

The spindle apparatus of a typical animal cell has three types of microtubules (see Figure 2.7).

- The **astral microtubules** emanate outward from the centrosome toward the plasma membrane. They are important for the positioning of the spindle apparatus within the cell.
- The **polar microtubules** project toward the region where the chromosomes will be found during mitosis—the region between the two spindle poles. Polar microtubules that overlap with each other play a role in the separation of the two poles. They help to “push” the poles away from each other.
- The **kinetochore microtubules** have attachments to **kinetochores**, which are protein complexes bound to the centromeres of individual chromosomes.

The spindle apparatus allows cells to organize and separate chromosomes so that each daughter cell receives the same complement of chromosomes. This sorting process, known as mitosis, is described next.



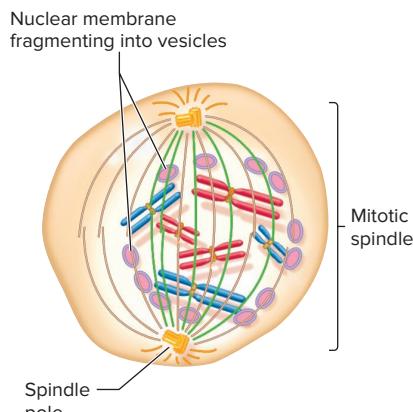
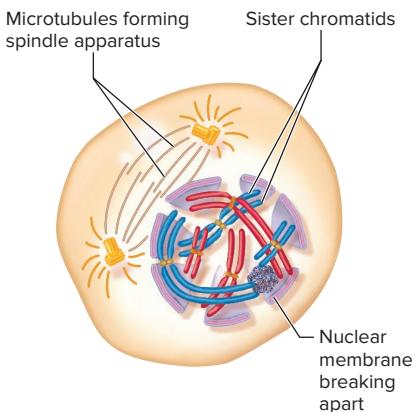
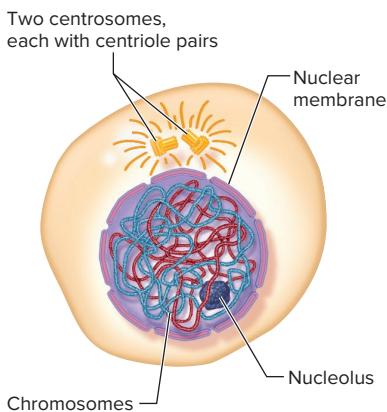
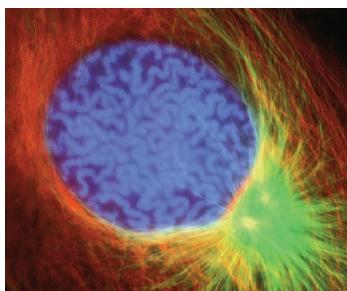
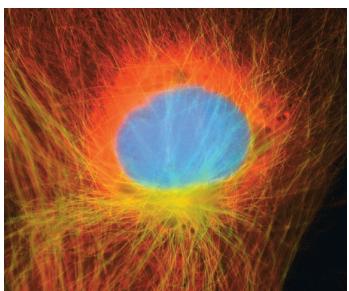
**FIGURE 2.7** The structure of the mitotic spindle apparatus in a typical animal cell. During the cell cycle, a single centrosome duplicates in S phase and the two centrosomes separate at the beginning of M phase. The spindle apparatus is formed from microtubules that are rooted in the centrosomes. Each centrosome is located at a spindle pole. The astral microtubules emanate away from the region between the poles. They help position the spindle apparatus within the cell. However, the spindle apparatus formed in many species, such as plants, does not have astral microtubules. The polar microtubules project into the region between the two poles; they play a role in pole separation. The kinetochore microtubules are attached to the kinetochores of sister chromatids. Note: For simplicity, only a single pair of homologous chromosomes is shown; eukaryotic cells typically have many pairs of homologous chromosomes.

**CONCEPT CHECK:** Where are the two ends of a kinetochore microtubule?

### The Transmission of Chromosomes During the Division of Eukaryotic Cells Requires a Process Known as Mitosis

The process of mitosis is shown for a diploid animal cell in Figure 2.8. In the simplified diagrams below the micrographs in the figure, the original mother cell contains six chromosomes; it is diploid ( $2n$ ) and has three chromosomes per set ( $n = 3$ ). One set is shown in blue, and the homologous set is shown in red. As discussed next, mitosis is subdivided into phases known as prophase, prometaphase, metaphase, anaphase, and telophase.

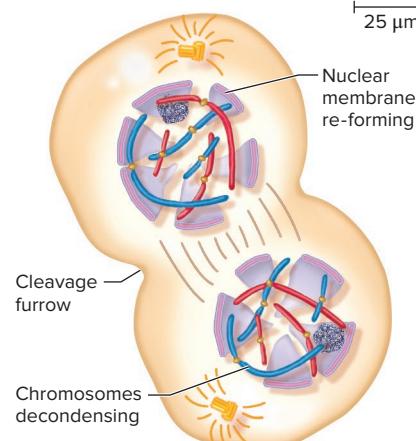
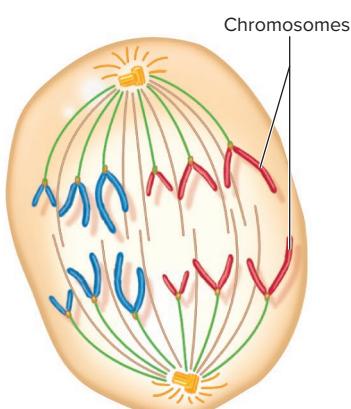
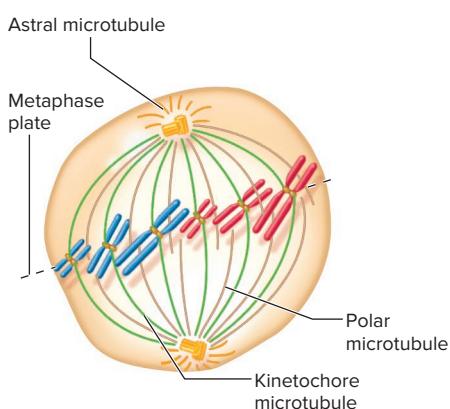
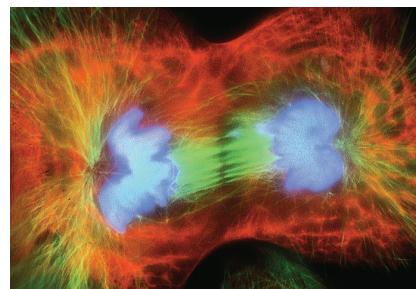
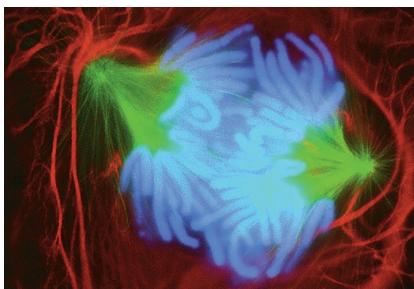
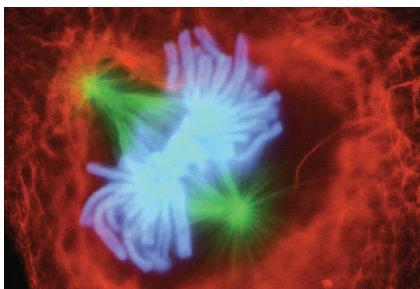
**Prophase** Prior to mitosis, the cells are in interphase, during which the chromosomes are **decondensed**—less tightly compacted—and found in the nucleus (Figure 2.8a). At the start of mitosis, in **prophase**, the chromosomes have already replicated, resulting in 12 chromatids that are joined as six pairs of sister chromatids (Figure 2.8b). As prophase proceeds, the nuclear membrane begins to dissociate into small vesicles and the nucleolus becomes less visible. At the same time, the chromatids become



(a) INTERPHASE

(b) PROPHASE

(c) PROMETAPHASE



**FIGURE 2.8** The process of mitosis in an animal cell. The two rows of micrographs illustrate cells of a fish embryo advancing through mitosis. The chromosomes are stained in blue and the microtubules are green. Below the micrographs are schematic diagrams that emphasize the sorting and separation of the chromosomes. In the diagrams, the original diploid cell is shown with six chromosomes (three in each set). At the start of mitosis, these have already replicated into 12 chromatids. The final result is two daughter cells, each containing six chromosomes.



(a-f): Photomicrographs by Dr. Conly L. Rieder, Wadsworth Center, Albany, New York 12201-0509

**CONCEPT CHECK:** During which phase of mitosis are sister chromatids separated and sent to opposite poles?

**condensed** into more compact structures that are readily visible by light microscopy. The two centrosomes move apart, and the spindle apparatus begins to form.

**Prometaphase** As mitosis advances from prophase to prometaphase, the centrosomes move to opposite ends of the cell and establish two spindle poles, one within each of the future daughter cells. During **prometaphase**, the nuclear membrane is completely fragmented into vesicles, allowing the spindle fibers to interact with the sister chromatids (Figure 2.8c).

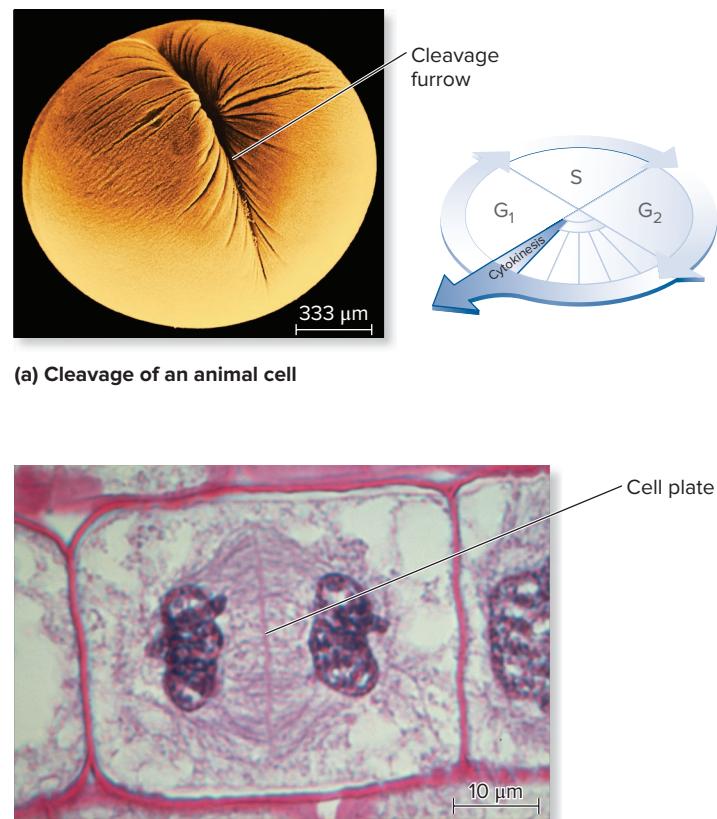
How do sister chromatids become attached to the spindle apparatus? Initially, microtubules form rapidly and can be seen growing out from the two poles. As a microtubule grows, if its end happens to make contact with a kinetochore, the end is said to be captured and remains firmly attached to the kinetochore. This random process is how sister chromatids become attached to kinetochore microtubules. Alternatively, if the end of a microtubule does not collide with a kinetochore, the microtubule eventually depolymerizes and retracts to the centrosome. As the end of prometaphase nears, the kinetochore on a pair of sister chromatids is attached to kinetochore microtubules from opposite poles. As these events are occurring, the sister chromatids undergo jerky movements as they are tugged, back and forth, between the two poles. By the end of prometaphase, the spindle apparatus is completely formed.

**Metaphase** Eventually, the pairs of sister chromatids align themselves along a plane called the **metaphase plate**. As shown in Figure 2.8d, when this alignment is complete, the cell is in **metaphase** of mitosis. At this point, each pair of chromatids (each dyad) is attached to both poles by kinetochore microtubules. The pairs of sister chromatids have become organized into a single row along the metaphase plate. When this organizational process is finished, the chromatids can be equally distributed into two daughter cells.

**Anaphase** At **anaphase**, the connection that is responsible for holding each pair of chromatids together is broken (Figure 2.8e). (We will examine the process of sister chromatid cohesion during prophase and separation during anaphase in more detail in Chapter 10; look ahead to Figure 10.30.) Each chromatid, or monad, now an individual chromosome, is linked to only one of the two poles. As anaphase proceeds, the chromosomes move toward the pole to which they are attached. This movement is due to the shortening of the kinetochore microtubules. In addition, the two poles themselves move farther apart due to the elongation of the polar microtubules, which slide in opposite directions as a result of the actions of motor proteins.

**Telophase** During **telophase**, the chromosomes reach their respective poles and decondense. The nuclear membrane now reforms to produce two separate nuclei. In Figure 2.8f, this membrane re-formation has produced two nuclei that contain six chromosomes each. The nucleoli have also reappeared.

**Cytokinesis** In most cases, mitosis is quickly followed by **cytokinesis**, in which the two nuclei are segregated into separate daughter cells. Likewise, cytokinesis also segregates cell organelles, such as mitochondria and chloroplasts, into daughter cells.



(a) Cleavage of an animal cell

(b) Formation of a cell plate in a plant cell

**FIGURE 2.9** Cytokinesis in animal and plant cells. (a) In an animal cell, cytokinesis involves the formation of a cleavage furrow. (b) In a plant cell, cytokinesis occurs via the formation of a cell plate between the two daughter cells.

(a): Don W. Fawcett/Science Source; (b): Ed Reschke

**CONCEPT CHECK:** What causes the cleavage furrow in a dividing animal cell to ingest?

In animal cells, cytokinesis begins shortly after anaphase. A contractile ring, composed of myosin motor proteins and actin filaments, assembles at the cytoplasmic surface of the plasma membrane. Myosin hydrolyzes ATP, which shortens the ring, thereby constricting the plasma membrane to form a **cleavage furrow** that ingresses, or moves inward (Figure 2.9a). Ingression continues until a midbody structure is formed that physically pinches the single cell into two cells.

In plants, the two daughter cells are separated by the formation of a **cell plate** (Figure 2.9b). At the end of anaphase, Golgi-derived vesicles carrying cell wall materials are transported to the equator of a dividing cell. The fusion of these vesicles gives rise to the cell plate, which is a membrane-bound compartment. The cell plate begins in the middle of the cell and expands until it attaches to the mother cell's wall. Once this attachment has taken place, the cell plate undergoes a process of maturation and eventually separates the mother cell into two daughter cells.

**Outcome of Mitotic Cell Division** Mitosis and cytokinesis ultimately produce two daughter cells having the same number of chromosomes as the mother cell. Barring rare mutations, the two

daughter cells are genetically identical to each other and to the mother cell from which they were derived. The critical consequence of this sorting process is to ensure genetic consistency from one generation of somatic cells to the next. The development of multicellularity relies on the repeated process of mitosis and cytokinesis. In diploid organisms that are multicellular, most of the somatic cells are diploid and genetically identical to each other.

### GENETIC TIPS

**THE QUESTION:** What are the functional roles of the mitotic spindle apparatus in an animal cell? Explain how these functions are related to the three types of microtubules: astral, polar, and kinetochore microtubules.

**T**OPIC: *What topic in genetics does this question address?* The topic is mitosis. More specifically, the question is about the roles of the mitotic spindle apparatus.

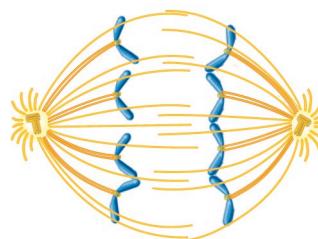
**I**NFORMATION: *What information do you know based on the question and your understanding of the topic?* From the question, you know there are three types of microtubules. From your understanding of the topic, you may remember the structure of the spindle apparatus, which is shown in Figure 2.7. Also, Figure 2.8 shows the roles that the spindle apparatus plays during mitosis.

**P**ROBLEM-SOLVING **S**TATEGY: *Define key terms.*  
**D**escribe the steps. One strategy to begin solving this problem is to make sure you understand the key terms. In particular, you may want to look up the meaning of *mitotic spindle apparatus* and *microtubules*, if you don't already know what those terms mean. After you understand the key terms, another useful problem-solving strategy is to describe the steps of mitosis, and think about the roles of the types of microtubules in the various steps. These steps are shown in Figure 2.8. You may also want to refer back to Figure 2.7 to appreciate the structure of the spindle apparatus.

**A**NSWER: The spindle apparatus is involved in sorting the chromosomes and promoting the division of one cell into two daughter cells.

- The polar microtubules overlap with each other and push the poles apart during anaphase.
- The astral microtubules help to orient the spindle apparatus in the cell.
- The kinetochore microtubules attach to chromosomes and aid in their sorting. Their roles are to align the chromosomes at the metaphase plate and to pull the chromosomes to the poles during anaphase.

2. Which phase of mitosis is depicted in the drawing below?



- Prophase
- Prometaphase
- Metaphase
- Anaphase
- Telophase

## 2.4 MEIOSIS

### Learning Outcomes:

1. List and describe the phases of meiosis.
2. Outline the key differences between mitosis and meiosis.

In the previous section, we considered the process in which a eukaryotic cell can divide by mitosis and cytokinesis so that a mother cell produces two genetically identical daughter cells. Diploid eukaryotic cells may also divide by an alternative process called **meiosis** (from the Greek meaning “less”). During meiosis, **haploid** cells, which contain a single set of chromosomes, are produced from a cell that was originally diploid. For this to occur, the chromosomes must be correctly sorted and distributed in a way that reduces the chromosome number to half its original value. For example, in humans, haploid gametes (sperm or egg cells) are produced by meiosis. Each gamete must receive half the total number of 46 chromosomes, but not just any 23 chromosomes will do. A gamete must receive one chromosome from each of the 23 pairs. In this section, we will examine how the phases of meiosis lead to the formation of cells with a haploid complement of chromosomes.

### Meiosis Produces Cells That Are Haploid

The process of meiosis bears striking similarities to mitosis. Like mitosis, meiosis begins after a cell has advanced through the G<sub>1</sub>, S, and G<sub>2</sub> phases of the cell cycle. However, meiosis involves two successive divisions rather than one (as in mitosis). Prior to meiosis, the chromosomes are replicated in S phase to produce pairs of sister chromatids. This single replication event is then followed by two sequential cell divisions called meiosis I and II. Like mitosis, each of these divisions is subdivided into prophase, prometaphase, metaphase, anaphase, and telophase.

**Prophase of Meiosis I** **Figure 2.10** emphasizes some of the important events that occur during prophase of meiosis I.

**Synapsis.** At the beginning of prophase, the replicated chromosomes begin to condense and become visible with a light microscope. The sister chromatids are connected to each other by

## 2.3 COMPREHENSION QUESTIONS

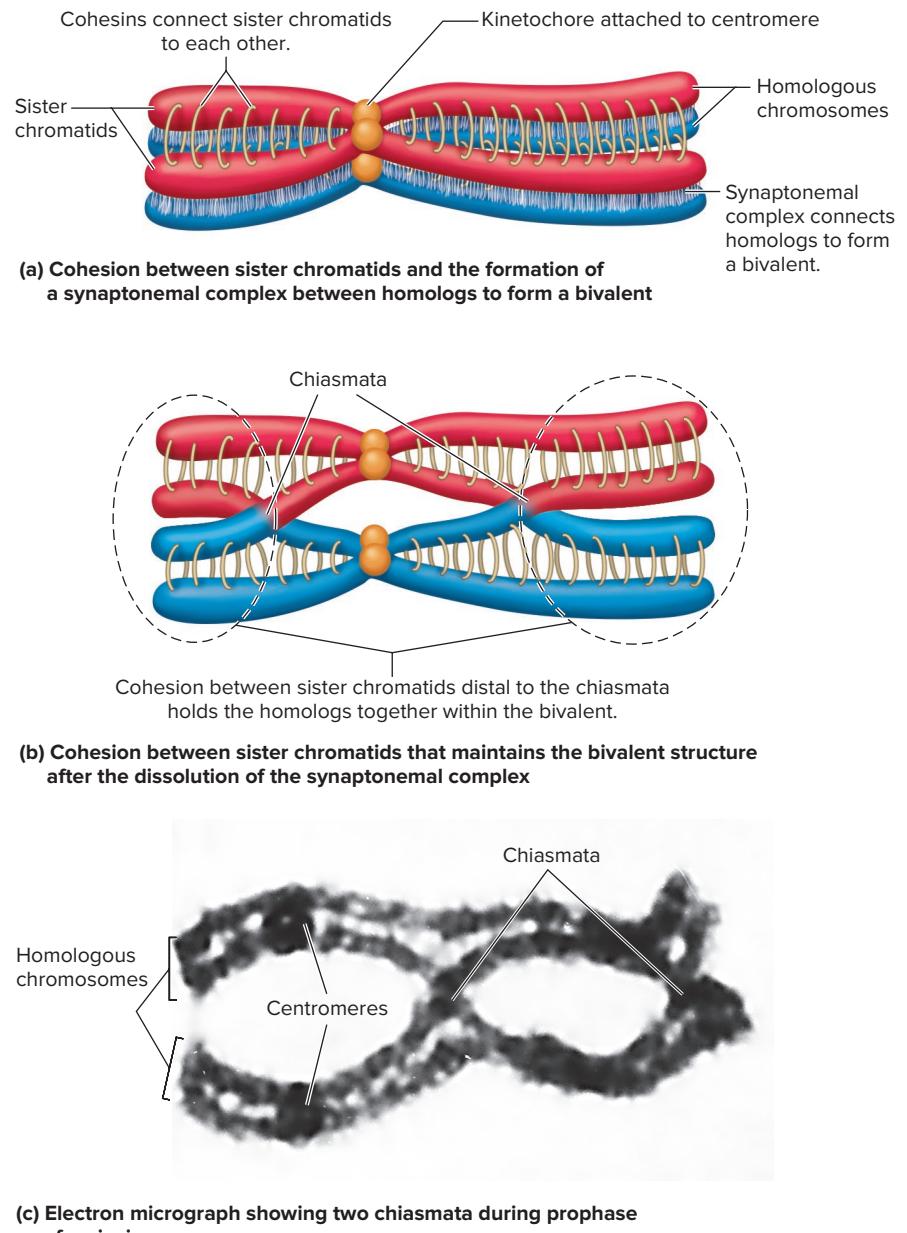
1. What is the function of the kinetochore during mitosis?
  - It promotes the replication of a chromosome to form a dyad.
  - It is a location where a kinetochore microtubule can attach to a chromosome.
  - It promotes the condensation of chromosomes during prophase.
  - Both a and b are correct.

proteins called cohesin. Next, a process called **synapsis** occurs in which the homologous chromosomes recognize each other and begin to align themselves along their entire length. In most species, this process involves the formation of a synaptonemal complex that physically connects the homologous chromosomes to each other (Figure 2.10a). The associated chromatids now form a structure called a **bivalent**, which contains two pairs of sister chromatids, or a total of four chromatids. A bivalent is also called a **tetrad** (from the prefix *tetra-*, meaning “four”) because it is composed of four chromatids—that is, four monads.

**Chiasma Formation.** The next key event is **chiasma formation**, also known as **crossing over**. Chiasma formation involves a physical exchange of chromosome pieces. At a chiasma, the DNA within a chromatid from each homolog breaks at the same location and then attaches to its homolog. The term **chiasma** (plural: **chiasmata**) was coined because a chiasma physically resembles the Greek letter chi,  $\chi$ . In Figure 2.10b, two chiasmata have formed. We will consider the genetic consequences of crossing over in Chapter 6 and the molecular process of crossing over in Chapter 19.

**Dissolution of the Synaptonemal Complex.** After chiasma formation, the synaptonemal complex dissociates from the chromatids. Even so, the homologs still remain attached to each other within a bivalent. What holds the homologs together? The answer is cohesin, which holds the sister chromatids together. In the distal region between the chiasmata and the ends of each chromosome, these cohesin links are responsible for keeping the homologs associated with each other and thereby maintain a bivalent structure. (See the regions within the dashed ovals in Figure 2.10b.)

**Multiple Chiasmata.** Depending on the size of the chromosome and the species, an average eukaryotic chromosome incurs from a couple to a couple of dozen crossovers. During spermatogenesis in humans, for example, an average chromosome undergoes slightly more than two crossovers, whereas chromosomes in certain plant species may undergo 20 or more crossovers. Figure 2.10c shows an electron micrograph of a bivalent with two chiasmata. Recent research has shown that crossing over is usually critical for the proper segregation of chromosomes. Abnormalities in chromosome segregation are often related to a defect in crossing over. In a high percentage of people with Down syndrome, in which an individual has three copies of chromosome 21 instead of two, research has shown that the presence of the extra chromosome is associated with a lack of crossing over between homologous chromosomes.

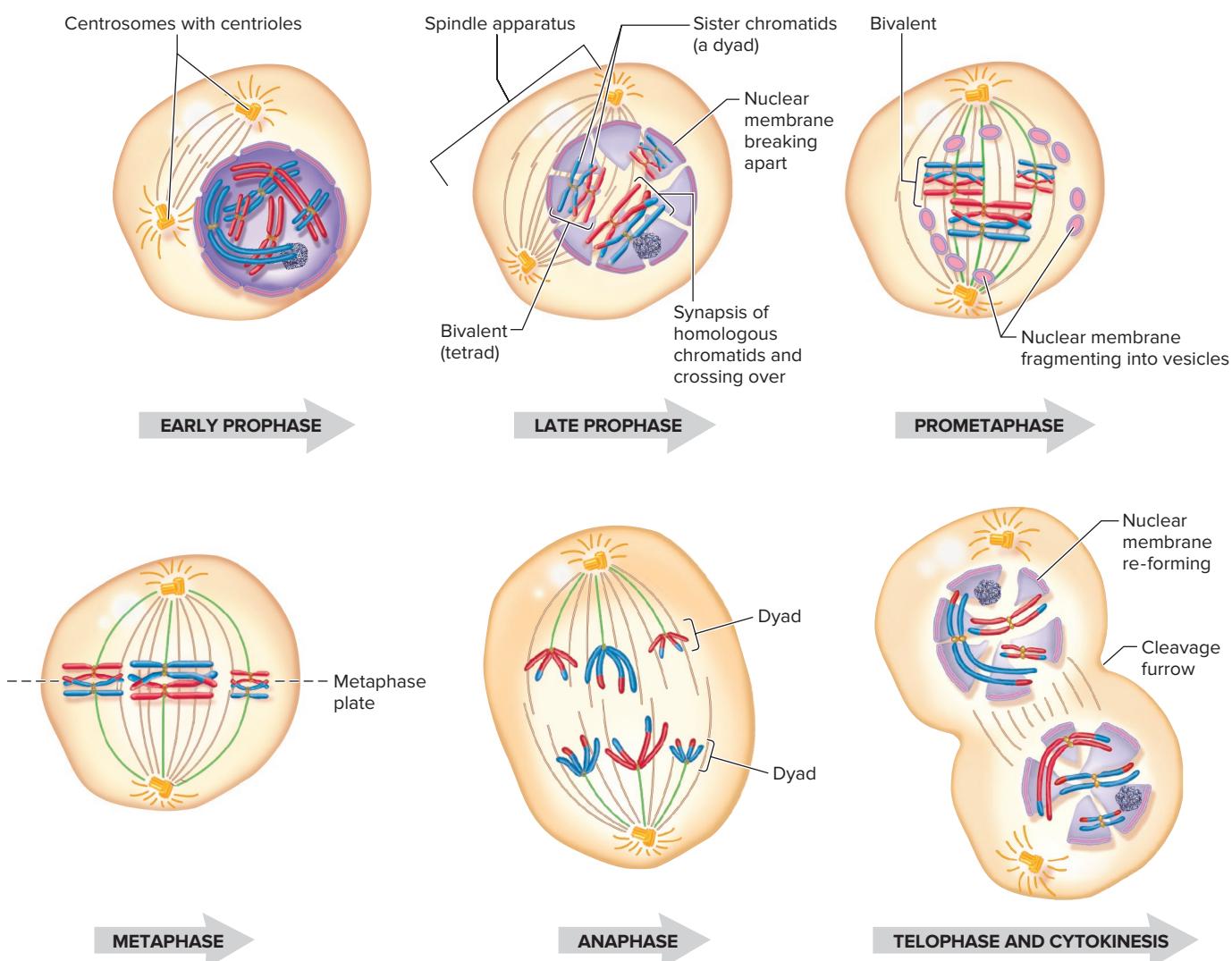
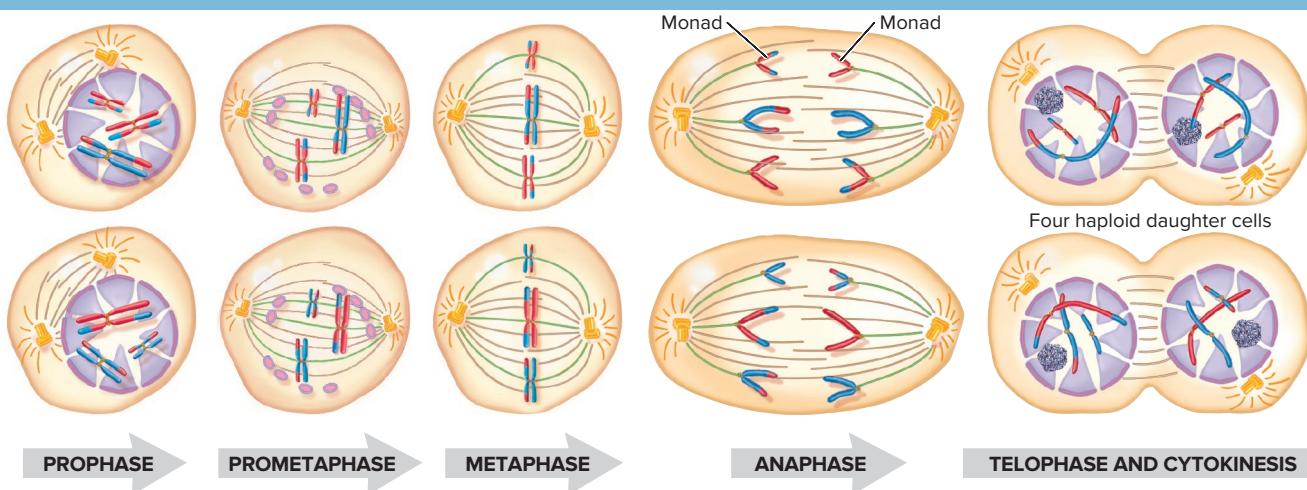


**FIGURE 2.10** Key events that occur during prophase of meiosis I. (a) Prior to prophase, sister chromatids are held together via protein complexes called cohesins. (Note: Cohesins are described in greater detail in Chapter 10; see Section 10.7.) During early prophase, the formation of a synaptonemal complex causes homologous pairs of sister chromatids to associate with each other in a structure called a bivalent. (b) In the middle of prophase, chiasma formation (i.e., crossing over) involves a physical exchange of chromosome pieces. After chiasma formation, the synaptonemal complex dissociates. In the distal region between the chiasmata and the ends of each chromosome, the cohesin links keep the homologs associated with each other to maintain a bivalent structure. (c) A transmission electron micrograph showing two chiasmata.

(c): Stanley K. Sessions

**CONCEPT CHECK:** What is the end result of crossing over?

**Prometaphase of Meiosis I** Figure 2.10 emphasizes the pairing and crossing over that occur during prophase of meiosis I. In **Figure 2.11**, we turn our attention to the general events in meiosis. Prophase of meiosis I is followed by prometaphase, in which the

**MEIOSIS I****MEIOSIS II**

**FIGURE 2.11** The phases of meiosis in an animal cell. See text for details.

**CONCEPT CHECK:** How do the four cells at the end of meiosis differ from the original mother cell?

spindle apparatus is complete, and the chromatids are attached via kinetochore microtubules.

**Metaphase of Meiosis I** At metaphase of meiosis I, the bivalents (tetrads) are organized along the metaphase plate. Before we consider the rest of meiosis I, a particularly critical feature for you to appreciate is how the bivalents are aligned along the metaphase plate. In particular, the pairs of sister chromatids are aligned in a double row rather than a single row, as occurs in mitosis (refer back to Figure 2.8d). Furthermore, the arrangement of sister chromatids (dyads) within this double row is random with regard to the blue and red homologs. In Figure 2.11, one of the blue homologs is above the metaphase plate and the other two are below, whereas one of the red homologs is below the metaphase plate and the other two are above.

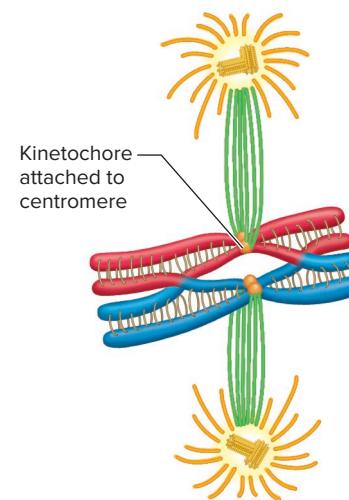
In an organism that produces many gametes, meiosis can produce many different arrangements of homologs in various cells—for example, three blues above and none below, or none above and three below, and so on. As discussed in Chapter 3 (see Section 3.4), the random arrangement of homologs is consistent with Mendel’s law of independent assortment.

Because most eukaryotic species have several chromosomes per set, the sister chromatids can be randomly aligned along the metaphase plate in many possible ways. Let’s consider humans, who have 23 chromosomes per set. The possible number of different random alignments equals  $2^n$ , where  $n$  is the number of chromosomes per set. Thus, in humans, there are  $2^{23}$ , or over 8 million, possibilities! Because the homologs are genetically similar but not identical, we see from this calculation that the random alignment of homologous chromosomes provides a mechanism to promote a vast amount of genetic diversity.

In addition to the random arrangement of homologs within a double row, a second distinctive feature of metaphase of meiosis I is the attachment of kinetochore microtubules to the sister chromatids (Figure 2.12). One pair of sister chromatids is linked to one of the poles, and the homologous pair is linked to the opposite pole. This arrangement is quite different from the kinetochore attachment sites during mitosis, in which a pair of sister chromatids is linked to both poles (see Figure 2.8).

**Anaphase of Meiosis I** At the start of anaphase of meiosis I, the cohesins along the arms of sister chromatids are released, thereby allowing the two pairs of sister chromatids within a bivalent to separate from each other (see Figure 2.11). However, the connection at the centromere remains intact so the sister chromatids remain attached to each other. Each joined pair of chromatids migrates to one pole, and the homologous pair of chromatids moves to the opposite pole. Another way of saying this is that the two dyads within a tetrad separate from each other and migrate to opposite poles.

**Telophase of Meiosis I** Finally, at telophase of meiosis I, the sister chromatids have reached their respective poles, and decondensation occurs in most, but not all, species. In many species, the nuclear membrane re-forms to produce two separate nuclei. In the example of Figure 2.11, the end result of meiosis I is two cells,



**FIGURE 2.12** Attachment of the kinetochore microtubules to replicated chromosomes at metaphase of meiosis I. The kinetochore microtubules from a given pole are attached to one pair of chromatids in a bivalent, but not both. Therefore, each pair of sister chromatids is attached to only one pole.

**CONCEPT CHECK:** How is the attachment of chromosomes to kinetochore microtubules during metaphase of meiosis I different from their attachment during metaphase of mitosis?

each with three pairs of sister chromatids. A reduction division has occurred. The original diploid cell had its chromosomes in homologous pairs, but the two cells produced at the end of meiosis I are considered to be haploid; they do not have pairs of homologous chromosomes. The reduction division occurs because the connection holding the sister chromatids together does not break during anaphase.

**Meiosis II** The sorting events that occur during meiosis II are similar to those that occur during mitosis, but the starting point is different. For a diploid organism with six chromosomes, mitosis begins with 12 chromatids that are joined as six pairs of sister chromatids (refer back to Figure 2.8). In other words, mitosis begins with six dyads in this case. By comparison, in such a diploid organism, the two cells that begin meiosis II each have six chromatids that are joined as three pairs of sister chromatids; meiosis II begins with three dyads in this case. Otherwise, the steps that occur during prophase, prometaphase, metaphase, anaphase, and telophase of meiosis II are analogous to a mitotic division.

**Meiosis Versus Mitosis** If we compare the outcome of meiosis (see Figure 2.11) to that of mitosis (see Figure 2.8), the results are quite different. In the examples we examined, mitosis produced two diploid daughter cells with six chromosomes each, whereas meiosis produced four haploid daughter cells with three chromosomes each. In other words, meiosis halved the number of chromosomes per cell. **Table 2.1** describes key differences between mitosis and meiosis that account for the different outcomes of the two processes.

**TABLE 2.1****A Comparison of Mitosis, Meiosis I, and Meiosis II**

Phase	Event	Mitosis	Meiosis I	Meiosis II
Prophase	Synapsis	No	Yes	No
Prophase	Crossing over	Rarely	Commonly	Rarely
Prometaphase	Attachment to the poles	A pair of sister chromatids to both poles	A pair of sister chromatids to one pole	A pair of sister chromatids to both poles
Metaphase	Alignment along the metaphase plate	Sister chromatids	Bivalents	Sister chromatids
Anaphase	Separation of:	Sister chromatids	Bivalents	Sister chromatids
End result		Two diploid cells		Four haploid cells

With regard to alleles, the results of mitosis and meiosis are also different. The daughter cells produced by mitosis are genetically identical. However, the haploid cells produced by meiosis are not genetically identical to each other because they contain only one homologous chromosome from each pair. In Section 3.4 of Chapter 3, we will consider how the haploid cells may differ in the alleles that they carry on their homologous chromosomes (look ahead to Figures 3.12 and 3.13).

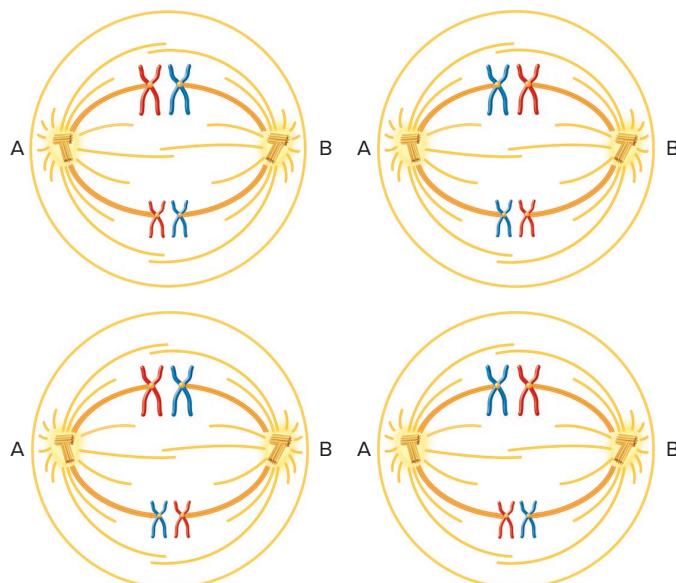
**GENETIC TIPS**

**THE QUESTION:** If a diploid cell contains four chromosomes (i.e., two per set), how many possible random arrangements of homologs can occur during metaphase of meiosis I?

**T**OPIC: **What topic in genetics does this question address?** The topic is meiosis. More specifically, the question is about metaphase of meiosis I.

**I**NFORMATION: **What information do you know based on the question and your understanding of the topic?** From the question, you know that a cell that started with two pairs of homologous chromosomes has entered meiosis and is now in metaphase of meiosis I. From your understanding of the topic, you may remember that bivalents align along the metaphase plate (see Figure 2.11). The orientations of the homologs within the bivalents are random.

**P**ROBLEM-SOLVING **S**TRATEGY: **Make a drawing. Make a calculation.** One strategy to solve this problem is to make a drawing in which the homologs are different colors, such as red and blue. Note: The spindle poles are labeled A and B in the drawing in the upper right column. The alignment occurs relative to the spindle poles.

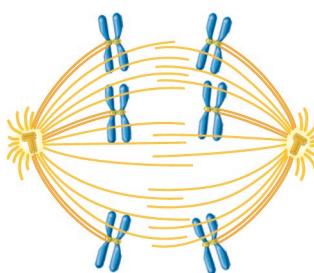


Another strategy is to make a calculation in which the number of different random alignments equals  $2^n$ , where  $n$  is the number of chromosomes per set.

**ANSWER:** In the drawing, the number of random alignments is 4. From a calculation, the number of random alignments equals  $2^n$ . So the possible number of arrangements in this case is  $2^2$ , which equals 4.

**2.4 COMPREHENSION QUESTIONS**

- When does crossing over usually occur, and what is the end result?
  - It occurs during prophase of meiosis I, and the end result is the exchange of pieces between homologous chromosomes.
  - It occurs during prometaphase of meiosis I, and the end result is the exchange of pieces between homologous chromosomes.
  - It occurs during prophase of meiosis I, and the end result is the separation of sister chromatids.
  - It occurs during prometaphase of meiosis I, and the end result is the separation of sister chromatids.
- Which phase of meiosis is depicted in the drawing to the right?
  - Metaphase of meiosis I
  - Metaphase of meiosis II
  - Anaphase of meiosis I
  - Anaphase of meiosis II



## 2.5 SEXUAL REPRODUCTION

### Learning Outcomes:

1. Define sexual reproduction.
2. Describe how animals make sperm and egg cells.
3. Explain how plants alternate between haploid and diploid generations.

In the previous section, we considered how a diploid cell divides by meiosis to produce cells with half the genetic material of the original mother cell. This process is critical for sexual reproduction, which is a common way for eukaryotic organisms to produce offspring. During **sexual reproduction**, two gametes fuse with each other in the process of fertilization to begin the development of a new organism.

Gametes are highly specialized cells that are produced by a process called **gametogenesis**. As discussed previously, gametes are typically haploid, which means they contain half the number of chromosomes found in diploid cells. Haploid cells are represented by  $1n$  and diploid cells by  $2n$ , where  $n$  refers to a set of chromosomes. A haploid gamete contains a single set of chromosomes, whereas a diploid cell has two sets. For example, a diploid human cell contains two sets of chromosomes, for a total of 46, but a human gamete (sperm or egg cell) contains only a single set of 23 chromosomes.

Some simple eukaryotic species are **isogamous**, which means that their gametes are morphologically similar. Examples of isogamous organisms include many species of fungi and algae. Most eukaryotic species, however, are **heterogamous**—they produce two morphologically different types of gametes. Male gametes, or **sperm cells**, are relatively small and usually travel relatively far distances to reach the female gamete—the **egg cell**, or **ovum**.

The mobility of the sperm is an important characteristic, making it likely that it will come in close proximity to the egg cell. The sperm of most animal species contain a single flagellum that enables them to swim. The sperm of ferns and nonvascular plants, such as bryophytes, may have multiple flagella. In flowering plants, however, the sperm are contained within pollen grains. A pollen grain is a small mobile structure that can be carried by the wind or on the feet or hairs of insects. In flowering plants, sperm are delivered to egg cells via pollen tubes. Compared with sperm cells, an egg cell is usually very large and nonmotile. In animal species, the egg stores a large amount of nutrients to nourish the growing embryo. In this section, we will examine how sperm and egg cells are made in animal and plant species.

### In Animals, Spermatogenesis Produces Four Haploid Sperm Cells and Oogenesis Produces a Single Haploid Egg Cell

In male animals, **spermatogenesis**, the production of sperm cells, occurs within glands known as the testes. The testes contain spermatogonial cells that divide by mitosis to produce two cells. One of these remains a spermatogonial cell, and the other cell becomes a primary spermatocyte. As shown in **Figure 2.13a**, the spermatocyte advances through meiosis I and meiosis II to produce four

haploid cells, which are known as spermatids. These cells then mature into sperm cells. The structure of a sperm cell includes a long flagellum and a head. The head of the sperm contains little more than a haploid nucleus and an organelle known as an acrosome, at its tip. The acrosome contains digestive enzymes that are released when a sperm meets an egg cell. These enzymes enable the sperm to penetrate the outer protective layers of the egg cell and gain entry into the cell's cytosol. In animal species without a mating season, sperm production is a continuous process in mature males. A mature human male, for example, may produce several hundred million sperm each day.

In female animals, **oogenesis**, the production of egg cells, occurs within specialized diploid cells of the ovary known as oogonia. Quite early in the development of the ovary, the oogonia initiate meiosis to produce primary oocytes. For example, in human females, approximately 1 million primary oocytes per ovary are produced before birth. These primary oocytes are arrested—enter a dormant phase—at prophase of meiosis I, and they remain at this stage until the female becomes sexually mature. At maturity, primary oocytes are periodically activated to advance through meiosis I to an early stage of meiosis II. If fertilization occurs, the oocyte nucleus completes meiosis II.

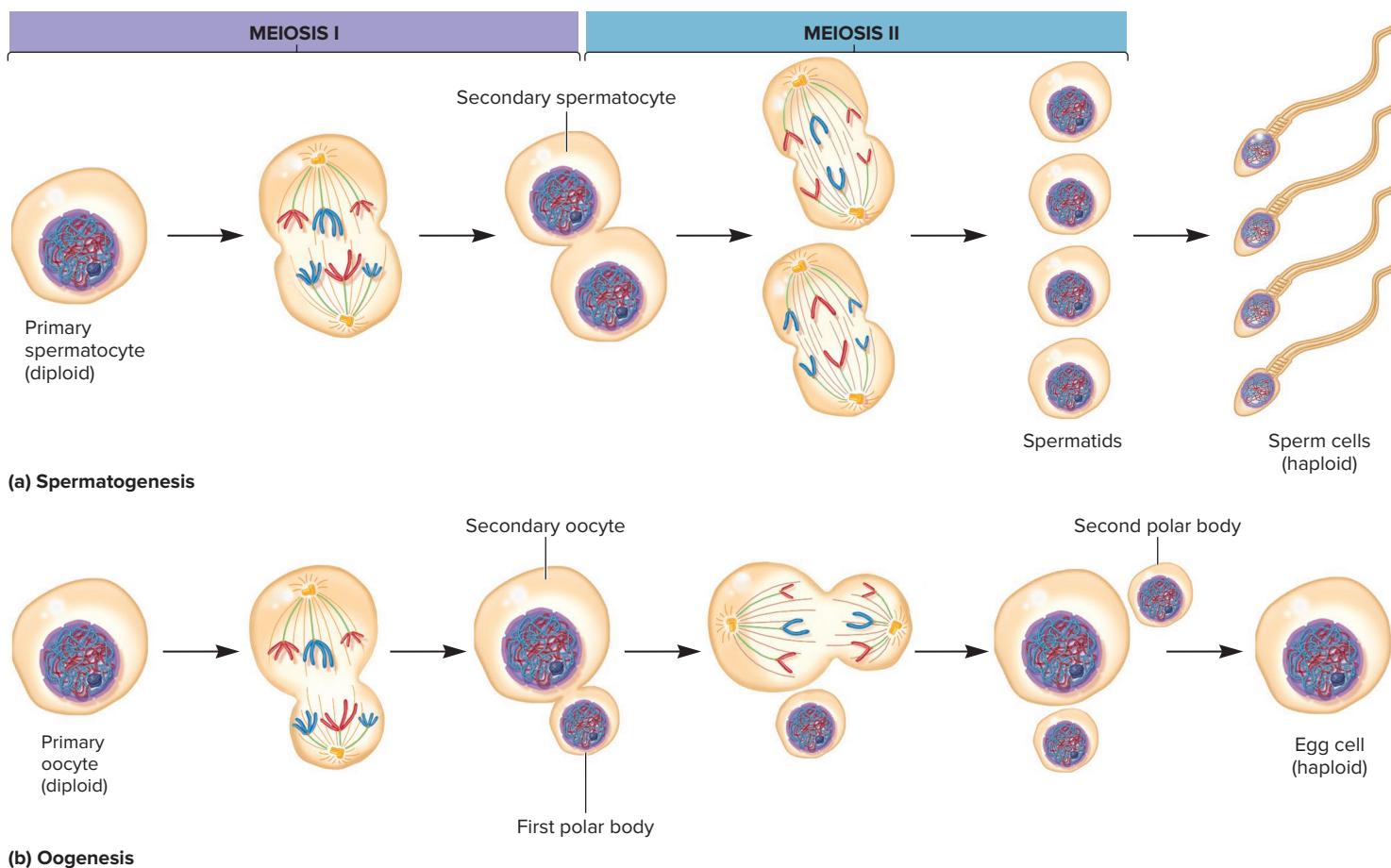
During oocyte maturation, meiosis produces only one cell that is destined to become an egg, as opposed to the four gametes produced from each primary spermatocyte during spermatogenesis. How does oogenesis occur? As shown in **Figure 2.13b**, the first meiotic division is asymmetrical and produces a secondary oocyte and a much smaller cell, known as a polar body. Most of the cytoplasm is retained by the secondary oocyte and very little by the polar body, making the oocyte the larger cell with more stored nutrients. The secondary oocyte then begins meiosis II.

In mammals, the secondary oocyte is released from the ovary—an event called ovulation—and travels down the oviduct toward the uterus. During this journey, if a sperm cell penetrates the secondary oocyte, it is stimulated to complete meiosis II; in this case, the secondary oocyte produces a haploid egg and a second polar body. The haploid nuclei of the egg and sperm then unite to create the diploid nucleus of a new individual.

### Plant Species Alternate Between Haploid (Gametophyte) and Diploid (Sporophyte) Generations

Most species of animals are diploid, and their haploid gametes are considered to be a specialized type of cell. By comparison, the life cycles of plant species alternate between haploid and diploid generations. The haploid generation is called the **gametophyte**, whereas the diploid generation is called the **sporophyte**. Certain cells in the sporophyte undergo meiosis and produce haploid cells called spores, which divide by mitosis to produce a gametophyte.

- In simpler plants, such as mosses, a haploid spore can produce a large multicellular gametophyte by repeated mitoses and cellular divisions.
- In flowering plants, spores develop into gametophytes that contain only a few cells. In this case, the organism that we think of as a plant is the sporophyte, whereas the gametophyte



**FIGURE 2.13** Gametogenesis in animals. (a) Spermatogenesis. A diploid spermatocyte undergoes meiosis to produce four haploid ( $1n$ ) spermatids. These differentiate during spermatogenesis to become mature sperm. (b) Oogenesis. A diploid oocyte undergoes meiosis to produce one haploid egg cell and two or three polar bodies. In some species, the first polar body divides; in other species, it does not. Because of asymmetrical cytokinesis, the amount of cytoplasm the egg receives is maximized. The polar bodies degenerate.

Note: In some species, such as humans, the oocyte completes meiosis II when fertilization takes place.

**CONCEPT CHECK:** What are polar bodies?

is very inconspicuous. The gametophytes of most plant species are small structures produced within the much larger sporophyte. Certain cells within the haploid gametophytes then become specialized as haploid gametes.

**Figure 2.14** provides an overview of gametophyte development and gametogenesis in flowering plants, using as an example a flower from an angiosperm (a plant that produces seeds within an ovary). Meiosis occurs within cells found in two different structures of the sporophyte: the anthers and the ovaries, which produce male and female gametophytes, respectively.

In the anther, diploid cells called microsporocytes undergo meiosis to produce four haploid microspores. These separate into individual microspores. In many angiosperms, each microspore undergoes mitosis to produce a two-celled structure containing one tube cell and one generative cell, both of which are haploid. This structure differentiates into a **pollen grain**, which is the male gametophyte and has a thick cell wall. Later, the generative cell undergoes a mitotic cell division to produce two haploid sperm

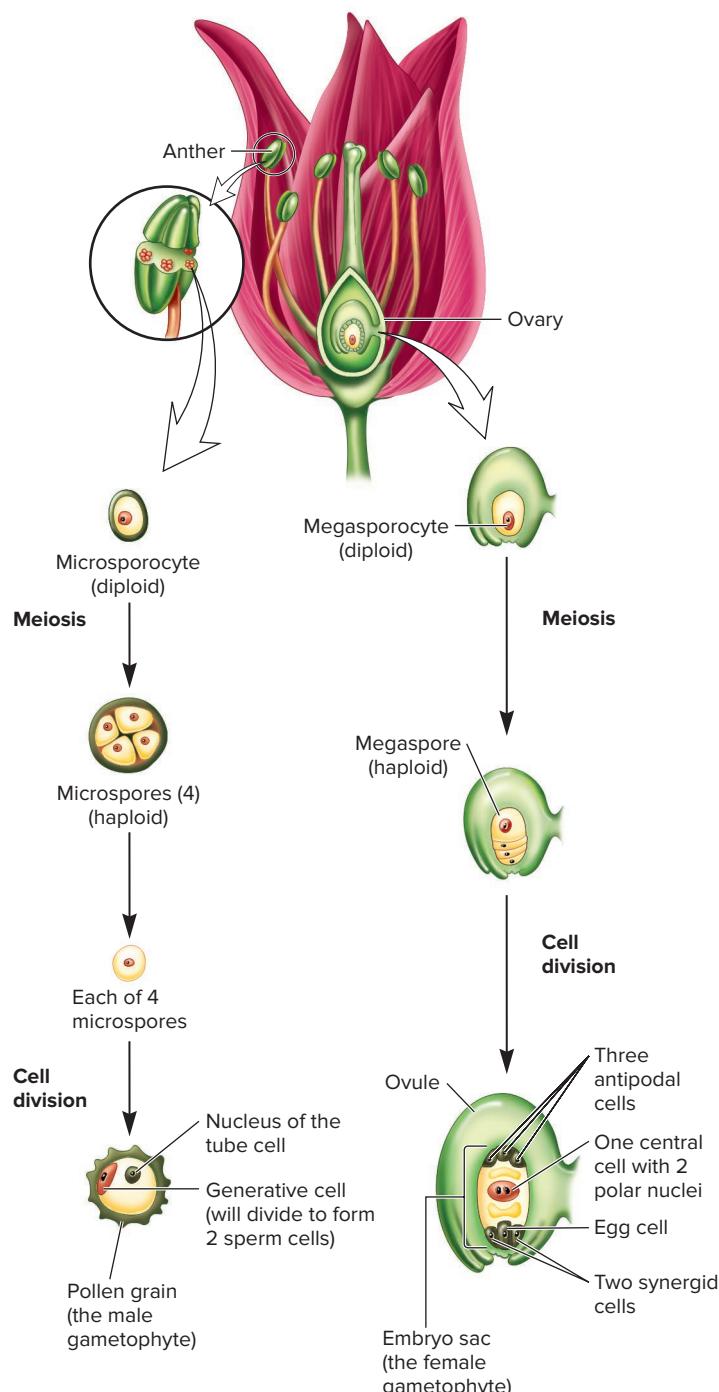
cells. In most plant species, this division occurs only if the pollen grain germinates—if it lands on a stigma and forms a pollen tube (look ahead to Figure 3.2c).

By comparison, female gametophytes are produced within ovules found in the plant ovaries. A type of cell known as a megasporocyte undergoes meiosis to produce four haploid megasporocytes. Three of the four megasporocytes degenerate. The remaining haploid megasporocyte then undergoes three successive mitotic divisions accompanied by asymmetric cytokinesis to produce seven individual cells—one egg, two synergids, three antipodal cells, and one central cell. This seven-celled structure, also known as the **embryo sac**, is the mature female gametophyte. Each embryo sac is contained within an ovule.

For fertilization to occur, specialized cells within the male and female gametophytes must meet. The steps of plant fertilization are described in Chapter 3.

1. To begin this process, a pollen grain lands on a stigma (look ahead to Figure 3.2c).





**FIGURE 2.14** The formation of male and female gametes by the gametophytes of angiosperms (flowering plants).

**CONCEPT CHECK:** Are all cell nuclei in the embryo sac haploid or is just the egg cell haploid?

- This stimulates the tube cell to sprout a pollen tube that grows through the style and eventually makes contact with an ovule. As this is occurring, the generative cell undergoes mitosis to produce two haploid sperm cells. The sperm cells migrate through the pollen tube and eventually reach the ovule.

- One of the sperm enters the central cell, which contains the two polar nuclei. This results in a cell that is triploid ( $3n$ ). This cell divides mitotically to produce **endosperm**, which acts as a food-storing tissue. The other sperm enters the egg cell. The egg and sperm nuclei fuse to create a diploid cell, the zygote, which becomes a plant embryo. Therefore, fertilization in flowering plants is actually a double fertilization. The result is that the endosperm, whose production uses a large amount of plant resources, will develop only when an egg cell has been fertilized.
- After fertilization is complete, the ovule develops into a seed, and the surrounding ovary develops into the fruit, which encloses one or more seeds.

When comparing animals and plants, it's interesting to consider how gametes are made. Animals produce gametes by meiosis. In contrast, plants produce gametes by mitosis. The gametophyte of plants is a haploid multicellular organism produced by mitotic cellular divisions of a haploid spore. Within the multicellular gametophyte, certain cells become specialized as gametes.

## 2.5 COMPREHENSION QUESTIONS

- In animals, a key difference between spermatogenesis and oogenesis is that
  - only oogenesis involves meiosis.
  - only spermatogenesis involves meiosis.
  - spermatogenesis produces four sperm, whereas oogenesis produces only one egg cell.
  - None of the above describes a difference between the two processes.
- Which of the following statements regarding plants is *false*?
  - Meiosis within anthers produces spores that develop into pollen.
  - Meiosis within ovules produces spores that develop into an embryo sac.
  - The male gametophyte is a pollen grain, and the female gametophyte is an embryo sac.
  - Meiosis directly produces sperm and egg cells in plants.

## 2.6 SEX CHROMOSOMES AND SEX DETERMINATION

### Learning Outcomes:

- Define *sex chromosomes* and *sex determination*.
- Outline different mechanisms of sex determination.

In the preceding section, we considered how sexual reproduction involves the production and subsequent union of male and female gametes—sperm and egg. In most species of animals, sperm are produced by males, whereas eggs are produced by females. Males and females are said to be of different sexes. However, some animal

species produce hermaphrodites in which the same individual can make both male and female gametes. In most species of flowering plants, a single individual (a sporophyte) produces both male gametophytes and female gametophytes. Such species are called **monoecious**. However, in other plant species, the sporophytes are divided into those that produce only male gametophytes and those that produce only female gametophytes. Such species are called **dioecious**.

In 1901, Clarence McClung, who studied grasshoppers, was the first to suggest that male and female sexes are due to the inheritance of particular chromosomes. The term **sex chromosomes** refers to chromosomes that differ between males and females. Sex chromosomes are found in most species of animals and a few species of dioecious plants. For example, in mammals and fruit flies, the sex chromosomes are designated X and Y. In this section, we will explore difference mechanisms that give rise to male or female individuals, a process called **sex determination**.

### Sex Differences May Depend on the Presence of Sex Chromosomes or on the Number of Sets of Chromosomes

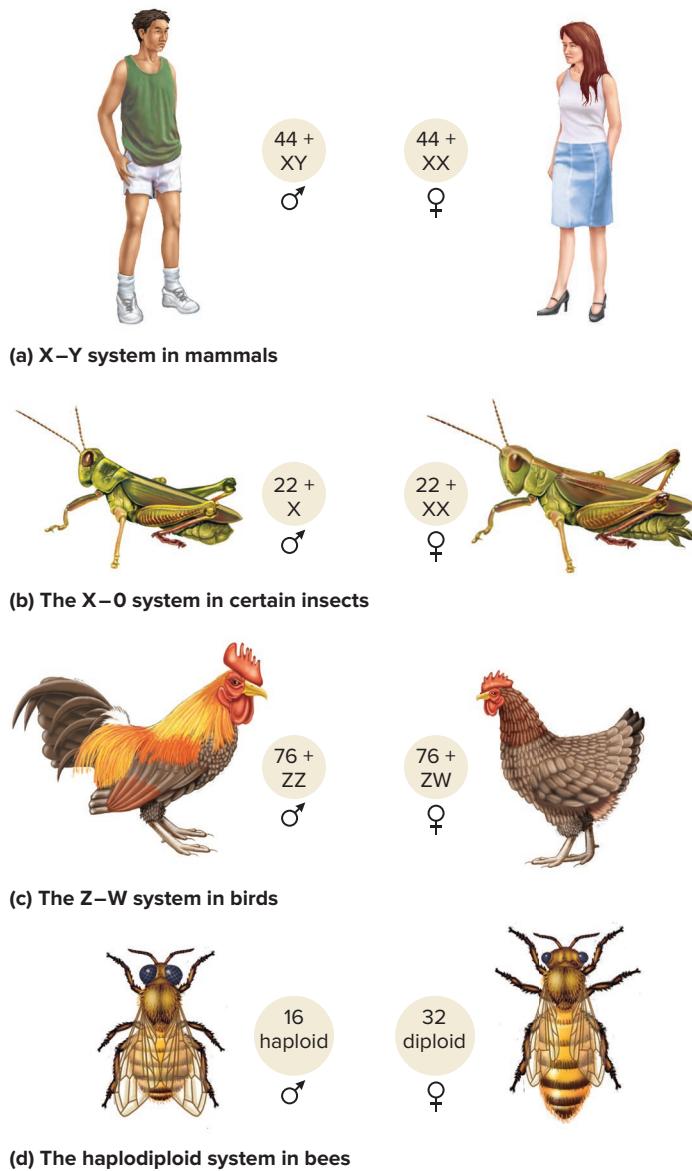
Since McClung's initial observations, we now know that a pair of chromosomes, called the sex chromosomes, determines sex in many different animal species. Some examples are described in **Figure 2.15**.

**X-Y System.** In the X-Y system of sex determination, which operates in mammals, the male has one X chromosome and one Y chromosome, whereas the female has two X chromosomes (Figure 2.15a). In this case, the male is called the **heterogametic sex**. Two types of sperm are produced: one type that carries only the X chromosome, and another type that carries the Y. The female is the **homogametic sex** because all eggs carry a single X chromosome.

The 46 chromosomes in humans consist of 1 pair of sex chromosomes and 22 pairs of **autosomes**—chromosomes that are not sex chromosomes. In the human male, each of the four sperm produced during gametogenesis contains 23 chromosomes. Two sperm contain an X chromosome, and the other two have a Y chromosome. The sex of the offspring is determined by whether the sperm that fertilizes the egg carries an X or a Y chromosome.

What causes an offspring to develop into a male or female? One possibility is that two X chromosomes are required for female development. A second possibility is that the Y chromosome promotes male development. In the case of mammals, the second possibility is correct. This is known from the analysis of rare individuals who carry chromosomal abnormalities. For example, mistakes that occasionally occur during meiosis may produce an individual who carries two X chromosomes and one Y chromosome. Such an individual develops into a male. As discussed in Chapter 26, the *SRY* gene on the Y chromosome plays a key role in causing the development of male characteristics.

**X-O System.** The X-O system of sex determination operates in many insects (Figure 2.15b). In such species, the male has one sex chromosome (the X) and is designated X0, whereas the female has a pair of sex chromosomes (two X's). In other insect species, such as *Drosophila melanogaster*, the male is XY. For both types of insect species (i.e., having X0 males and XX females or having XY males and XX females), the ratio between X chromosomes



**FIGURE 2.15** Different mechanisms of sex determination in animals. See the text for a description.

**CONCEPT CHECK:** What is the difference between the X-Y and X-O systems of sex determination?

and the number of autosomal sets determines sex. If a fly has one X chromosome and is diploid for the autosomes ( $2n$ ), the ratio is  $1/2$ , or 0.5. This fly will become a male even if it does not receive a Y chromosome. In contrast to the X-Y system of mammals, the Y chromosome in the X-O system does not determine maleness. If a fly receives two X chromosomes and is diploid, the ratio is  $2/2$ , or 1.0, and the fly becomes a female.

**Z-W System.** In the Z-W system, which determines sex in birds and some fish, the male is ZZ and the female is ZW (Figure 2.15c). The letters Z and W are used to distinguish these types of sex chromosomes from those found in the X-Y pattern of sex determination of other species. In the Z-W system, the male is the homogametic sex, and the female is heterogametic.

**Haplodiploid System.** In addition to sex chromosomes, sex determination in other species is determined by the number of sets of chromosomes. For example, the haplodiploid system is found in bees (Figure 2.15d). The male bee, called the drone, is produced from unfertilized haploid eggs. Female bees, both worker bees and queen bees, are produced from fertilized eggs and therefore are diploid.

## Sex Differences May Depend on the Environment

Although sex in many species is determined by chromosomes, other mechanisms are also known. In certain reptiles and fish, sex is controlled by environmental factors such as temperature. For example, in the American alligator (*Alligator mississippiensis*), temperature controls sex development (Figure 2.16a). The temperature-sensitive period is between 7 and 21 days after laying. Temperatures  $\leq 30^{\circ}\text{C}$  produce all female offspring, whereas those  $\geq 34^{\circ}\text{C}$  yield all male offspring. Temperatures between  $30^{\circ}\text{C}$  and  $34^{\circ}\text{C}$  result in batches of both sexes.

Recent research suggests that a thermosensitive protein called TRPV4 is present within the developing alligator gonad inside the egg shell. This protein is functional at warm temperatures, at or above  $34^{\circ}\text{C}$ , and can activate cell signaling by inducing calcium ion influx into cells. The results indicate that TRPV4 may play a key role in promoting the sex determination pathway that gives rise to males.

Another way that sex can be environmentally determined is via behavior. Clownfish of the genus *Amphiprion* are coral reef fish that live among anemones on the ocean floor (Figure 2.16b). One anemone typically harbors a harem of clownfish consisting of a large female, a medium-sized reproductive male, and small nonreproductive juveniles. Clownfish are **protandrous hermaphrodites**—they can switch from male to female! When the female of a harem dies, the reproductive male changes sex to become a female and the largest of the juveniles matures into a reproductive male. Unlike male and female humans, the sexes of clownfish are not determined by chromosome differences. Male and female clownfish have the same chromosomal composition.

How can a clownfish switch from female to male? A juvenile clownfish has both male and female immature sexual organs. Hormone levels, particularly those of an androgen called testosterone and an estrogen called estradiol, control the expression of particular genes. In nature, the first sexual change that usually happens is that a juvenile clownfish becomes a male. This occurs when the testosterone level becomes high, which promotes the expression of genes that code proteins that cause the male organs to mature. Later, when the female of the harem dies, the estradiol level in the reproductive male becomes high and testosterone is decreased. This alters gene expression in a way that leads to the synthesis of some new proteins and prevents the synthesis of others. When this occurs, the female organs grow and the male reproductive system degenerates. The male fish becomes female.

What factor determines the hormone levels in clownfish? A female seems to control the other clownfish in the harem through aggressive dominance, thereby preventing the formation of other females. This aggressive behavior suppresses an area of the brain in the other clownfish that is responsible for the production of certain hormones that are needed to promote female development.



(a) Sex determination via temperature:  
American alligator (*A. mississippiensis*)



(b) Sex determination via behavior:  
Clownfish (*Amphiprion ocellaris*)

**FIGURE 2.16** Sex determination caused by environmental factors. (a) In the alligator, temperature determines whether an individual develops into a female or male. (b) In clownfish, males can change into females due to behavioral changes that occur when a dominant female dies.

(a) NASA; (b) Krzysztof Odziomek/iStock/Getty Images

**CONCEPT CHECK:** How might global warming affect alligator populations?

If a clownfish is left by itself in an aquarium, it will automatically develop into a female because this suppression does not occur.

## Dioecious Plant Species Have Opposite Sexes

As mentioned, in most flowering plants, including pea plants discussed in Chapter 3, a single diploid individual (a sporophyte) produces both female and male gametophytes, which are haploid and produce egg or sperm cells, respectively (see Figure 2.14). However, some plant species are dioecious, which means that some individuals produce only male gametophytes, whereas others produce only female gametophytes. These species include holies (Figure 2.17a), willows, and ginkgo trees.

(a) American holly (*I. opaca*)(b) Female and male flowers on separate individuals in white campion (*S. latifolia*)**FIGURE 2.17 Examples of dioecious plants in which individuals produce only male gametophytes or only female gametophytes.**

(a) American holly (*Ilex opaca*). The female sporophyte, which produces red berries, is shown here. (b) White campion (*Silene latifolia*), which is often studied by researchers.

(a) valentino cazzanti/Shutterstock; (b, c) Arco Images GmbH/Alamy Stock Photo

The genetics of sex determination in dioecious plant species is beginning to be understood. To study this process, many researchers have focused their attention on the white campion, *Silene latifolia*, which is a relatively small dioecious plant with a short generation time (Figure 2.17b). In this species, sex chromosomes, designated X and Y, are responsible for sex determination. The male plant has X and Y chromosomes, whereas the female plant is XX. Sex chromosomes are also found in other plant species such as papaya and spinach. However, in other dioecious species, cytological examination of the chromosomes does not reveal distinct types of sex chromosomes. Even so, in these plant species, the male plants usually appear to be the heterogametic sex.

**2.6 COMPREHENSION QUESTIONS**

1. Among different species, sex may be determined by
  - a. differences in sex chromosomes.
  - b. differences in the number of sets of chromosomes.
  - c. environmental factors.
  - d. all of the above.
2. In mammals, sex is determined by
  - a. the *SRY* gene on the Y chromosome.
  - b. having two copies of the X chromosome.
  - c. having one copy of the X chromosome.
  - d. both a and c.
3. An abnormal fruit fly has two sets of autosomes and is XXY. Such a fly is
  - a. a male.
  - b. a female.
  - c. a hermaphrodite.
  - d. none of the above.

**K E Y T E R M S**

**2.1:** chromosomes, chromatin, prokaryotes, nucleoid, eukaryotes, organelles, nucleus, cytogenetics, cytogeneticist, somatic cell, gametes, germ cells, karyotype, diploid, homologs, alleles, locus (loci)

**2.2:** asexual reproduction, multicellularity, binary fission, cell cycle, interphase, G<sub>1</sub> phase, restriction point, S phase, chromatids, centromere, sister chromatids, dyad, monad, kinetochore, G<sub>2</sub> phase, M phase, mitosis

**2.3:** mitotic spindle apparatus (spindle apparatus, mitotic spindle), microtubule-organizing centers (MTOCs), centrosomes, spindle pole, centrioles, astral microtubules, polar microtubules, kinetochore microtubules, kinetochore, decondensed,

prophase, condensed, prometaphase, metaphase plate, metaphase, anaphase, telophase, cytokinesis, cleavage furrow, cell plate

**2.4:** meiosis, haploid, synapsis, bivalent, tetrad, chiasma formation (crossing over), chiasma (chiasmata)

**2.5:** sexual reproduction, gametogenesis, isogamous, heterogamous, sperm cell, egg cell, ovum, spermatogenesis, oogenesis, gametophyte, sporophyte, pollen grain, embryo sac, endosperm

**2.6:** monoecious, dioecious, sex chromosomes, sex determination, heterogametic sex, homogametic sex, autosomes, protandrous hermaphrodites

## CHAPTER SUMMARY

### 2.1 General Features of Chromosomes

- Chromosomes are structures that contain the genetic material, which is DNA.
- Prokaryotic cells are simple and lack cell compartmentalization, whereas eukaryotic cells contain a cell nucleus and other compartments (see Figure 2.1).
- Chromosomes can be examined under the microscope. An organized representation of the chromosomes from a single cell is called a karyotype (see Figure 2.2).
- In eukaryotic species, the chromosomes are found in sets. Eukaryotic cells are often diploid, which means that each type of chromosome occurs in a homologous pair (see Figure 2.3).

### 2.2 Cell Division

- Bacteria divide by binary fission (see Figure 2.4).
- To divide, eukaryotic cells advance through a cell cycle (see Figure 2.5).
- Prior to cell division, eukaryotic chromosomes are replicated to form sister chromatids (see Figure 2.6).

### 2.3 Mitosis and Cytokinesis

- Chromosome sorting in eukaryotes is achieved via the mitotic spindle apparatus (see Figure 2.7).
- A common way for eukaryotic cells to divide is by mitosis and cytokinesis. Mitosis is divided into prophase, prometaphase, metaphase, anaphase, and telophase (see Figure 2.8).

- During cytokinesis, animal cells divide by forming a cleavage furrow and plant cells form a cell plate (Figure 2.9).

### 2.4 Meiosis

- Another way for eukaryotic cells to divide is via meiosis, which produces four haploid cells. During prophase of meiosis I, homologs synapse and crossing over may occur (see Figures 2.10, 2.11, 2.12, Table 2.1).

### 2.5 Sexual Reproduction

- Animals produce gametes via spermatogenesis and oogenesis (see Figure 2.13).
- Plants exhibit alternation of generations between a diploid sporophyte and a haploid gametophyte. The gametophyte produces gametes (see Figure 2.14).

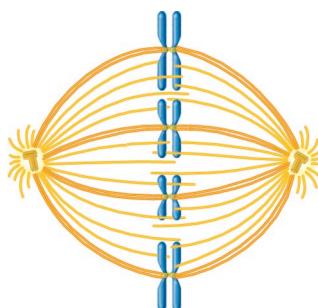
### 2.6 Sex Chromosomes and Sex Determination

- Sex chromosomes are chromosomes that differ between males and females. Sex determination is the process that gives rise to male and female individuals.
- Mechanisms of sex determination may involve differences in chromosome composition or environmental factors (see Figures 2.15, 2.16, 2.17).

## PROBLEM SETS & INSIGHTS

### MORE GENETIC TIPS

**1.** A diploid cell begins with eight chromosomes, four per set, and then proceeds through cell division. In the following diagram, in what phase of mitosis, meiosis I, or meiosis II is the cell?



**T**

**OPIC:** *What topic in genetics does this question address?* The topic is cell division. More specifically, the question is asking you to look at a diagram and discern which phase of cell division it shows.

**I** **INFORMATION:** *What information do you know based on the question and your understanding of the topic?* In the question, you are given a diagram of a cell in a particular phase of the cell cycle. This cell is derived from a mother cell with four pairs of chromosomes. From your understanding of the topic, you may remember the various phases of mitosis, meiosis I, and meiosis II, which are described in Figures 2.8 and 2.11. If so, you may initially realize that the cell is in metaphase.

**P**

**ROBLEM-SOLVING** **S** **TRATEGY:** *Describe the steps.* To solve this problem, you may need to describe the steps, starting with a mother cell that has four pairs of chromosomes. Keep in mind that a mother cell with four pairs of chromosomes has eight chromosomes during G<sub>1</sub>, which then replicate to form eight pairs of sister chromatids during S phase. Therefore, at the beginning of M phase, this mother cell will have eight pairs of sister chromatids. During metaphase of mitosis, the eight pairs of sister chromatids in the mother cell will align in a single row. During meiosis I, four bivalents will align along the metaphase plate in the mother cell. During meiosis II, four pairs of sister chromatids in the two daughter cells will align along the metaphase plate in a single row.

**ANSWER:** The cell is in metaphase of meiosis II. You can tell because the pairs of sister chromatids are lined up in a single row along the metaphase plate, and the cell has only four pairs of sister chromatids. If the diagram was showing mitosis, the cell would have eight pairs of sister chromatids in a single row. If it was showing meiosis I, four bivalents would be aligned along the metaphase plate.

2. What are the key differences in anaphase when comparing mitosis, meiosis I, and meiosis II?

**T OPIC:** *What topic in genetics does this question address?* The topic is cell division. More specifically, the question is about the events that occur during anaphase.

**I NFORMATION:** *What information do you know based on the question and your understanding of the topic?* From the question, you know you are supposed to distinguish the key differences among anaphase of mitosis, anaphase of meiosis I, and anaphase of meiosis II. From your understanding of the topic, you may remember that the separation of chromosomes is distinctly different in meiosis I compared to mitosis and meiosis II. Compare Figures 2.8 and 2.11.

**P ROBLEM-SOLVING S TRATEGY:** *Make a drawing. Compare and contrast.* One strategy to solve this problem is to make a drawing. If you make drawings of a cell in anaphase, like those shown in Figures 2.8 and 2.11, you may appreciate that sister chromatids (dyads) move to opposite poles during anaphase of meiosis I, whereas individual chromatids (monads) move to opposite poles during anaphase of mitosis and meiosis II. Another strategy is to compare and contrast what happens during meiosis I with the events of mitosis and meiosis II. During meiosis I, anaphase does not involve the splitting of centromeres, whereas centromeres split during mitosis and meiosis II, thereby separating sister chromatids.

**ANSWER:** During anaphase in mitosis and meiosis II, the centromeres split and individual chromatids move to their respective poles. In anaphase of meiosis I, the centromeres do not split. Instead, the bivalents separate and pairs of sister chromatids move to opposite poles.

## Conceptual Questions

- C1. The process of binary fission begins with a single mother cell and ends with two daughter cells. Would you expect the mother and daughter cells to be genetically identical? Explain why or why not.
- C2. What is a homolog? With regard to genes and alleles, how are homologs similar to and different from each other?
- C3. What is a sister chromatid? Are sister chromatids genetically similar or identical? Explain.
- C4. With regard to sister chromatids, which phase of mitosis is the organization phase, and which is the separation phase?
- C5. A species is diploid and has three chromosomes per set. Make a drawing that shows what the chromosomes look like in the G<sub>1</sub> and G<sub>2</sub> phases of the cell cycle.
- C6. How does the attachment of kinetochore microtubules to the kinetochore differ in metaphase of meiosis I compared to metaphase of mitosis? Discuss what you think would happen if a sister chromatid was not attached to a kinetochore microtubule.
- C7. For the following events, specify whether each occurs during mitosis, meiosis I, or meiosis II:
  - A. Separation of conjoined chromatids within a pair of sister chromatids
  - B. Pairing of homologous chromosomes
  - C. Alignment of chromatids along the metaphase plate
  - D. Attachment of sister chromatids to both poles

3. Assuming that such a fly would be viable, what would be the sex of a fruit fly with each of the following chromosomal compositions?

- A. One X chromosome and two sets of autosomes
- B. Two X chromosomes, one Y chromosome, and two sets of autosomes
- C. Two X chromosomes and four sets of autosomes
- D. Four X chromosomes, two Y chromosomes, and four sets of autosomes

**T OPIC:** *What topic in genetics does this question address?* The topic is sex determination. More specifically, the question is about sex determination in fruit flies.

**I NFORMATION:** *What information do you know based on the question and your understanding of the topic?* In the question, you are given four examples that describe how many sex chromosomes and how many sets of autosomes a fruit fly has. From your understanding of the topic, you may remember that sex determination in fruit flies follows the X-0 system, in which the ratio of the number of X chromosomes to the number of sets of autosomes determines sex. If that ratio is 1, the fly becomes a female. If it is 0.5, the fly becomes a male. The presence of a Y chromosome does not determine sex in the X-0 system.

**P ROBLEM-SOLVING S TRATEGY:** *Make a calculation.* For each example, you divide the number of X chromosomes by the number of sets of autosomes.
 

- A. 1 divided by 2 equals 0.5.
- B. 2 divided by 2 equals 1.
- C. 2 divided by 4 equals 0.5.
- D. 4 divided by 4 equals 1.

**ANSWER:**

- A. Male
- B. Female
- C. Male
- D. Female

- C8. Identify the key events during meiosis that result in a 50% reduction in the amount of genetic material per cell.
- C9. A cell is diploid and contains three chromosomes per set. Draw the arrangement of the chromosomes during metaphase of mitosis and during metaphase of meiosis I and II. In your drawings, make the sets of chromosomes different colors.
- C10. The alignment of homologs along the metaphase plate during metaphase of meiosis I is random. In your own words, explain what this means.
- C11. A eukaryotic cell is diploid and contains 10 chromosomes (5 in each set). In mitosis and meiosis, how many daughter cells will be produced, and how many chromosomes will each one contain?
- C12. If a diploid cell contains six chromosomes (i.e., three per set), how many possible random arrangements of homologs can occur during metaphase of meiosis I?
- C13. A cell has four pairs of chromosomes. Assuming that crossing over does not occur, what is the probability that a gamete will contain all of the paternal chromosomes? If  $n$  is the number of chromosomes in a set, which of the following expressions can be used to calculate the probability that a gamete will receive all of the paternal chromosomes:  $(1/2)^n$ ,  $(1/2)^{n-1}$ , or  $n^{1/2}$ ?
- C14. With regard to question C13, how would the phenomenon of crossing over affect the results? In other words, would the probability of a gamete inheriting only paternal chromosomes be higher or lower? Explain your answer.
- C15. Eukaryotic cells must sort their chromosomes during mitosis so that each daughter cell receives the correct number of chromosomes. Why don't bacteria need to sort their chromosomes?
- C16. Why is it necessary for the chromosomes to condense during mitosis and meiosis? What do you think might happen if the chromosomes were not condensed?
- C17. Nine-banded armadillos almost always give birth to four offspring that are genetically identical quadruplets. Explain how you think this happens.
- C18. A diploid species has four chromosomes per set for a total of eight chromosomes in its somatic cells. Draw a diagram showing how such a cell would look in late prophase of meiosis II and in prophase of mitosis. Discuss how prophase of meiosis II and prophase of mitosis differ from each other, and explain how the difference originates.
- C19. Explain why the products of meiosis may not be genetically identical, whereas the products of mitosis are.
- C20. The period between meiosis I and meiosis II is called interphase II. Does DNA replication take place during interphase II?
- C21. List several ways in which telophase appears to be the reverse of prophase and prometaphase.
- C22. Corn has 10 chromosomes per set, and the sporophyte of the species is diploid. If you made karyotypes, what is the total number of chromosomes you would expect to see in each of the following types of corn cells?
- A. A leaf cell
  - B. The sperm nucleus of a pollen grain
  - C. An endosperm cell after fertilization
  - D. A root cell
- C23. The arctic fox has 50 chromosomes (25 per set), and the common red fox has 38 chromosomes (19 per set). These species can interbreed to produce viable but infertile offspring. How many chromosomes will the offspring have? What problems do you think may occur during meiosis that would explain the offspring's infertility?
- C24. Let's suppose that a gene affecting pigmentation is found on the X chromosome (in mammals or insects) or the Z chromosome (in birds) but not on the Y or W chromosome. It is found on an autosome in bees. This gene exists in two alleles: *D* (dark) is dominant to *d* (light). What would be the phenotypic results of crosses between true-breeding dark females and true-breeding light males and of the reciprocal crosses involving true-breeding light females and true-breeding dark males for each of the following species? Refer to Figure 2.15 for the mechanism of sex determination in these species.
- A. Birds
  - B. Fruit flies
  - C. Bees
  - D. Humans
- C25. Describe the cellular differences between male and female gametes.
- C26. At puberty in humans, the testes contain a finite number of cells but produce an enormous number of sperm cells during the life span of a male. Explain why testes do not run out of spermatogonial cells.
- C27. Describe the timing of meiosis I and II during human oogenesis.
- C28. Three genes (*A*, *B*, and *C*) are found on three different chromosomes. For the following diploid genotypes, list all of the possible gamete combinations.
- A. *Aa Bb Cc*
  - B. *AA Bb CC*
  - C. *Aa BB Cc*
  - D. *Aa bb cc*
- C29. A female with an abnormally long chromosome 13 (and a normal homolog of chromosome 13) has children with a male with an abnormally short chromosome 11 (and a normal homolog of chromosome 11). What is the probability of producing an offspring that will have both a long chromosome 13 and a short chromosome 11? If such a child is produced, what is the probability that this child will eventually pass both abnormal chromosomes to one of their offspring?
- C30. *Anopheles gambiae* is the mosquito that transmits malaria to humans. Like *Drosophila*, the mosquitos carry X and Y sex chromosomes and follow the X-O mechanism of sex determination. Assuming that such a mosquito would be viable, what would be the sex of a mosquito with each of the following chromosomal compositions?
- A. One X chromosome, one Y chromosome, and two sets of autosomes
  - B. Two X chromosomes, one Y chromosome, and two sets of autosomes
  - C. Two X chromosomes, four Y chromosomes, and four sets of autosomes
  - D. Four X chromosomes, two Y chromosomes, and four sets of autosomes
- C31. What would be the sex of a human with each of the following sets of sex chromosomes?
- A. XXX
  - B. X (also described as X0)
  - C. XYY
  - D. XXY

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## Experimental Questions

- E1. When studying living cells in a laboratory, researchers sometimes use drugs to cause cells to remain in a particular phase of the cell cycle. For example, aphidicolin inhibits DNA synthesis in eukaryotic cells and causes them to remain in the G<sub>1</sub> phase because they cannot replicate their DNA. In what phase of the cell cycle—G<sub>1</sub>, S, G<sub>2</sub>, prophase, metaphase, anaphase, or telophase—would you expect somatic cells to stay if they were treated with each of following types of drug?
- A. A drug that inhibits microtubule formation
  - B. A drug that allows microtubules to form but prevents them from shortening
  - C. A drug that inhibits cytokinesis
  - D. A drug that prevents chromosomal condensation
- E2. How would you set up crosses to determine if a gene is located on the Y chromosome versus one that is located on the X chromosome?
- E3. With regard to thickness and length, what do you think chromosomes would look like if you examined them microscopically during interphase? How would that compare with their appearance during metaphase?
- E4. A rare form of very tall stature that also included hearing loss was found to run in a particular family. It is inherited as a dominant trait. It was discovered that an affected individual had one normal copy of chromosome 15 and one abnormal copy of chromosome 15 that was unusually long. How would you determine if the unusually long chromosome 15 was causing this disorder?
- E5. Experimentally, how do you think researchers were able to determine that the Y chromosome causes maleness in mammals, whereas the ratio of X chromosomes to the sets of autosomes causes sex determination in fruit flies?
- E6. The amount of DNA per cell can be measured experimentally. It is typically expressed in picograms (pg). Let's suppose a human cell in the G<sub>1</sub> phase contains 9 pg of DNA. How much DNA would you expect in a single cell in each of the following phases?
- A. Metaphase of mitosis
  - B. Metaphase of meiosis I
  - C. Metaphase of meiosis II
  - D. After telophase of meiosis II and after cytokinesis

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## Questions for Student Discussion/Collaboration

1. Sex determination among different species is caused by a variety of mechanisms. With regard to evolution, discuss why you think this has happened. During the evolution of life on Earth over the past 4 billion years, do you think the phenomenon of opposite sexes is a relatively recent event?
2. A diploid eukaryotic cell has 10 chromosomes (5 per set). As a group, take turns having one student draw the cell as it would look

during a phase of mitosis, meiosis I, or meiosis II; then have the other students guess which phase it is.

*Note: All answers are available for the instructor in Connect; the answers to the even-numbered questions and all of the Concept Check and Comprehension Questions are in Appendix B.*