# CHAPTER 11
# Meiosis and Sexual Reproduction

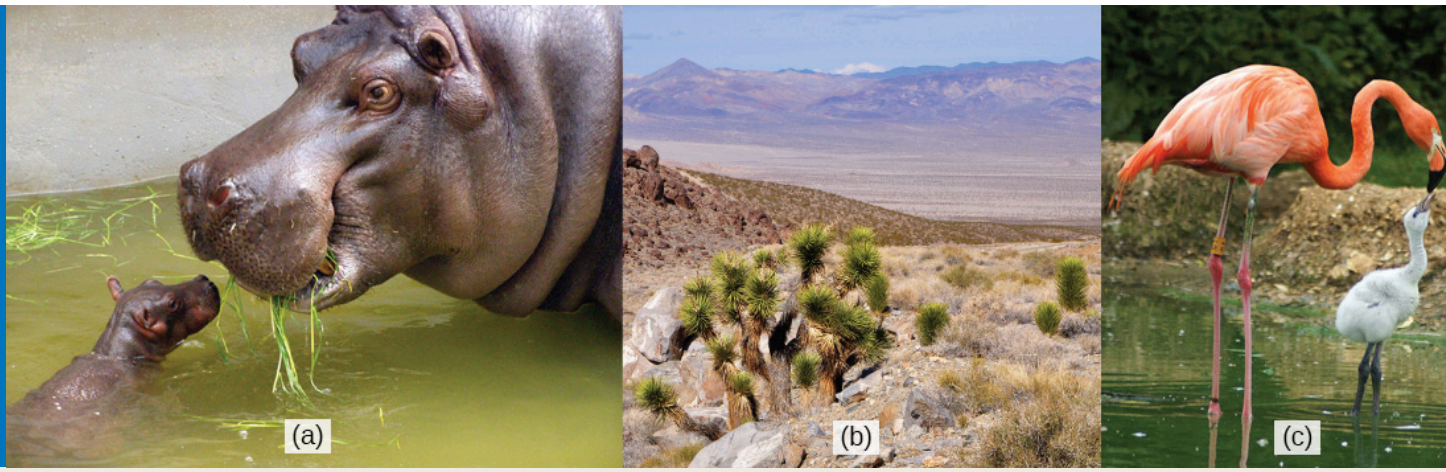



**Figure 11.1** Each of us, like the organisms shown above, begins life as a fertilized egg (zygote). After trillions of cell divisions, each of us develops into a complex, multicellular organism. (credit a: modification of work by Frank Wouters; credit b: modification of work by Ken Cole, USGS; credit c: modification of work by Martin Pettitt)

**INTRODUCTION** The ability to reproduce is a basic characteristic of all organisms: Hippopotamuses give birth to hippopotamus calves; Joshua trees produce seeds from which Joshua tree seedlings emerge; and adult flamingos lay eggs that hatch into flamingo chicks. However, unlike the organisms shown above, offspring may or may not resemble their parents. For example, in the case of most insects such as butterflies (with a complete metamorphosis), the larval forms rarely resemble the adult forms.

Although many unicellular organisms and a few multicellular organisms can produce genetically identical clones of themselves through ***asexual reproduction***, many single-celled organisms and most multicellular organisms reproduce regularly using another method—***sexual reproduction***. This highly evolved method involves the production by parents of two haploid cells and the fusion of two haploid cells to form a single, genetically recombined diploid cell—a genetically unique organism. Haploid cells that are part of the sexual reproductive cycle are produced by a type of cell division called **meiosis**. Sexual reproduction, involving both meiosis and fertilization, introduces variation into offspring that may account for the evolutionary success of sexual reproduction. The vast majority of eukaryotic organisms, both multicellular and unicellular, can or must employ some form of meiosis and fertilization to reproduce.

In most plants and animals, through thousands of rounds of mitotic cell division, diploid cells (whether produced by asexual or sexual reproduction) will develop into an adult organism.

Chapter Outline

# 11.1 The Process of Meiosis

*By the end of this section, you will be able to do the following:*

- Describe the behavior of chromosomes during meiosis, and the differences between the first and second meiotic divisions
- Describe the cellular events that take place during meiosis
- Explain the differences between meiosis and mitosis
- Explain the mechanisms within the meiotic process that produce genetic variation among the haploid gametes

Sexual reproduction requires the union of two specialized cells, called **gametes**, each of which contains one set of chromosomes. When gametes unite, they form a **zygote**, or fertilized egg that contains two sets of chromosomes. (Note: Cells that contain one set of chromosomes are called **haploid**; cells containing two sets of chromosomes are called **diploid**.) If the reproductive cycle is to continue for any sexually reproducing species, then the diploid cell must somehow reduce its number of chromosome sets to produce haploid gametes; otherwise, the number of chromosome sets will double with every future round of fertilization. Therefore, sexual reproduction requires a nuclear division that reduces the number of chromosome sets by half.

Most animals and plants and many unicellular organisms are diploid and therefore have two sets of chromosomes. In each **somatic cell** of the organism (all cells of a multicellular organism except the gametes or reproductive cells), the nucleus contains two copies of each chromosome, called **homologous chromosomes**. Homologous chromosomes are matched pairs containing the same genes in identical locations along their lengths. Diploid organisms inherit one copy of each homologous chromosome from each parent.

**Meiosis** is the *nuclear division* that forms haploid cells from diploid cells, and it employs many of the same cellular mechanisms as mitosis. However, as you have learned, **mitosis** produces daughter cells whose nuclei are genetically identical to the original parent nucleus. In mitosis, both the parent and the daughter nuclei are at the same "ploidy level"—diploid in the case of most multicellular most animals. Plants use mitosis to grow as sporophytes, and to grow and produce eggs and sperm as gametophytes; so they use mitosis for both haploid and diploid cells (as well as for all other ploidies). In meiosis, the starting nucleus is always diploid and the daughter nuclei that result are haploid. To achieve this reduction in chromosome number, meiosis consists of one round of chromosome replication followed by two rounds of nuclear division. Because the events that occur during each of the division stages are analogous to the events of mitosis, the same stage names are assigned. However, because there are two rounds of division, the major process and the stages are designated with a "I" or a "II." Thus, **meiosis I** is the first round of meiotic division and consists of prophase I, prometaphase I, and so on. Likewise, **Meiosis II** (during which the second round of meiotic division takes place) includes prophase II, prometaphase II, and so on.

## Meiosis I

Meiosis is preceded by an interphase consisting of $G_1$, S, and $G_2$ phases, which are nearly identical to the phases preceding mitosis. The $G_1$ phase (the "first gap phase") is focused on cell growth. During the S phase—the second phase of interphase—the cell copies or *replicates* the DNA of the chromosomes. Finally, in the $G_2$ phase (the "second gap phase") the cell undergoes the final preparations for meiosis.

During DNA duplication in the S phase, each chromosome is replicated to produce two identical copies—*sister chromatids* that are held together at the centromere by **cohesin** proteins, which hold the chromatids together until anaphase II.

### Prophase I

Early in prophase I, before the chromosomes can be seen clearly with a microscope, the homologous chromosomes are attached at their tips to the nuclear envelope by proteins. As the nuclear envelope begins to break down, the proteins associated with homologous chromosomes bring the pair closer together. Recall that in mitosis, homologous chromosomes do not pair together. The **synaptonemal complex**, a lattice of proteins between the homologous chromosomes, first forms at specific locations and then spreads outward

to cover the entire length of the chromosomes. The tight pairing of the homologous chromosomes is called *synapsis*. In **synapsis**, the genes on the chromatids of the homologous chromosomes are aligned precisely with each other. The synaptonemal complex supports the exchange of chromosomal segments between homologous nonsister chromatids—a process called **crossing over**. Crossing over can be observed visually after the exchange as *chiasmata* (singular = chiasma) (Figure 11.2).

In humans, even though the X and Y sex chromosomes are not completely homologous (that is, most of their genes differ), there is a small region of homology that allows the X and Y chromosomes to pair up during prophase I. A partial synaptonemal complex develops only between the regions of homology.

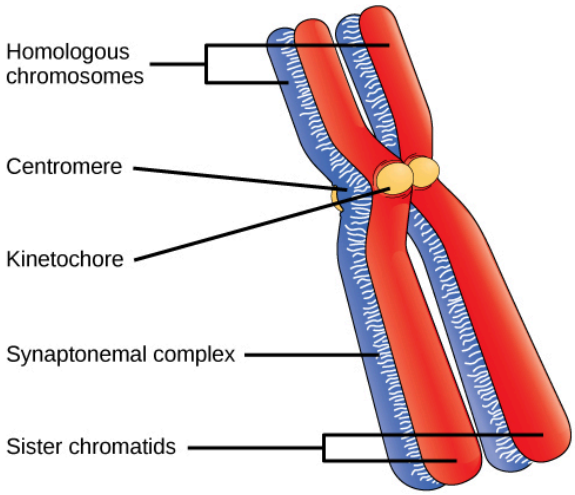



**Figure 11.2** Early in prophase I, homologous chromosomes come together to form a synapse. The chromosomes are bound tightly together and in perfect alignment by a protein lattice called a synaptonemal complex and by cohesin proteins at the centromere.

Located at intervals along the synaptonemal complex are large protein assemblies called **recombination nodules**. These assemblies mark the points of later chiasmata and mediate the multistep process of **crossover**—or genetic recombination—between the nonsister chromatids. Near the recombination nodule, the double-stranded DNA of each chromatid is cleaved, the cut ends are modified, and a new connection is made between the nonsister chromatids. As prophase I progresses, the synaptonemal complex begins to break down and the chromosomes begin to condense. When the synaptonemal complex is gone, the homologous chromosomes remain attached to each other at the centromere and at chiasmata. The chiasmata remain until anaphase I. The number of chiasmata varies according to the species and the length of the chromosome. There must be at least one chiasma per chromosome for proper separation of homologous chromosomes during meiosis I, but there may be as many as 25. Following crossover, the synaptonemal complex breaks down and the cohesin connection between homologous pairs is removed. At the end of prophase I, the pairs are held together only at the chiasmata (Figure 11.3). These pairs are called **tetrads** because the four sister chromatids of each pair of homologous chromosomes are now visible.

The crossover events are the first source of genetic variation in the nuclei produced by meiosis. A single crossover event between homologous nonsister chromatids leads to a reciprocal exchange of equivalent DNA between a maternal chromosome and a paternal chromosome. When a recombinant sister chromatid is moved into a gamete cell it will carry some DNA from one parent and some DNA from the other parent. The recombinant chromatid has a combination of maternal and paternal genes that did not exist before the crossover. Crossover events can occur almost anywhere along the length of the synapsed chromosomes. Different cells undergoing meiosis will therefore produce different recombinant chromatids, with varying combinations of maternal and parental genes. Multiple crossovers in an arm of the chromosome have the same effect, exchanging segments of DNA to produce genetically recombined chromosomes.

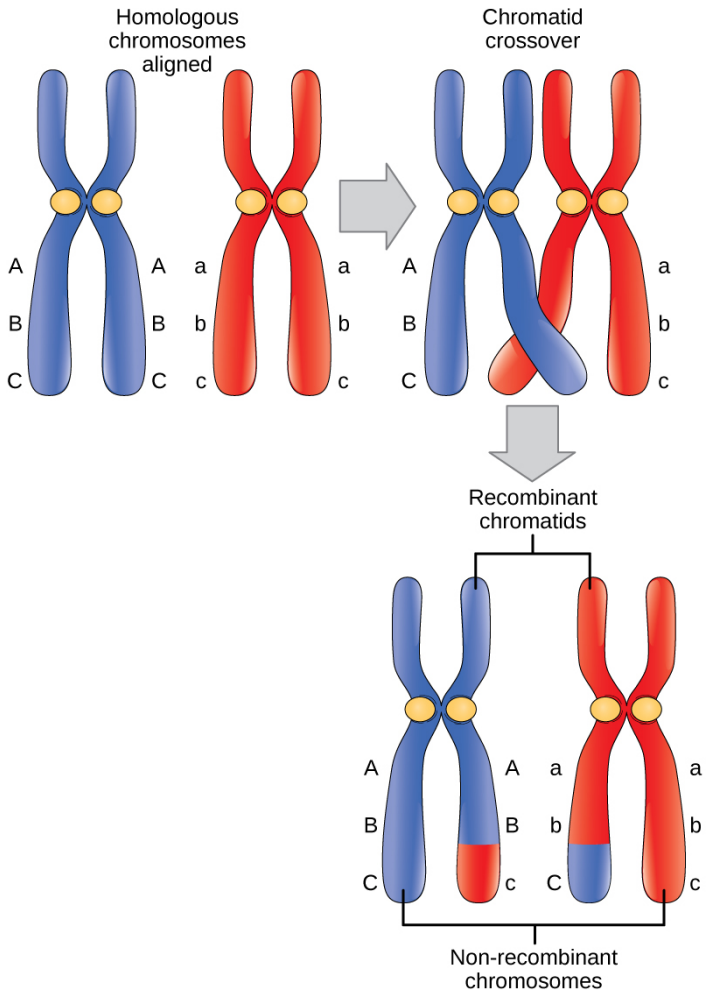



**Figure 11.3** Crossover occurs between *nonsister chromatids of homologous chromosomes.* The result is an exchange of genetic material between homologous chromosomes.

## Prometaphase I

The key event in prometaphase I is the attachment of the spindle fiber microtubules to the kinetochore proteins at the centromeres. Kinetochore proteins are multiprotein complexes that bind the centromeres of a chromosome to the microtubules of the mitotic spindle. Microtubules grow from microtubule-organizing centers (MTOCs). In animal cells, MTOCs are centrosomes located at opposite poles of the cell. The microtubules from each pole move toward the middle of the cell and attach to one of the kinetochores of the two fused homologous chromosomes. Each member of the homologous pair attaches to a microtubule extending from opposite poles of the cell so that in the next phase, the microtubules can pull the homologous pair apart. A spindle fiber that has attached to a kinetochore is called a *kinetochore microtubule*. At the end of prometaphase I, each tetrad is attached to microtubules from both poles, with one homologous chromosome facing each pole. The homologous chromosomes are still held together at the chiasmata. In addition, the nuclear membrane has broken down entirely.

## Metaphase I

During metaphase I, the homologous chromosomes are arranged at the **metaphase plate**—roughly in the midline of the cell, with the kinetochores facing opposite poles. The homologous pairs orient themselves randomly at the equator. For example, if the two homologous members of chromosome 1 are labeled *a* and *b*, then the chromosomes could line up a-b or b-a. This is important in determining the genes carried by a gamete, as each will only receive one of the two homologous chromosomes. (Recall that after crossing over takes place, homologous chromosomes are not identical. They contain slight differences in their genetic information, causing each gamete to have a unique genetic makeup.)

The randomness in the alignment of recombined chromosomes at the metaphase plate, coupled with the crossing over events between nonsister chromatids, are responsible for much of the genetic variation in the offspring. To clarify this further, remember that the homologous chromosomes of a sexually reproducing organism are originally inherited as two separate sets,

one from each parent. Using humans as an example, one set of 23 chromosomes is present in the egg donated by the mother. The father provides the other set of 23 chromosomes in the sperm that fertilizes the egg. Every cell of the multicellular offspring has copies of the original two sets of homologous chromosomes. In prophase I of meiosis, the homologous chromosomes form the tetrads. In metaphase I, these pairs line up at the midway point between the two poles of the cell to form the metaphase plate. Because there is an equal chance that a microtubule fiber will encounter a maternally or paternally inherited chromosome, the arrangement of the tetrads at the metaphase plate is random. Thus, any maternally inherited chromosome may face either pole. Likewise, any paternally inherited chromosome may also face either pole. *The orientation of each tetrad is independent of the orientation of the other 22 tetrads.*

This event—the *random* (or *independent*) assortment of homologous chromosomes at the metaphase plate—is the second mechanism that introduces variation into the gametes or spores. In each cell that undergoes meiosis, the arrangement of the tetrads is different. The number of variations is dependent on the number of chromosomes making up a set. There are two possibilities for orientation at the metaphase plate; the possible number of alignments therefore equals $2^n$ in a diploid cell, where $n$ is the number of chromosomes per haploid set. Humans have 23 chromosome pairs, which results in over eight million ($2^{23}$) possible genetically-distinct gametes just from the random alignment of chromosomes at the metaphase plate. This number does not include the variability that was previously produced by crossing over between the nonsister chromatids. Given these two mechanisms, it is highly unlikely that any two haploid cells resulting from meiosis will have the same genetic composition (Figure 11.4).

To summarize, meiosis I creates genetically diverse gametes in two ways. First, during prophase I, crossover events between the nonsister chromatids of each homologous pair of chromosomes generate recombinant chromatids with new combinations of maternal and paternal genes. Second, the random assortment of tetrads on the metaphase plate produces unique combinations of maternal and paternal chromosomes that will make their way into the gametes.

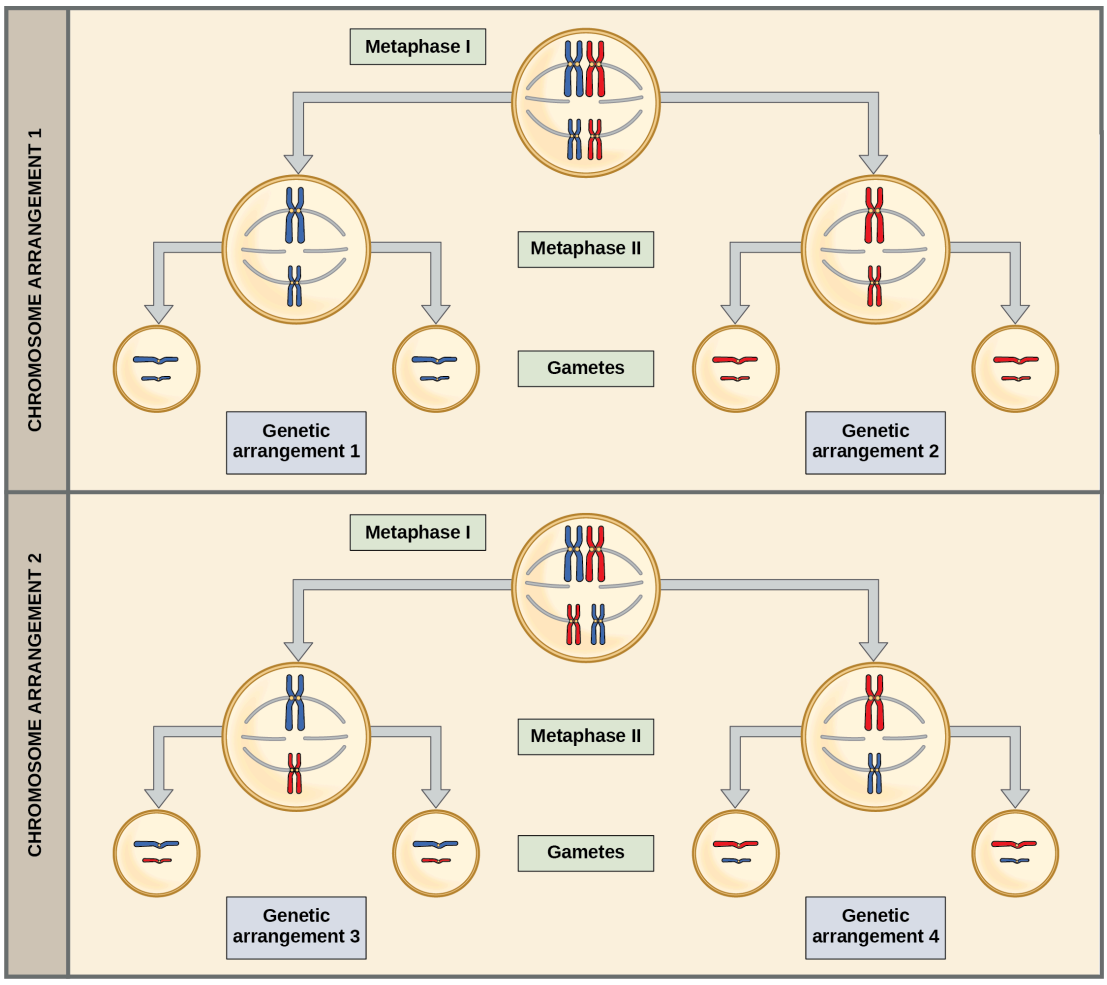



**Figure 11.4** Random, independent assortment during metaphase I can be demonstrated by considering a cell with a set of two

chromosomes ($n = 2$). In this case, there are two possible arrangements at the equatorial plane in metaphase I. The total possible number of different gametes is $2^n$, where $n$ equals the number of chromosomes in a set. In this example, there are four possible genetic combinations for the gametes. With $n = 23$ in human cells, there are over eight million possible combinations of paternal and maternal chromosomes.

### Anaphase I

In anaphase I, the microtubules pull the linked chromosomes apart. The sister chromatids remain tightly bound together at the centromere. The chiasmata are broken in anaphase I as the microtubules attached to the fused kinetochores pull the homologous chromosomes apart (Figure 11.5).

### Telophase I and Cytokinesis

In telophase, the separated chromosomes arrive at opposite poles. The remainder of the typical telophase events may or may not occur, depending on the species. In some organisms, the chromosomes "decondense" and nuclear envelopes form around the separated sets of chromatids produced during telophase I. In other organisms, **cytokinesis**—the physical separation of the cytoplasmic components into two daughter cells—occurs without reformation of the nuclei. In nearly all species of animals and some fungi, cytokinesis separates the cell contents via a *cleavage furrow* (constriction of the actin ring that leads to cytoplasmic division). In plants, a *cell plate* is formed during cell cytokinesis by Golgi vesicles fusing at the metaphase plate. This cell plate will ultimately lead to the formation of cell walls that separate the two daughter cells.

Two haploid cells are the result of the first meiotic division of a diploid cell. The cells are haploid because at each pole, there is just one of each pair of the homologous chromosomes. Therefore, only one full set of the chromosomes is present. This is why the cells are considered haploid—there is only one chromosome set, *even though each chromosome still consists of two sister chromatids.* Recall that sister chromatids are merely duplicates of one of the two homologous chromosomes (except for changes that occurred during crossing over). In meiosis II, these two sister chromatids will separate, creating four haploid daughter cells.

### LINK TO LEARNING

Review the process of meiosis, observing how chromosomes align and migrate, at Meiosis: An Interactive Animation (http://openstax.org/l/animal_meiosis) .

## Meiosis II

In some species, cells enter a brief interphase, or **interkinesis**, before entering meiosis II. Interkinesis lacks an S phase, so chromosomes are not duplicated. The two cells produced in meiosis I go through the events of meiosis II in synchrony. During meiosis II, the sister chromatids within the two daughter cells separate, forming four new haploid gametes. The mechanics of meiosis II are similar to mitosis, except that each dividing cell has only one set of homologous chromosomes, each with two chromatids. Therefore, each cell has half the number of sister chromatids to separate out as a diploid cell undergoing mitosis. In terms of chromosomal content, cells at the start of meiosis II are similar to haploid cells in $G_2$, preparing to undergo mitosis.

### Prophase II

If the chromosomes decondensed in telophase I, they condense again. If nuclear envelopes were formed, they fragment into vesicles. The MTOCs that were duplicated during interkinesis move away from each other toward opposite poles, and new spindles are formed.

### Prometaphase II

The nuclear envelopes are completely broken down, and the spindle is fully formed. Each sister chromatid forms an individual kinetochore that attaches to microtubules from opposite poles.

### Metaphase II

The sister chromatids are maximally condensed and aligned at the equator of the cell.

### Anaphase II

The sister chromatids are pulled apart by the kinetochore microtubules and move toward opposite poles. Nonkinetochore microtubules elongate the cell.

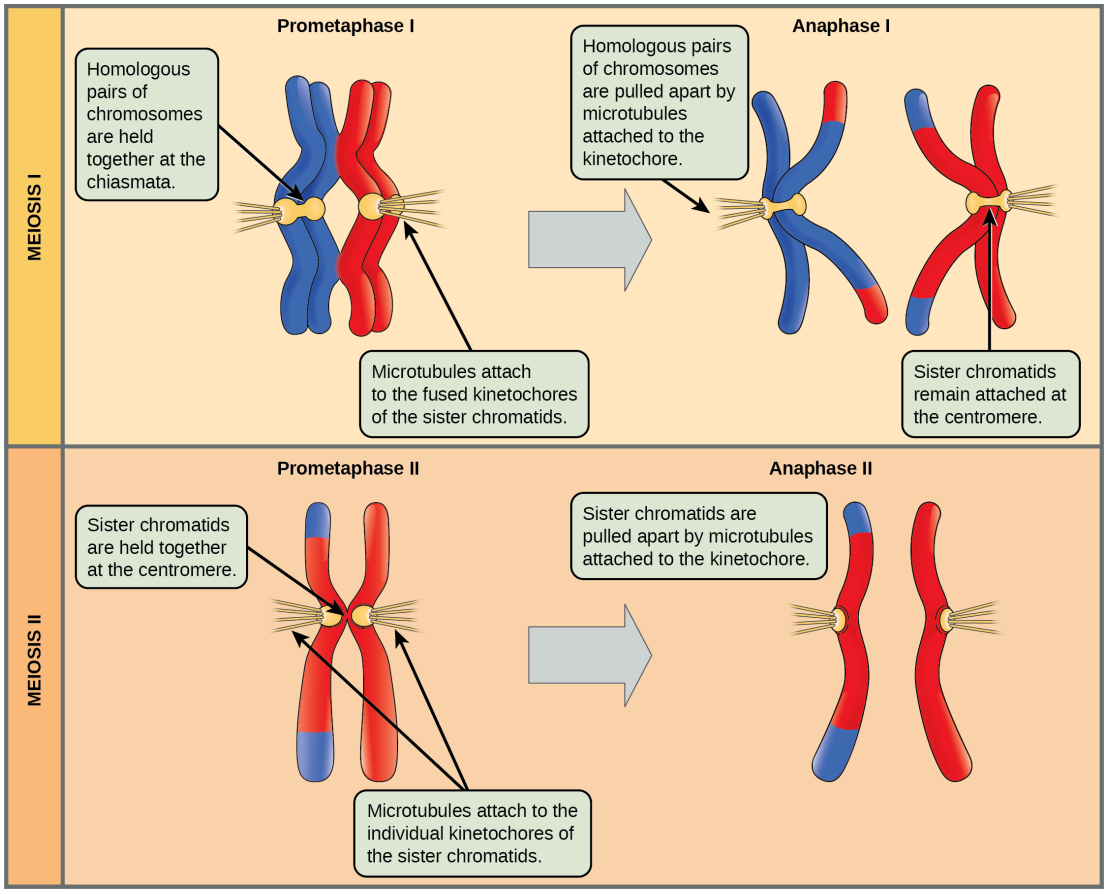



**Figure 11.5** The process of chromosome alignment differs between meiosis I and meiosis II. In prometaphase I, microtubules attach to the fused kinetochores of homologous chromosomes, and the homologous chromosomes are arranged at the midline of the cell (the metaphase plate) in metaphase I. In anaphase I, the homologous chromosomes separate. In prometaphase II, microtubules attach to the kinetochores of sister chromatids, and the sister chromatids are arranged at the midpoint of the cells in metaphase II. In anaphase II, the sister chromatids separate.

## Telophase II and Cytokinesis

The chromosomes arrive at opposite poles and begin to decondense. Nuclear envelopes form around the chromosomes. If the parent cell was diploid, as is most commonly the case, then cytokinesis now separates the two cells into four unique haploid cells. The cells produced are genetically unique because of the random assortment of paternal and maternal homologs and because of the recombination of maternal and paternal segments of chromosomes (with their sets of genes) that occurs during crossover. The entire process of meiosis is outlined in Figure 11.6.

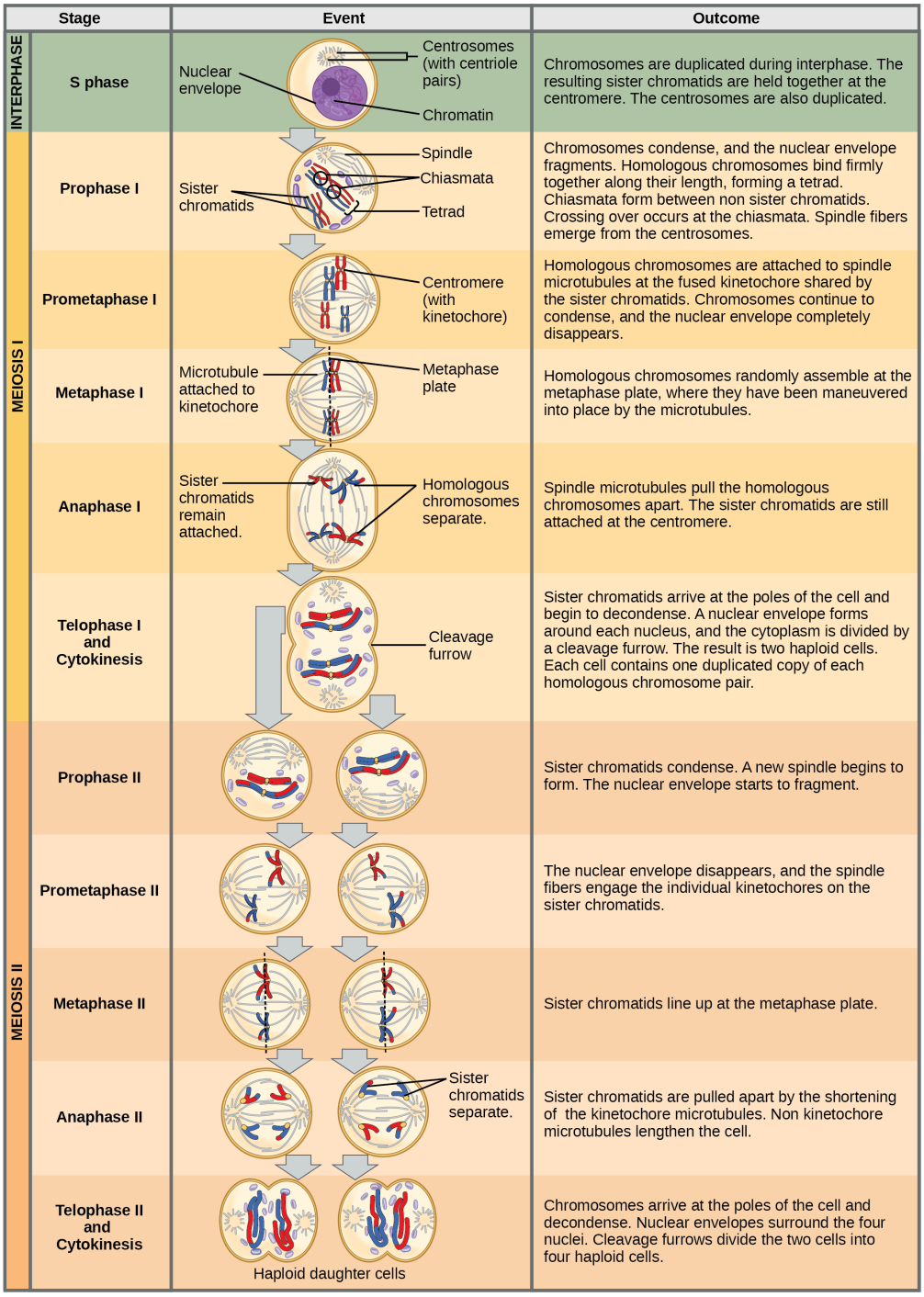



**Figure 11.6** An animal cell with a diploid number of four ($2n = 4$) proceeds through the stages of meiosis to form four haploid daughter cells.

## Comparing Meiosis and Mitosis

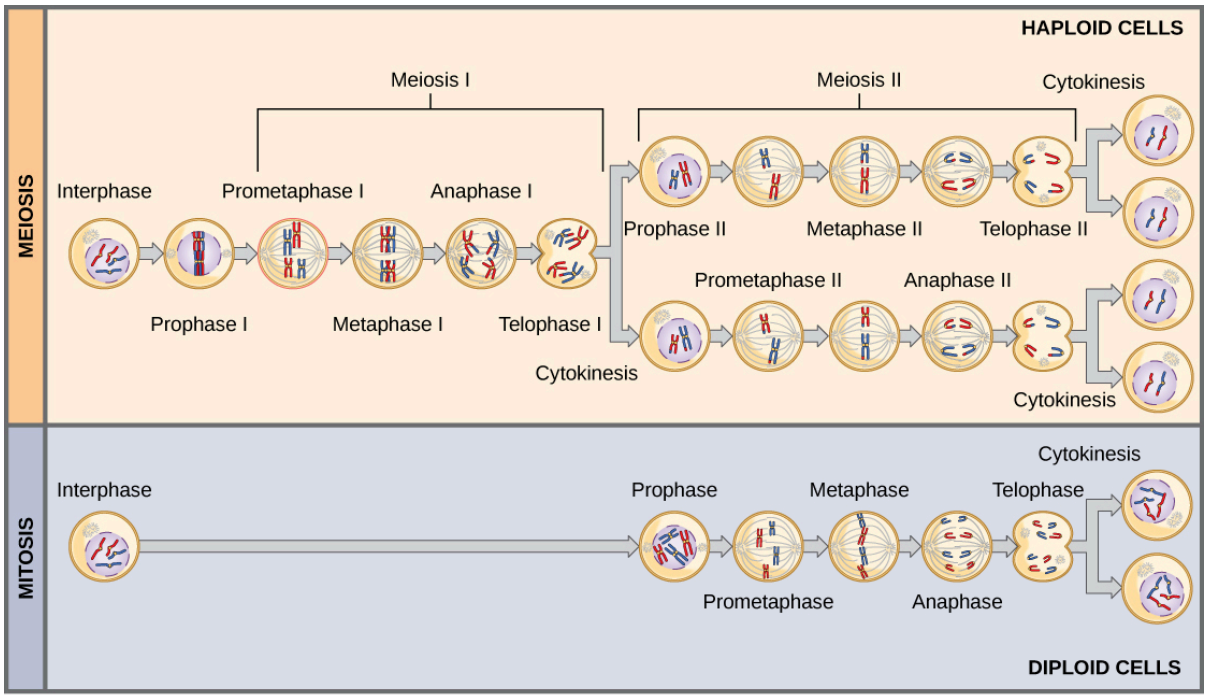
Mitosis and meiosis are both forms of division of the nucleus in eukaryotic cells. They share some similarities, but also exhibit a number of important and distinct differences that lead to very different outcomes (Figure 11.7). Mitosis is a single nuclear division that results in two nuclei that are usually partitioned into two new cells. The nuclei resulting from a mitotic division are genetically identical to the original nucleus. They have the same number of sets of chromosomes: one set in the case of haploid cells and two sets in the case of diploid cells. In contrast, meiosis consists of two nuclear divisions resulting in four nuclei that are usually partitioned into four new, genetically distinct cells. The four nuclei produced during meiosis are not genetically identical, and they contain one chromosome set only. This is half the number of chromosome sets in the original cell, which is

diploid.

The main differences between mitosis and meiosis occur in meiosis I, which is a very different nuclear division than mitosis. In meiosis I, the homologous chromosome pairs physically meet and are bound together with the synaptonemal complex. Following this, the chromosomes develop chiasmata and undergo crossover between nonsister chromatids. In the end, the chromosomes line up along the metaphase plate as tetrads—with kinetochore fibers from opposite spindle poles attached to each kinetochore of a homolog to form a tetrad. *All of these events occur only in meiosis I.*

When the chiasmata resolve and the tetrad is broken up with the homologs moving to one pole or another, the ploidy level—the number of sets of chromosomes in each future nucleus—has been reduced from two to one. For this reason, meiosis I is referred to as a **reductional division**. There is no such reduction in ploidy level during mitosis.

Meiosis II is analogous to a mitotic division. In this case, the duplicated chromosomes (only one set of them) line up on the metaphase plate with divided kinetochores attached to kinetochore fibers from opposite poles. During anaphase II, as in mitotic anaphase, the kinetochores divide and one sister chromatid—now referred to as a chromosome—is pulled to one pole while the other sister chromatid is pulled to the other pole. If it were not for the fact that there had been crossover, the two products of each individual meiosis II division would be identical (as in mitosis). Instead, they are different because there has always been at least one crossover per chromosome. Meiosis II is not a reduction division because although there are fewer copies of the genome in the resulting cells, there is still one set of chromosomes, as there was at the end of meiosis I.




| | OUTCOME | | | | | |
|---|---|---|---|---|---|---|
| PROCESS | DNA synthesis | Synapsis of homologous chromosomes | Crossover | Homologous chromosomes line up at metaphase plate | Sister chromatids line up at metaphase plate | Number and genetic composition of daughter cells |
| MEIOSIS | Occurs in S phase of interphase | During prophase I | During prophase I | During metaphase I | During metaphase II | Four haploid cells at the end of meiosis II |
| MITOSIS | Occurs in S phase of interphase | Does not occur in mitosis | Does not occur in mitosis | Does not occur in mitosis | During metaphase | Two diploid cells at the end of mitosis |

Figure 11.7 Meiosis and mitosis are both preceded by one cycle of DNA replication; however, meiosis includes two nuclear divisions. The four daughter cells resulting from meiosis are haploid and genetically distinct. The daughter cells resulting from mitosis are diploid and

identical to the parent cell.

## EVOLUTION CONNECTION

### The Mystery of the Evolution of Meiosis

Some characteristics of organisms are so widespread and fundamental that it is sometimes difficult to remember that they evolved like other simple traits. Meiosis is such an extraordinarily complex series of cellular events that biologists have had trouble testing hypotheses concerning how it may have evolved. Although meiosis is inextricably entwined with sexual reproduction and its advantages and disadvantages, it is important to separate the questions of the evolution of meiosis and the evolution of sex, because early meiosis may have been advantageous for different reasons than it is now. Thinking outside the box and imagining what the early benefits from meiosis might have been is one approach to uncovering how it may have evolved.

Meiosis and mitosis share obvious cellular processes, and it makes sense that meiosis evolved from mitosis. The difficulty lies in the clear differences between meiosis I and mitosis. Adam Wilkins and Robin Holliday[1] summarized the unique events that needed to occur for the evolution of meiosis from mitosis. These steps are homologous chromosome pairing and synapsis, crossover exchanges, sister chromatids remaining attached during anaphase, and suppression of DNA replication in interphase. They argue that the first step is the hardest and most important and that understanding how it evolved would make the evolutionary process clearer. They suggest genetic experiments that might shed light on the evolution of synapsis.

There are other approaches to understanding the evolution of meiosis in progress. Different forms of meiosis exist in single-celled protists. Some appear to be simpler or more "primitive" forms of meiosis. Comparing the meiotic divisions of different protists may shed light on the evolution of meiosis. Marilee Ramesh and colleagues[2] compared the genes involved in meiosis in protists to understand when and where meiosis might have evolved. Although research is still ongoing, recent scholarship into meiosis in protists suggests that some aspects of meiosis may have evolved later than others. This kind of genetic comparison can tell us what aspects of meiosis are the oldest and what cellular processes they may have borrowed from in earlier cells.

## LINK TO LEARNING

Click through the steps of this interactive animation to compare the meiotic process of cell division to that of mitosis at How Cells Divide (http://openstax.org/l/how_cells_dvide) .

# 11.2 Sexual Reproduction

*By the end of this section, you will be able to do the following:*

- Explain that meiosis and sexual reproduction are highly evolved traits
- Identify variation among offspring as a potential evolutionary advantage of sexual reproduction
- Describe the three different life-cycle types among sexually reproducing multicellular organisms.

Sexual reproduction was likely an early evolutionary innovation after the appearance of eukaryotic cells. It appears to have been very successful because most eukaryotes are able to reproduce sexually and, in many animals, it is the only mode of reproduction. And yet, scientists also recognize some real disadvantages to sexual reproduction. On the surface, creating offspring that are genetic clones of the parent appears to be a better system. If the parent organism is successfully occupying a habitat, offspring with the same traits should be similarly successful. There is also the obvious benefit to an organism that can produce offspring whenever circumstances are favorable by asexual budding, fragmentation, or by producing eggs asexually. These methods of reproduction do not require another organism of the opposite sex. Indeed, some organisms that lead a solitary lifestyle have retained the ability to reproduce asexually. In addition, in asexual populations, every individual is capable of reproduction. In sexual populations, the males are not producing the offspring themselves, so hypothetically an asexual

1Adam S. Wilkins and Robin Holliday, "The Evolution of Meiosis from Mitosis," *Genetics* 181 (2009): 3–12.

2Marilee A. Ramesh, Shehre-Banoo Malik and John M. Logsdon, Jr, "A Phylogenetic Inventory of Meiotic Genes: Evidence for Sex in *Giardia* and an Early Eukaryotic Origin of Meiosis," *Current Biology* 15 (2005):185–91.

population could grow twice as fast.

However, multicellular organisms that exclusively depend on asexual reproduction are exceedingly rare. Why are meiosis and sexual reproductive strategies so common? These are important (and as yet unanswered) questions in biology, even though they have been the focus of much research beginning in the latter half of the 20th century. There are several possible explanations, one of which is that the variation that sexual reproduction creates among offspring is very important to the survival and reproduction of the population. Thus, on average, a sexually reproducing population will leave more descendants than an otherwise similar asexually reproducing population. The only source of variation in asexual organisms is mutation. Mutations that take place during the formation of germ cell lines are also the ultimate source of variation in sexually reproducing organisms. However, in contrast to mutation during asexual reproduction, the mutations during sexual reproduction can be continually reshuffled from one generation to the next when different parents combine their unique genomes and the genes are mixed into different combinations by crossovers during prophase I and random assortment at metaphase I.

## EVOLUTION CONNECTION

### The Red Queen Hypothesis

Genetic variation is the outcome of sexual reproduction, but why are ongoing variations necessary, even under seemingly stable environmental conditions? Enter the Red Queen hypothesis, first proposed by Leigh Van Valen in 1973.[3] The concept was named in reference to the Red Queen's race in Lewis Carroll's book, *Through the Looking-Glass*.

All species **coevolve** (evolve together) with other organisms. For example, predators evolve with their prey, and parasites evolve with their hosts. Each tiny advantage gained by favorable variation gives a species a reproductive edge over close competitors, predators, parasites, or even prey. However, survival of any given genotype or phenotype in a population is dependent on the reproductive fitness of other genotypes or phenotypes within a given species. The only method that will allow a coevolving species to maintain its own share of the resources is to also *continually improve its* **fitness** (the capacity of the members to produce more reproductively viable offspring relative to others within a species). As one species gains an advantage, this increases selection on the other species; they must also develop an advantage or they will be outcompeted. No single species progresses too far ahead because genetic variation among the progeny of sexual reproduction provides all species with a mechanism to improve rapidly. Species that cannot keep up become extinct. The Red Queen's catchphrase was, "It takes all the running you can do to stay in the same place." This is an apt description of coevolution between competing species.

## Life Cycles of Sexually Reproducing Organisms

Fertilization and meiosis alternate in sexual **life cycles**. What happens between these two events depends on the organism's "reproductive strategy." The process of meiosis reduces the chromosome number by half. Fertilization, the joining of two haploid gametes, restores the diploid condition. Some organisms have a multicellular diploid stage that is most obvious and only produce haploid reproductive cells. Animals, including humans, have this type of life cycle. Other organisms, such as fungi, have a multicellular haploid stage that is most obvious. Plants and some algae have alternation of generations, in which they have multicellular diploid and haploid life stages that are apparent to different degrees depending on the group.

Nearly all animals employ a diploid-dominant life-cycle strategy in which the only haploid cells produced by the organism are the gametes. Early in the development of the embryo, specialized diploid cells, called **germ cells**, are produced within the gonads (such as the testes and ovaries). Germ cells are capable of mitosis to perpetuate the germ cell line and meiosis to produce haploid gametes. Once the haploid gametes are formed, they lose the ability to divide again. There is no multicellular haploid life stage. Fertilization occurs with the fusion of two gametes, usually from different individuals, restoring the diploid state (Figure 11.8).

3Leigh Van Valen, "A New Evolutionary Law," *Evolutionary Theory* 1 (1973): 1–30

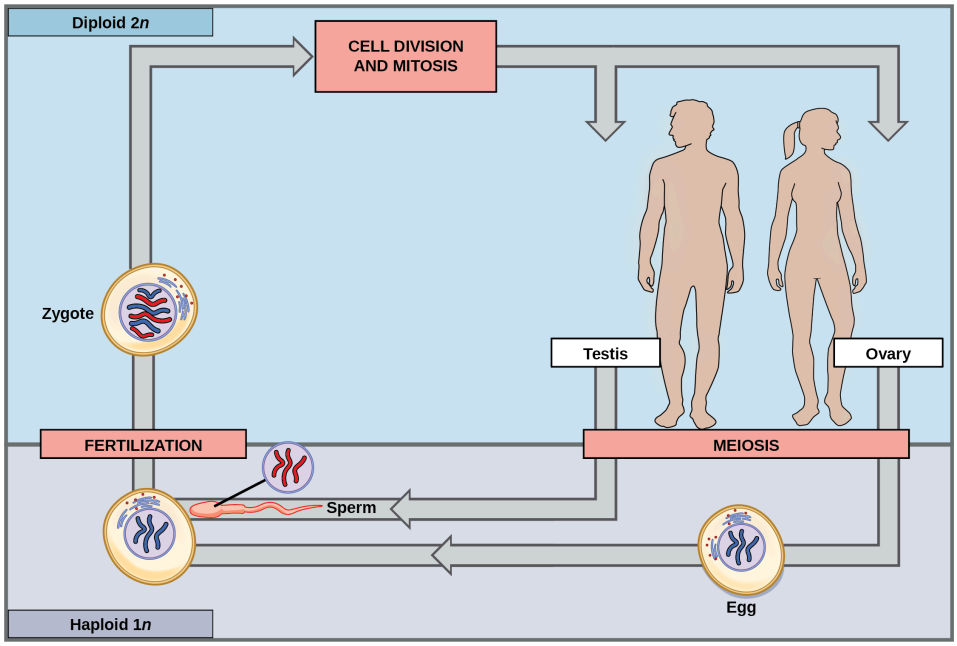



**Figure 11.8** In animals, sexually reproducing adults form haploid gametes from diploid germ cells. Fusion of the gametes gives rise to a fertilized egg cell, or zygote. The zygote will undergo multiple rounds of mitosis to produce a multicellular offspring. The germ cells are generated early in the development of the zygote.

Most fungi and algae employ a life-cycle type in which the "body" of the organism—the ecologically important part of the life cycle—is haploid. The haploid cells that make up the tissues of the dominant multicellular stage are formed by mitosis. During sexual reproduction, specialized haploid cells from two individuals—designated the (+) and (–) mating types—join to form a diploid zygote. The zygote immediately undergoes meiosis to form four haploid cells called *spores*. Although these spores are haploid like the "parents," they contain a new genetic combination from two parents. The spores can remain dormant for various time periods. Eventually, when conditions are favorable, the spores form multicellular haploid structures through many rounds of mitosis (Figure 11.9).

## VISUAL CONNECTION

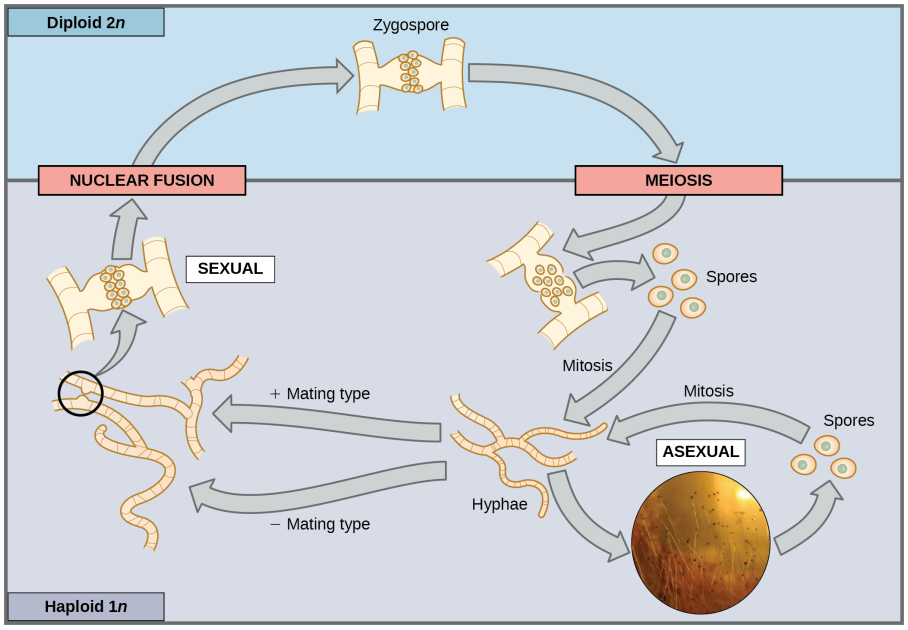



**Figure 11.9** Fungi, such as black bread mold (*Rhizopus nigricans*), have a haploid multicellular stage that produces specialized haploid cells by mitosis that fuse to form a diploid zygote. The zygote undergoes meiosis to produce haploid spores. Each spore gives rise to a multicellular haploid organism by mitosis. Above, different mating hyphae types (denoted as + and –) join to form a zygospore through nuclear fusion. (credit "zygomycota" micrograph: modification of work by "Fanaberka"/Wikimedia Commons)

If a mutation occurs so that a fungus is no longer able to produce a minus mating type, will it still be able to reproduce?

The third life-cycle type, employed by some algae and all plants, is a blend of the haploid-dominant and diploid-dominant extremes. Species with alternation of generations have both haploid and diploid multicellular organisms as part of their life cycle. The haploid multicellular plants are called **gametophytes**, because they produce gametes from specialized cells. Meiosis is not directly involved in the production of gametes in this case, because the organism that produces the gametes is already haploid. Fertilization between the gametes forms a diploid zygote. The zygote will undergo many rounds of mitosis and give rise to a diploid multicellular plant called a **sporophyte**. Specialized cells of the sporophyte will undergo meiosis and produce haploid spores. The spores will subsequently develop into the gametophytes (Figure 11.10).

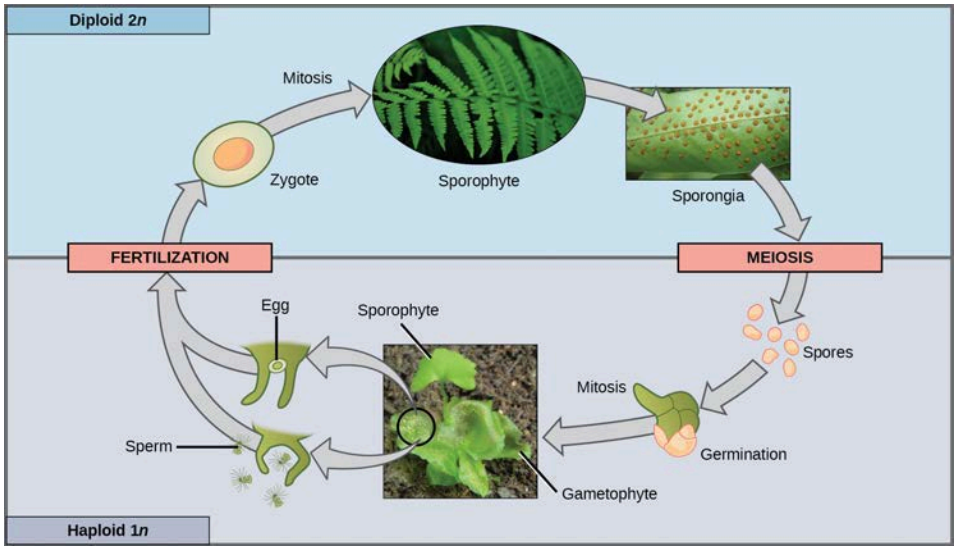



**Figure 11.10** Plants have a life cycle that alternates between a multicellular haploid organism and a multicellular diploid organism. In some plants, such as ferns, both the haploid and diploid plant stages are free-living. The diploid plant is called a sporophyte because it produces haploid spores by meiosis. The spores develop into multicellular, haploid plants that are called *gametophytes* because they produce gametes. The gametes of two individuals will fuse to form a diploid zygote that becomes the sporophyte. (credit "fern": modification of work by Cory Zanker; credit "sporangia": modification of work by "Obsidian Soul"/Wikimedia Commons; credit "gametophyte and sporophyte": modification of work by "Vlmastra"/Wikimedia Commons)

Although all plants utilize some version of the alternation of generations, the relative size of the sporophyte and the gametophyte and the relationship between them vary greatly. In plants such as moss, the gametophyte organism is the free-living plant and the sporophyte is physically dependent on the gametophyte. In other plants, such as ferns, both the gametophyte and sporophyte plants are free-living; however, the sporophyte is much larger. In seed plants, such as magnolia trees and daisies, the gametophyte is composed of only a few cells and, in the case of the female gametophyte, is completely retained within the sporophyte.

Sexual reproduction takes many forms in multicellular organisms. The fact that nearly every multicellular organism on Earth employs sexual reproduction is strong evidence for the benefits of producing offspring with unique gene combinations, though there are other possible benefits as well.

# KEY TERMS

**alternation of generations** life-cycle type in which the diploid and haploid stages alternate

**chiasmata** (singular, *chiasma*) the structure that forms at the crossover points after genetic material is exchanged

**cohesin** proteins that form a complex that seals sister chromatids together at their centromeres until anaphase II of meiosis

**crossover** exchange of genetic material between nonsister chromatids resulting in chromosomes that incorporate genes from both parents of the organism

**fertilization** union of two haploid cells from two individual organisms

**gametophyte** a multicellular haploid life-cycle stage that produces gametes

**germ cells** specialized cell line that produces gametes, such as eggs or sperm

**interkinesis** (also, *interphase II*) brief period of rest between meiosis I and meiosis II

**life cycle** the sequence of events in the development of an organism and the production of cells that produce offspring

**meiosis** a nuclear division process that results in four haploid cells

**meiosis I** first round of meiotic cell division; referred to as *reduction division* because the ploidy level is reduced from diploid to haploid

**meiosis II** second round of meiotic cell division following meiosis I; sister chromatids are separated into individual chromosomes, and the result is four unique haploid cells

**recombination nodules** protein assemblies formed on the synaptonemal complex that mark the points of crossover events and mediate the multistep process of genetic recombination between nonsister chromatids

**reduction division** nuclear division that produces daughter nuclei each having one-half as many chromosome sets as the parental nucleus; meiosis I is a reduction division

**somatic cell** all the cells of a multicellular organism except the gametes or reproductive cells

**spore** haploid cell that can produce a haploid multicellular organism or can fuse with another spore to form a diploid cell

**sporophyte** a multicellular diploid life-cycle stage that produces haploid spores by meiosis

**synapsis** formation of a close association between homologous chromosomes during prophase I

**synaptonemal complex** protein lattice that forms between homologous chromosomes during prophase I, supporting crossover

**tetrad** two duplicated homologous chromosomes (four chromatids) bound together by chiasmata during prophase I

# CHAPTER SUMMARY

## 11.1 The Process of Meiosis

Sexual reproduction requires that organisms produce cells that can fuse during fertilization to produce offspring. In most animals, meiosis is used to produce haploid eggs and sperm from diploid parent cells so that the fusion of an egg and sperm produces a diploid zygote. As with mitosis, DNA replication occurs prior to meiosis during the S-phase of the cell cycle so that each chromosome becomes a pair of sister chromatids. In meiosis, there are two rounds of nuclear division resulting in four nuclei and usually four daughter cells, each with half the number of chromosomes as the parent cell. The first division separates homologs, and the second—like mitosis—separates chromatids into individual chromosomes. Meiosis generates variation in the daughter nuclei during crossover in prophase I as well as during the random alignment of tetrads at metaphase I. The cells that are produced by meiosis are genetically unique.

Meiosis and mitosis share similar processes, but have distinct outcomes. Mitotic divisions are single nuclear divisions that produce genetically identical daughter nuclei (i.e., each daughter nucleus has the same number of chromosome sets as the original cell). In contrast, meiotic divisions include two nuclear divisions that ultimately produce four genetically different daughter nuclei that have only one chromosome set (instead of the two sets of chromosomes in the parent cell). The main differences between the two nuclear division processes take place during the first division of meiosis: homologous chromosomes pair, crossover, and exchange homologous nonsister chromatid segments. The homologous chromosomes separate into different nuclei during meiosis I, causing a *reduction of ploidy level in the first division*. The second division of meiosis is similar to a mitotic division, except that the daughter cells do not contain identical genomes because of crossover and chromosome recombination in prophase I.

## 11.2 Sexual Reproduction

Nearly all eukaryotes undergo sexual reproduction. The variation introduced into the reproductive cells by meiosis provides an important advantage that has made sexual reproduction evolutionarily successful. Meiosis and fertilization alternate in sexual life cycles. The process of meiosis produces unique reproductive cells called gametes, which have half the number of chromosomes as the parent cell. When two haploid gametes fuse, this restores the

diploid condition in the new zygote. Thus, most sexually reproducing organisms alternate between haploid and diploid stages. However, the ways in which reproductive cells are produced and the timing between meiosis and fertilization vary greatly.

## VISUAL CONNECTION QUESTIONS

**1.** Figure 11.9 If a mutation occurs so that a fungus is no longer able to produce a minus mating type, will it still be able to reproduce?

## REVIEW QUESTIONS

**2.** Meiosis usually produces _____ daughter cells.
   a. two haploid
   b. two diploid
   c. four haploid
   d. four diploid

**3.** What structure is most important in forming the tetrads?
   a. centromere
   b. synaptonemal complex
   c. chiasma
   d. kinetochore

**4.** At which stage of meiosis are sister chromatids separated from each other?
   a. prophase I
   b. prophase II
   c. anaphase I
   d. anaphase II

**5.** At metaphase I, homologous chromosomes are connected only at what structures?
   a. chiasmata
   b. recombination nodules
   c. microtubules
   d. kinetochores

**6.** Which of the following is *not* true in regard to crossover?
   a. Spindle microtubules guide the transfer of DNA across the synaptonemal complex.
   b. Nonsister chromatids exchange genetic material.
   c. Chiasmata are formed.
   d. Recombination nodules mark the crossover point.

**7.** What phase of mitotic interphase is missing from meiotic interkinesis?
   a. $G_0$ phase
   b. $G_1$ phase
   c. S phase
   d. $G_2$ phase

**8.** The part of meiosis that is similar to mitosis is _____.
   a. meiosis I
   b. anaphase I
   c. meiosis II
   d. interkinesis

**9.** If a muscle cell of a typical organism has 32 chromosomes, how many chromosomes will be in a gamete of that same organism?
   a. 8
   b. 16
   c. 32
   d. 64

**10.** Which statement best describes the genetic content of the two daughter cells in prophase II of meiosis?
   a. haploid with one copy of each gene
   b. haploid with two copies of each gene
   c. diploid with two copies of each gene
   d. diploid with four copies of each gene

**11.** The pea plants used in Mendel's genetic inheritance studies were diploid, with 14 chromosomes in somatic cells. Assuming no crossing over events occur, how many unique gametes could one pea plant produce?
   a. 28
   b. 128
   c. 196
   d. 16,384

**12.** How do telophase I and telophase II differ during meiosis in animal cells?
   a. Cells remain diploid at the end of telophase I, but are haploid at the end of telophase II.
   b. Daughter cells form a cell plate to divide during telophase I, but divide by cytokinesis during telophase II.
   c. Cells enter interphase after telophase I, but not after telophase II.
   d. Chromosomes can remain condensed at the end of telophase I, but decondense after telophase II.

**13.** What is a likely evolutionary advantage of sexual reproduction over asexual reproduction?
   a. Sexual reproduction involves fewer steps.
   b. There is a lower chance of using up the resources in a given environment.
   c. Sexual reproduction results in variation in the offspring.
   d. Sexual reproduction is more cost-effective.

**14.** Which type of life cycle has both a haploid and diploid multicellular stage?
   a. asexual life cycles
   b. most animal life cycles
   c. most fungal life cycles
   d. alternation of generations

**15.** What is the ploidy of the most conspicuous form of most fungi?
   a. diploid
   b. haploid
   c. alternation of generations
   d. asexual

**16.** A diploid, multicellular life-cycle stage that gives rise to haploid cells by meiosis is called a _____.
   a. sporophyte
   b. gametophyte
   c. spore
   d. gamete

**17.** Hydras and jellyfish both live in a freshwater lake that is slowly being acidified by the runoff from a chemical plant built upstream. Which population is predicted to be better able to cope with the changing environment?
   a. jellyfish
   b. hydra
   c. The populations will be equally able to cope.
   d. Both populations will die.

**18.** Many farmers are worried about the decreasing genetic diversity of plants associated with generations of artificial selection and inbreeding. Why is limiting random sexual reproduction of food crops concerning?
   a. Mutations during asexual reproduction decrease plant fitness.
   b. Consumers do not trust identical-appearing produce.
   c. Larger portions of the plant populations are susceptible to the same diseases.
   d. Spores are not viable in an agricultural setting.

## CRITICAL THINKING QUESTIONS

**19.** Describe the process that results in the formation of a tetrad.

**20.** Explain how the random alignment of homologous chromosomes during metaphase I contributes to the variation in gametes produced by meiosis.

**21.** What is the function of the fused kinetochore found on sister chromatids in prometaphase I?

**22.** In a comparison of the stages of meiosis to the stages of mitosis, which stages are unique to meiosis and which stages have the same events in both meiosis and mitosis?

**23.** Why would an individual with a mutation that prevented the formation of recombination nodules be considered less fit than other members of its species?

**24.** Does crossing over occur during prophase II? From an evolutionary perspective, why is this advantageous?

**25.** List and briefly describe the three processes that lead to variation in offspring with the same parents.

**26.** Animals and plants both have diploid and haploid cells. How does the animal life cycle differ from the alternation of generations exhibited by plants?

**27.** Explain why sexual reproduction is beneficial to a population but can be detrimental to an individual offspring.

**28.** How does the role of meiosis in gamete production differ between organisms with a diploid-dominant life cycle and organisms with an alternation of generations life cycle?

**29.** How do organisms with haploid-dominant life cycles ensure continued genetic diversification in offspring without using a meiotic process to make gametes?