11 | MEIOSIS AND SEXUAL REPRODUCTION

(a) (b) (c)

Figure 11.1 Each of us, like these other large multicellular organisms, begins life as a fertilized egg. 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)

Chapter Outline

Introduction

The ability to reproduce “in kind” is a basic characteristic of all living things. “In kind” means that the offspring of an organism closely resembles its parent or parents. Hippopotamuses give birth to hippopotamus calves, Joshua trees produce Joshua tree seedlings, and flamingos lay eggs that hatch into flamingo chicks. In kind can mean exactly the same. Many unicellular organisms, such as yeast, and a few multicellular organisms, such as sponges, can produce genetically identical clones of themselves through cell division. However, many single-celled organisms and most multicellular organisms reproduce regularly using a method requiring two parents. Sexual reproduction occurs through the production by each parent of a haploid cell (containing one half of an offspring’s required genetic material) and the fusion of these two haploid cells to form a single, unique diploid cell with a complete set of genetic information. In most plants and animals, through multiple rounds of mitotic cell division, this diploid cell will develop into an adult organism. Haploid cells that are necessary for sexual reproduction are produced by a type of cell division called meiosis. Sexual reproduction, specifically meiosis and fertilization, introduces variation into offspring. Variation is an important component of a species evolutionary success. The vast majority of eukaryotic organisms employs some form of meiosis and fertilization to reproduce.

Not all sexually reproducing eukaryotes reproduce solely by sexual reproduction. For example, an Asian termite species, *Reticulitermes speratus*, can reproduce sexually or asexually. In a young colony, a single termite pair—the king and queen—produce worker offspring sexually by the union of haploid cells. However, after several years, as the queen begins to age, she produces some offspring asexually in a process called parthenogenesis. These offspring, which are destined to become new queens, are not fertilized by the king. They are genetic clones of the queen. More information about parthenogenesis in these termites can be found at **this article (http://openstaxcollege.org/l/32termitequeen)** .

11.1 | The Process of Meiosis

In this section, you will explore the following questions:

- How do chromosomes behave during meiosis?
- What cellular events occur during meiosis?
- What are the similarities and differences between meiosis and mitosis?
- How can the process of meiosis generate genetic variation?

Connection for AP® Courses

As we explored the cell cycle and mitosis in a previous chapter, we learned that cells divide to grow, replace other cells, and reproduce asexually. Without mutation, or changes in the DNA, the daughter cells produced by mitosis receive a set of genetic instructions that is identical to that of the parent cell. Because changes in genes drive both the unity and diversity of life, organisms without genetic variation cannot evolve through natural selection. Evolution occurs only because organisms have developed ways to vary their genetic material. This occurs through mutations in DNA, recombination of genes during meiosis, and meiosis followed by fertilization in sexually reproducing organisms.

Sexual reproduction requires that diploid ($2n$) organisms produce haploid ($1n$) cells through meiosis and that these haploid cells fuse to form new, diploid offspring. The union of these two haploid cells, one from each parent, is fertilization. Although the processes of meiosis and mitosis share similarities, their end products are different. Recall that eukaryotic DNA is contained in chromosomes, and that chromosomes occur in homologous pairs (homologues). At fertilization, the male parent contributes one member of each homologous pair to the offspring, and the female parent contributes the other. With the exception of the sex chromosomes, homologous chromosomes contain the same genes, but these genes can have different variations, called alleles. (For example, you might have inherited an allele for brown eyes from your father and an allele for blue eyes from your mother.) As in mitosis, homologous chromosomes are duplicated during the S-stage (synthesis) of interphase. However, unlike mitosis, in which there is just one nuclear division, meiosis has two complete rounds of nuclear division—meiosis I and meiosis II. These result in four nuclei and (usually) four daughter cells, each with half the number of chromosomes as the parent cell ($1n$). The first division, meiosis I, separates homologous chromosomes, and the second division, meiosis II, separates chromatids. (Remember: during meiosis, DNA replicates ONCE but divides TWICE, whereas in mitosis, DNA replicates ONCE but divides only ONCE.).

Although mitosis and meiosis are similar in many ways, they have different outcomes. The main difference is in the type of cell produced: mitosis produces identical cells, allowing growth or repair of tissues; meiosis generates reproductive cells, or gametes. Gametes, often called sex cells, unite with other sex cells to produce new, unique organisms.

Genetic variation occurs during meiosis I, in which homologous chromosomes pair and exchange non-sister chromatid segments (crossover). Here the homologous chromosomes separate into different nuclei, causing a reduction in “ploidy.” During meiosis II—which is more similar to a mitotic division—the chromatids separate and segregate into four haploid sex cells. However, because of crossover, the resultant daughter cells do not contain identical genomes. As in mitosis, external factors and internal signals regulate the meiotic cell cycle. As we will explore in more detail in a later chapter, errors in meiosis can cause genetic disorders, such as Down syndrome.

Information presented and the examples highlighted in the section support concepts and learning objectives outlined in Big Idea 3 of the AP® Biology Curriculum Framework. The learning objectives listed in the Curriculum Framework provide a transparent foundation for the AP® Biology course, an inquiry-based laboratory experience, instructional activities, and AP® exam questions. A learning objective merges required content with one or more of the seven science practices.

Big Idea 3	Living systems store, retrieve, transmit and respond to information essential to life processes.
Enduring Understanding 3.A	Heritable information provides for continuity of life.

Essential Knowledge	**3.A.2** In eukaryotes, heritable information is passed to the next generation via processes that include the cell cycle and mitosis or meiosis plus fertilization.
Science Practice	**6.2** The student can construct explanations of phenomena based on evidence produced through scientific practices.
Learning Objective	**3.9** The student is able to construct an explanation, using visual representations or narratives, as to how DNA in chromosomes is transmitted to the next generation via mitosis, or meiosis followed by fertilization.
Essential Knowledge	**3.A.2** In eukaryotes, heritable information is passed to the next generation via processes that include the cell cycle and mitosis or meiosis plus fertilization.
Science Practice	**7.1** The student can connect phenomena and models across spatial and temporal scales.
Learning Objective	**3.10** The student is able to represent the connection between meiosis and increased genetic diversity necessary for evolution.

The Science Practice Challenge Questions contain additional test questions for this section that will help you prepare for the AP exam. These questions address the following standards:
[APLO 1.9][APLO 2.15][APLO 2.39][APLO 3.11][APLO 3.9]

You read that **fertilization** is the union of two sex cells from two individual organisms. If these two cells each contain one set of chromosomes, the resulting fertilized cell contains two sets of chromosomes. Haploid cells contain one set of chromosomes. Cells containing two sets of chromosomes are called diploid. The number of sets of chromosomes in a cell is called its ploidy level. If the reproductive cycle is to continue, a diploid cell must reduce the number of its chromosome sets before fertilization can occur again. Otherwise, the number of chromosome sets would double, and continue to double in every generation. So, in addition to fertilization, sexual reproduction includes a nuclear division that reduces the number of chromosome sets.

Most animals and plants are diploid, containing two sets of chromosomes. In an organism's **somatic cells**, sometimes referred to as "body" cells (all cells of a multicellular organism except the 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 length. Diploid organisms inherit one copy of each homologous chromosome from each parent; all together, they are considered a full set of chromosomes. Haploid cells, containing a single copy of each homologous chromosome, are found only within an organism''s reproductive structures, such as the ovaries and testes. Haploid cells can be either gametes or spores. Male gametes are sperm and female gametes are eggs. All animals and most plants produce gametes. Spores are haploid cells that can produce a haploid organism or can fuse with another spore to form a diploid cell. Some plants and all fungi produce spores.

As you have learned, the nuclear division that forms haploid cells— **meiosis**—is closely related to mitosis. Mitosis is the part of a cell reproduction cycle that results in identical daughter nuclei that are also genetically identical to the original parent nucleus. In mitosis, both the parent and the daughter nuclei are at the same ploidy level—diploid for most plants and animals. Meiosis employs many of the same mechanisms as mitosis. However, the starting nucleus is always diploid and the nuclei that result at the end of a meiotic cell division are haploid. To achieve this reduction in chromosome number, meiosis consists of one round of chromosome duplication and 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. **Meiosis II**, in 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 the G_1, S, and G_2 phases, which are nearly identical to the phases preceding mitosis. The G_1 phase, which is also called the first gap phase, is the first phase of the interphase and is focused on cell growth. The S phase is the second phase of interphase, during which the DNA of the chromosomes is replicated. Finally, the G_2 phase, also called the second gap phase, is the third and final phase of interphase; in this 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, called sister chromatids, that are held together at the centromere by **cohesin** proteins. Cohesin holds the chromatids together until

anaphase II. The centrosomes, which are the structures that organize the microtubules of the meiotic spindle, also replicate. This prepares the cell to enter prophase I, the first meiotic phase.

Prophase I

Early in prophase I, before the chromosomes can be seen clearly microscopically, 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 close to each other. Recall that, in mitosis, homologous chromosomes do not pair together. In mitosis, homologous chromosomes line up end-to-end so that when they divide, each daughter cell receives a sister chromatid from both members of the homologous pair. The **synaptonemal complex**, a lattice of proteins between the homologous chromosomes, first forms at specific locations and then spreads 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 non-sister homologous chromatids, a process called crossing over. Crossing over can be observed visually after the exchange as **chiasmata** (singular = chiasma) (Figure 11.2).

In species such as humans, even though the X and Y sex chromosomes are not homologous (most of their genes differ), they have 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.

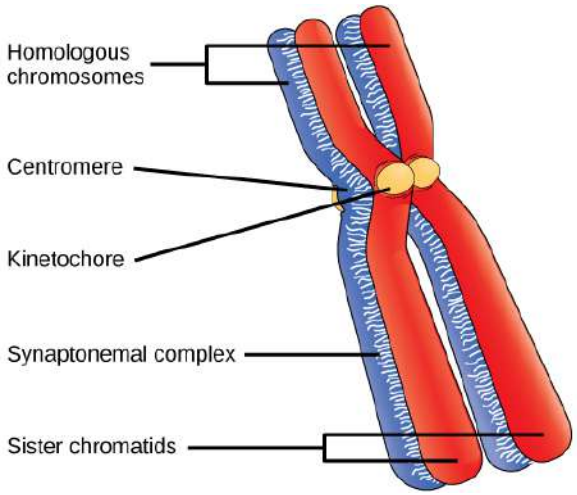


Figure 11.2 Early in prophase I, homologous chromosomes come together to form a synapse. The chromosomes are bound tightly together and in perfect alignment by a protein lattice called a synaptonemal complex and by cohesin proteins at the centromere.

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 non-sister chromatids. Near the recombination nodule on each chromatid, the double-stranded DNA is cleaved, the cut ends are modified, and a new connection is made between the non-sister 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 also removed. At the end of prophase I, the pairs are held together only at the chiasmata (Figure 11.3) and 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 non-sister chromatids leads to a reciprocal exchange of equivalent DNA between a maternal chromosome and a paternal chromosome. Now, when that sister chromatid is moved into a gamete cell it will carry some DNA from one parent of the individual and some DNA from the other parent. The sister recombinant chromatid has a combination of maternal and paternal genes that did not exist before the crossover. Multiple crossovers in an arm of the chromosome have the same effect, exchanging segments of DNA to create recombinant chromosomes.

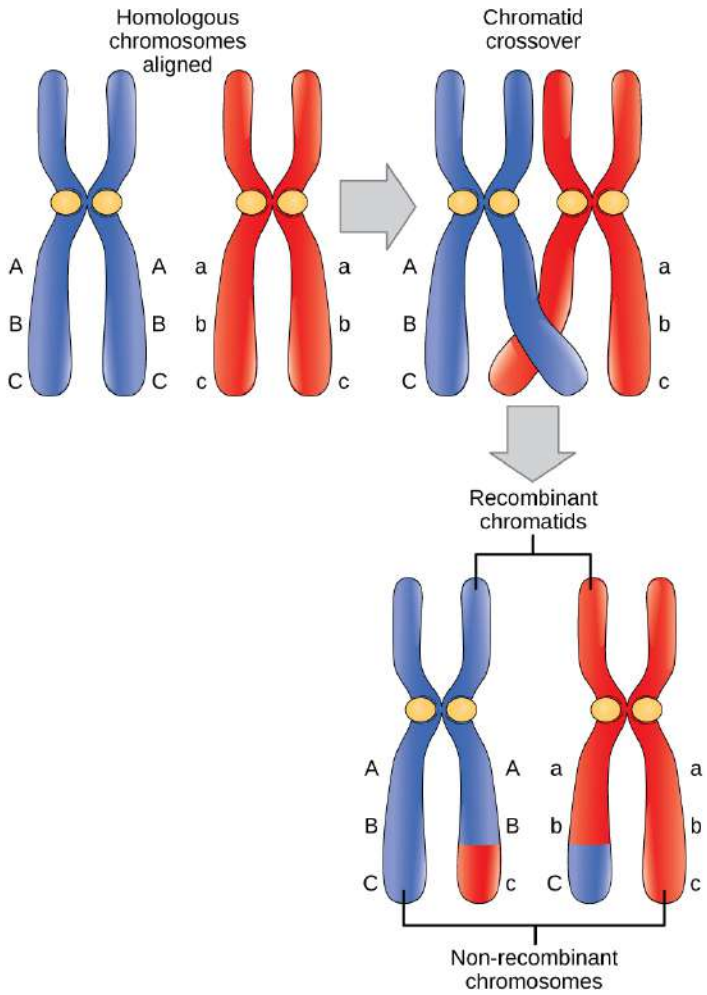


Figure 11.3 Crossover occurs between non-sister chromatids of homologous chromosomes. The result is an exchange of genetic material between homologous chromosomes.

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 centrosomes placed at opposite poles of the cell. The microtubules move toward the middle of the cell and attach to one of the two fused homologous chromosomes. The microtubules attach at each chromosomes' kinetochores. With each member of the homologous pair attached to opposite poles of the cell, 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 chiasmata. In addition, the nuclear membrane has broken down entirely.

Metaphase I

During metaphase I, the homologous chromosomes are arranged in the center 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 homologous chromosomes are not identical. They contain slight differences in their genetic information, causing each gamete to have a unique genetic makeup.

This randomness is the physical basis for the creation of the second form of genetic variation in offspring. Consider 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. Any maternally inherited chromosome may face either pole. 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*, where *n* is the number of chromosomes per set. Humans have 23 chromosome pairs, which results in over eight million (2^{23}) possible genetically-distinct gametes. This number does not include the variability that was previously created in the sister chromatids by crossover. 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 the genetic consequences of meiosis I, the maternal and paternal genes are recombined by crossover events that occur between each homologous pair during prophase I. In addition, the random assortment of tetrads on the metaphase plate produces a unique combination of maternal and paternal chromosomes that will make their way into the gametes.

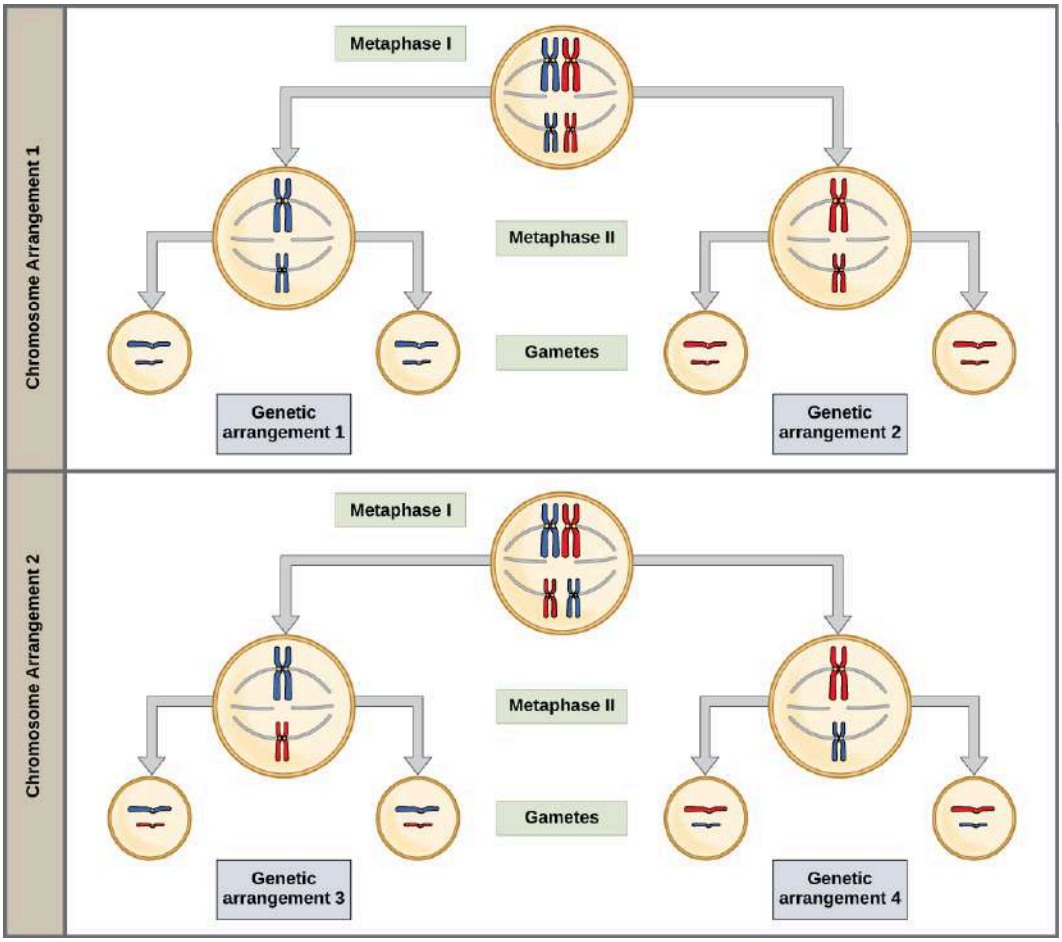


Figure 11.4 Random, independent assortment during metaphase I can be demonstrated by considering a cell with a set of two chromosomes (*n* = 2). In this case, there are two possible arrangements at the equatorial plane in metaphase I. The total possible number of different gametes is 2*n*, where *n* 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 8 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 chromatids in 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 end result of the first meiotic division. 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 homolog 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.

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

Human males typically have XY chromosomes and females have XX chromosomes, but there are rare instances in which a male can inherit an XXY or an XYY, or a female can have three X chromosomes. Explain how an error in meiosis can cause these aberrations.

a. Errors can arise only during the recombination process which may result in deletions, duplications or translocations causing such abnormalities.

b. Aberrations caused when a pair of homologous chromosomes fails to separate during anaphase I or when sister chromatids fail to separate during anaphase II, the daughter cells will inherit unequal numbers of chromosomes.

c. Errors during anaphase I of meiosis only cause such aberrations resulting in unequal numbers of chromosomes.

d. Errors during meiosis introduce variations in the DNA sequence, which depends specifically on the size of the variant only.

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 is similar to mitosis, except that each dividing cell has only one set of homologous chromosomes. Therefore, each cell has half the number of sister chromatids to separate out as a diploid cell undergoing mitosis.

Prophase II

If the chromosomes decondensed in telophase I, they condense again. If nuclear envelopes were formed, they fragment into vesicles. The centrosomes 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. Non-kinetochore microtubules elongate the cell.

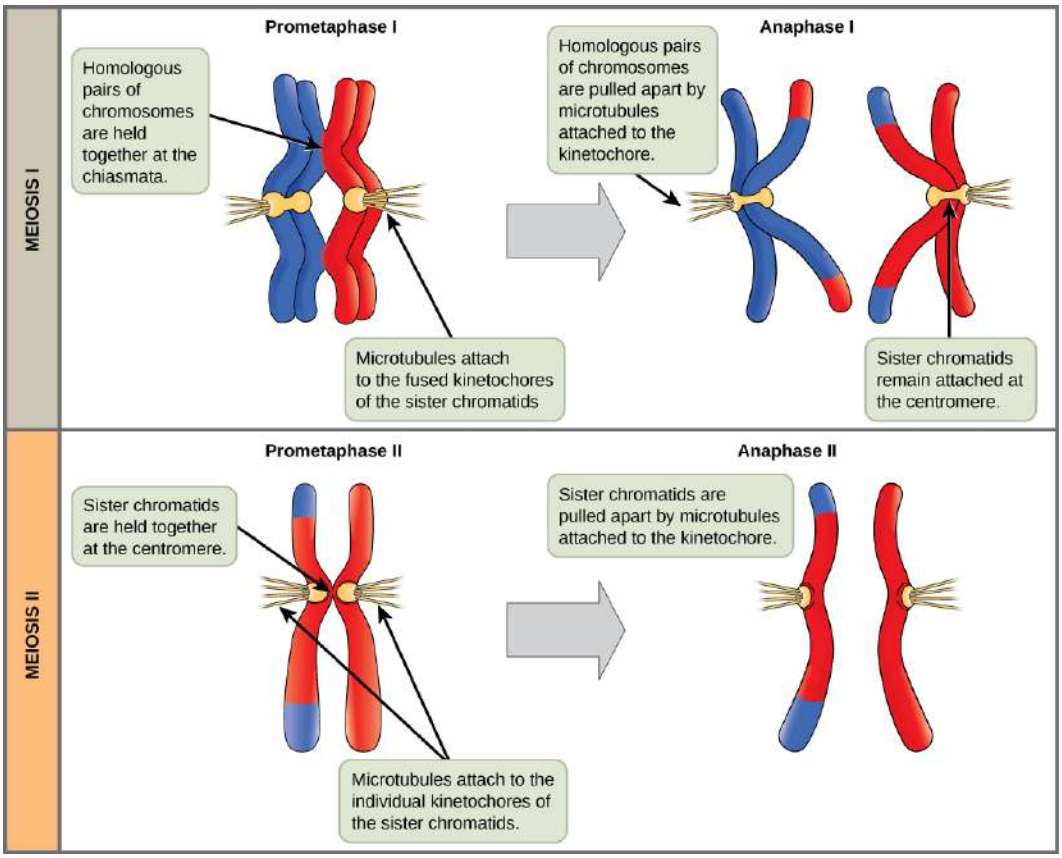


Figure 11.5 The process of chromosome alignment differs between meiosis I and meiosis II. In prometaphase I, microtubules attach to the fused kinetochores of homologous chromosomes, and the homologous chromosomes are arranged at the midpoint of the cell in metaphase I. In anaphase I, the homologous chromosomes are separated. 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 are separated.

Telophase II and Cytokinesis

The chromosomes arrive at opposite poles and begin to decondense. Nuclear envelopes form around the chromosomes. Cytokinesis separates the two cells into four unique haploid cells. At this point, the newly formed nuclei are both haploid. The cells produced are genetically unique because of the random assortment of paternal and maternal homologs and because of the recombining 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**.

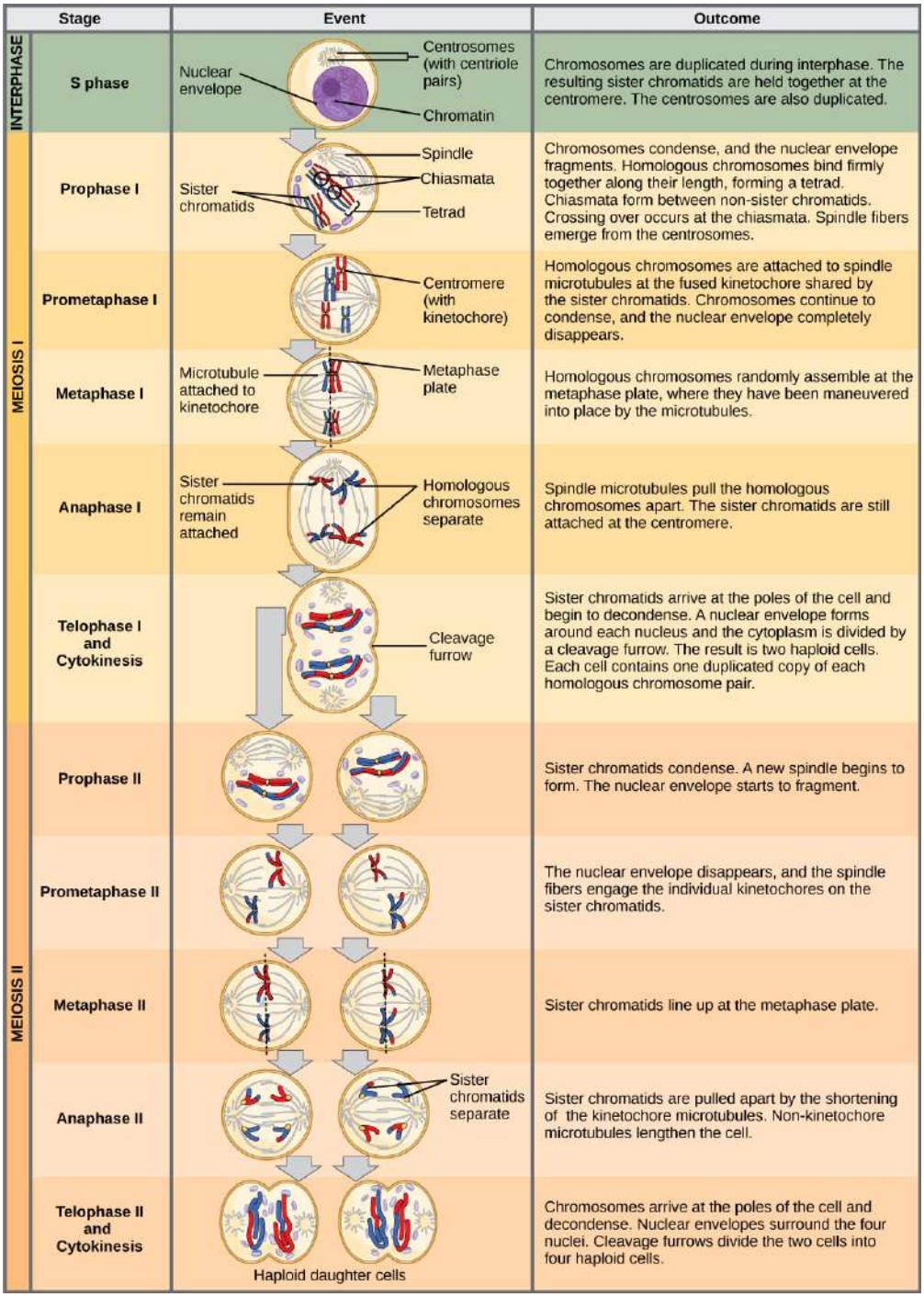


Figure 11.6 An animal cell with a diploid number of four ($2n = 4$) proceeds through the stages of meiosis to form four haploid daughter cells.

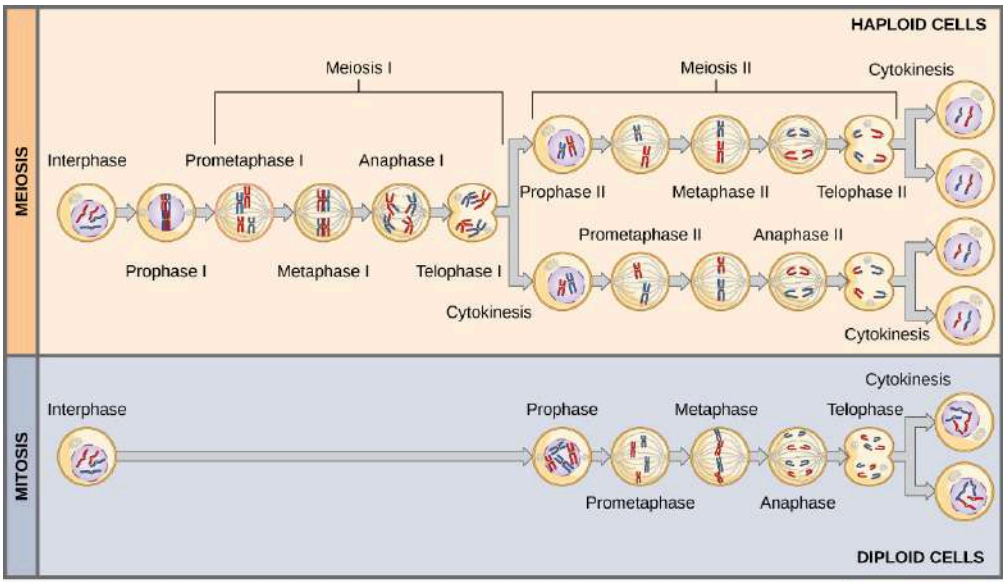
Comparing Meiosis and Mitosis

Mitosis and meiosis are both forms of division of the nucleus in eukaryotic cells. They share some similarities, but also exhibit 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 most plants and all animal species, it is typically diploid cells that undergo mitosis to form new diploid cells. In contrast, meiosis consists of two nuclear divisions resulting in four nuclei that are usually partitioned into four new cells. The nuclei resulting from 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 become associated with each other, are bound together with the synaptonemal complex, develop chiasmata and undergo crossover between sister chromatids, and line up along the metaphase plate in tetrads with kinetochore fibers from opposite spindle poles attached to each kinetochore of a homolog in 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 **reduction division**. There is no such reduction in ploidy level during mitosis.

Meiosis II is much more 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 (like 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 round 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 simpler traits. Meiosis is such an extraordinarily complex series of cellular events that biologists have had trouble hypothesizing and testing 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, 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.

Which of the following events occurs in both mitosis and meiosis I?

a. Homologous chromosomes pair together.
b. Crossover occurs between chromosomes.
c. Chromosomes line up at the metaphase plate.
d. Sister chromatids remain attached during anaphase.

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

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

Single-celled organisms, like amoebas, reproduce by mitosis. Explain how the genetic makeup of these organisms differs from organisms that undergo meiosis.

a. Organisms reproducing through mitosis produce genetically different daughter cells whereas those producing through meiosis have genetically identical daughter cells.

b. Crossing over or mixing of chromosomes does not occur in meiosis whereas it is prevalent in mitosis.

c. Mitosis is a process of asexual reproduction in which the number of chromosomes are reduced by half producing two haploid cells whereas in meiosis two diploid cells are produced by cell division.

d. Organisms producing through mitosis create genetically identical offspring as only a single parent copies its entire genetic material to the offspring. In meiosis, two parents produces gametes and the offspring have only half the number of chromosomes of each parent and hence genetic variation is introduced.

science practices CONNECTION for AP® Courses

Activity

Create a series of diagrams with annotations to compare and contrast the processes of mitosis and meiosis in an organism with a haploid number of six. Then, using specific examples, explain how meiosis followed by fertilization increases genetic variation in a family of organisms.

11.2 | Sexual Reproduction

In this section, you will explore the following questions:

- Why are meiosis and sexual reproduction considered evolved traits?
- Why is variation among offspring a potential evolutionary advantage to sexual reproduction?
- What are the three different life-cycles among sexual multicellular organisms and their commonalities?

Connection for AP® Courses

Nearly all eukaryotes undergo sexual reproduction. The variation introduced into the reproductive cells (gametes or spores) by meiosis is advantageous for evolution via natural selection. Meiosis and fertilization alternate as the organisms pass through the haploid and diploid stages of their life cycles. In most animals, the diploid stage dominates, whereas in fungi, the haploid stage dominates. Identifying the haploid and diploid stages within the life cycles of different organisms is vital in understanding how organisms reproduce and in determining when mitosis and meiosis occur.

Information presented and the examples highlighted in the section support concepts and learning objectives outlined in Big Idea 3 of the AP® Biology Curriculum Framework. The learning objectives listed in the Curriculum Framework provide

a transparent foundation for the AP® Biology course, an inquiry-based laboratory experience, instructional activities, and AP® exam questions. A Learning Objective merges required content with one or more of the seven science practices.

Big Idea 3	Living systems store, retrieve, transmit and respond to information essential to life processes.
Enduring Understanding 3.C	The processing of genetic information is imperfect and is a source of genetic variation.
Essential Knowledge	**3.C.2** Biological systems have multiple processes that increase genetic variation.
Science Practice	**7.2** The student can connect concepts in and across domain(s) to generalize or extrapolate in and/or across enduring understandings and/or big ideas.
Learning Objective	**3.27** The student is able to compare and contrast processes by which genetic variation is produced and maintained in organisms from multiple domains.

The Science Practice Challenge Questions contain additional test questions for this section that will help you prepare for the AP exam. These questions address the following standards:
[APLO 3.7][APLO 3.9][APLO 3.24][APLO 3.28]

Sexual reproduction was 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 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 would 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 asexual eggs. 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 in theory an asexual population could grow twice as fast.

However, multicellular organisms that exclusively depend on asexual reproduction are exceedingly rare. Why is sexuality (and meiosis) so common? This is one of the important unanswered questions in biology and has been the focus of much research beginning in the latter half of the twentieth 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. This is the ultimate source of variation in sexual organisms, but in addition, those different mutations are 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

It is not in dispute that sexual reproduction provides evolutionary advantages to organisms that employ this mechanism to produce offspring. But why, even in the face of fairly stable conditions, does sexual reproduction persist when it is more difficult and costly for individual organisms? Variation is the outcome of sexual reproduction, but why are ongoing variations necessary? 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 co-evolve 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 an edge over close competitors, predators, parasites, or even prey. The only method that will allow a co-evolving species to maintain its own share of the resources is to also continually improve its fitness. As one species gains an advantage, this increases selection pressure 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 co-evolution between competing species.

Which of the following scenarios provides the best support for the Red Queen Hypothesis?

a. An asexually reproducing plant rapidly populates a hillside left barren by a fire.
b. Individuals of a snail population that reproduce asexually die out after a parasite invades its territory.
c. A widely dispersed population of ruffed grouse disappears because individuals have difficulty finding mates.
d. A sexually-reproducing species of gophers goes extinct after a new predator is introduced.

Life Cycles of Sexually Reproducing Organisms

Fertilization and meiosis alternate in sexual **life cycles**. What happens between these two events depends on the organism. The process of meiosis reduces the chromosome number by half. Fertilization, the joining of two haploid gametes, restores the diploid condition. There are three main categories of life cycles in multicellular organisms: **diploid-dominant**, in which the multicellular diploid stage is the most obvious life stage, such as with most animals including humans; **haploid-dominant**, in which the multicellular haploid stage is the most obvious life stage, such as with all fungi and some algae; and **alternation of generations**, in which the two stages are apparent to different degrees depending on the group, as with plants and some algae.

Diploid-Dominant Life Cycle

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 cell line and meiosis to produce 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**).

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

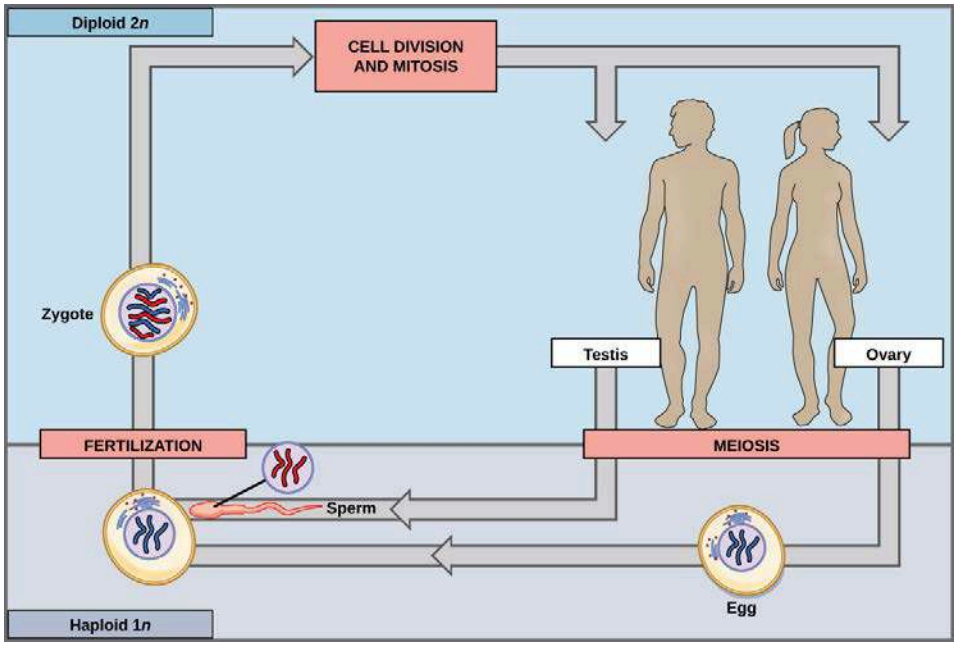


Figure 11.8 In animals, sexually reproducing adults form haploid gametes from diploid germ cells. Fusion of the gametes gives rise to a fertilized egg cell, or zygote. The zygote will undergo multiple rounds of mitosis to produce a multicellular offspring. The germ cells are generated early in the development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

Haploid-Dominant Life Cycle

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 haploid like the "parents," these spores contain a new genetic combination from two parents. The spores can remain dormant for various time periods. Eventually, when conditions are conducive, the spores form multicellular haploid structures by many rounds of mitosis (**Figure 11.9**).

visual CONNECTION

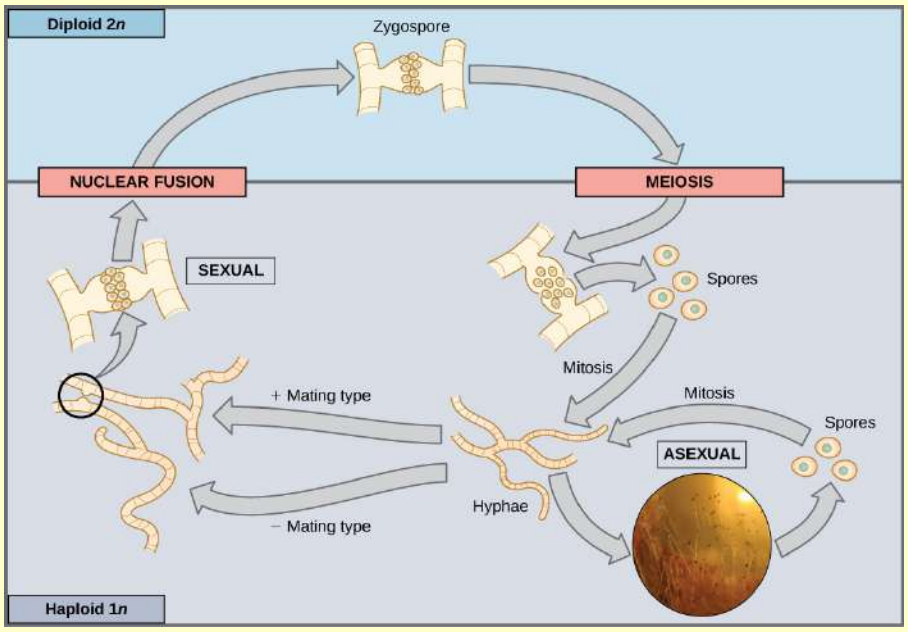


Figure 11.9 Fungi, such as black bread mold (*Rhizopus nigricans*), have haploid-dominant life cycles. The haploid multicellular stage produces specialized haploid cells by mitosis that fuse to form a diploid zygote. The zygote undergoes meiosis to produce haploid spores. Each spore gives rise to a multicellular haploid organism by mitosis. (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?

a. No, sexual mode of reproduction is the only mode of reproduction in fungi.

b. No, absence of minus mating types will disrupt functions in fungi.

c. Yes, it will be able to reproduce asexually by the mitotic divisions of spores.

d. Yes, by action of some enzymes, it will be able to reproduce asexually.

Alternation of Generations

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 a 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**).

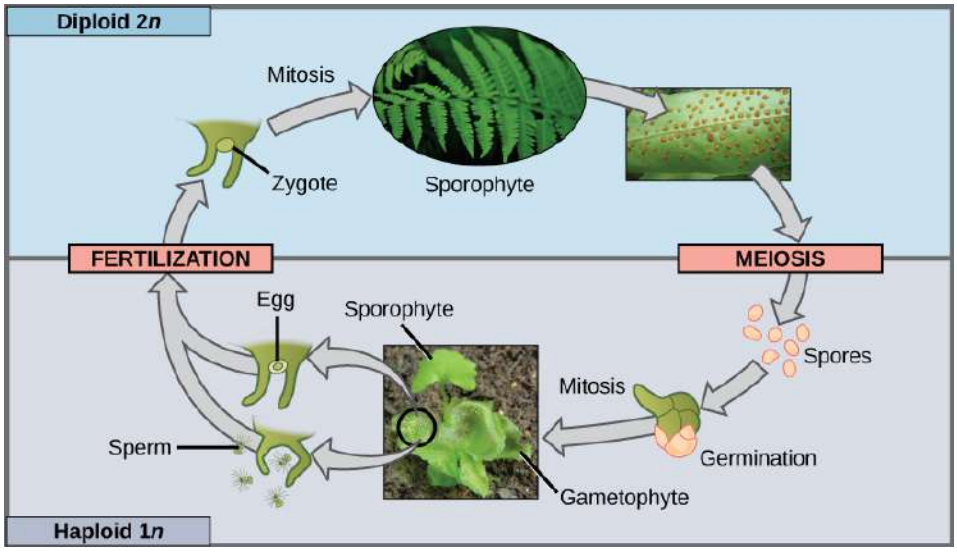


Figure 11.10 Plants have a life cycle that alternates between a multicellular haploid organism and a multicellular diploid organism. In some plants, such as ferns, both the haploid and diploid plant stages are free-living. The diploid plant is called a sporophyte because it produces haploid spores by meiosis. The spores develop into multicellular, haploid plants 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. However, at some point in each type of life cycle, meiosis produces haploid cells that will fuse with the haploid cell of another organism. The mechanisms of variation—crossover, random assortment of homologous chromosomes, and random fertilization—are present in all versions of sexual reproduction. 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.

science practices CONNECTION for AP® Courses

Think About It

Compare and contrast the three main types of life cycles in multicellular organisms and give an example of an organism that employs each.

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 non-sister chromatids resulting in chromosomes that incorporate genes from both parents of the organism

diploid-dominant life-cycle type in which the multicellular diploid stage is prevalent

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

haploid-dominant life-cycle type in which the multicellular haploid stage is prevalent

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 non-sister 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 diploid organisms produce haploid cells that can fuse during fertilization to form diploid offspring. As with mitosis, DNA replication occurs prior to meiosis during the S-phase of the cell cycle. Meiosis is a series of events that arrange and separate chromosomes and chromatids into daughter cells. During the interphases of meiosis, each chromosome is duplicated. 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 separates homologs, and the second—like mitosis—separates chromatids into individual chromosomes. During meiosis, variation in the daughter

nuclei is introduced because of crossover in prophase I and random alignment of tetrads at metaphase I. The cells that are produced by meiosis are genetically unique.

Meiosis and mitosis share similarities, but have distinct outcomes. Mitotic divisions are single nuclear divisions that produce daughter nuclei that are genetically identical and have the same number of chromosome sets as the original cell. Meiotic divisions include two nuclear divisions that produce four daughter nuclei that are genetically different and have one chromosome set instead of the two sets of chromosomes in the parent cell. The main differences between the processes occur in the first division of meiosis, in which homologous chromosomes are paired and exchange non-sister 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 more similar to a mitotic division, except that the daughter cells do not contain identical genomes because of crossover.

11.2 Sexual Reproduction

Nearly all eukaryotes undergo sexual reproduction. The variation introduced into the reproductive cells by meiosis appears to be one of the advantages of sexual reproduction that has made it so 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. Fertilization, the fusion of haploid gametes from two individuals, restores the diploid condition. Thus, 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. There are three main categories of life cycles: diploid-dominant, demonstrated by most animals; haploid-dominant, demonstrated by all fungi and some algae; and the alternation of generations, demonstrated by plants and some algae.

REVIEW QUESTIONS

1. How many and what type of daughter cells does meiosis produce?

a. four haploid
b. four diploid
c. two haploid
d. two diploid

2. What structure is most important in forming the tetrads?

a. centromere
b. chiasmata
c. kinetochore
d. Synaptonemal complex

3. At which stage of meiosis are sister chromatids separated from each other?

a. anaphase I
b. anaphase II
c. prophase I
d. prophase II

4. At metaphase I, homologous chromosomes are connected only at what structures?

a. chiasmata
b. kinetochores
c. microtubules
d. recombination nodules

5. What phase(s) of mitotic interphase is missing from meiotic interkinesis?

a. G_0 phase
b. G_1 phase
c. G_2 phase
d. S-phase

6. What part of meiosis is most similar to mitosis?

a. reduction division
b. interkinesis
c. meiosis I
d. meiosis II

7. Which of the following is not true during crossing over?

a. Chiasmata are formed.
b. Non-sister chromatids exchange genetic material.
c. Recombination nodules mediate cross over events.
d. Spindle microtubules guide the movement of chromosomal material.

8. During which phase does the second round of genetic variation occur during meiosis?

a. anaphase I
b. metaphase I
c. prophase II
d. Genetic variation only occurs during prophase I.

9. Which type of life cycle has both a haploid and a

diploid multicellular stage?

a. alternation of generations
b. asexual
c. diploid-dominant
d. haploid-dominant

10. What is a source of variation in asexual reproduction?

a. crossing over of chromosomes
b. mutation of DNA
c. random assortment of chromosomes
d. There is no variation in asexual reproduction.

11. What is a likely evolutionary advantage of sexual reproduction over asexual reproduction?

a. Sexual reproduction involves fewer steps.
b. Sexual reproduction results in variation in the offspring.
c. Sexual reproduction is more metabolically efficient.
d. Sexual reproduction uses up fewer resources in a given environment.

12. What is a disadvantage of sexual reproduction over asexual forms of reproduction?

a. Half the population is capable of carrying offspring.
b. Identical offspring are not produced.
c. Adaptation to rapidly changing environments is more difficult.
d. Mutation rates are slower.

13. Fungi typically display which type of life cycle?

a. alternation of generations
b. asexual
c. diploid-dominant
d. haploid-dominant

14. What is a haploid cell produced in a diploid-dominant organism by meiosis called?

a. gamete
b. gametophyte
c. spore
d. sporophyte

CRITICAL THINKING QUESTIONS

15. Describe what happens to the tetrads after they form.

a. Prophase I of meiosis forms the tetrads. They line up at the midway point between the two poles of the cell to form the metaphase plate. There is equal chance of a microtubule fiber to encounter a maternally or a paternally inherited chromosome. Orientation of each tetrad is independent of the orientation of other tetrads.
b. Prophase II of meiosis forms the tetrads. They line up at the midway point between the two poles of the cell to form the metaphase plate. There is equal chance of microtubule fiber to encounter maternally or paternally inherited chromosome. Orientation of each tetrad is independent of the orientation of other tetrads.
c. Prophase I of mitosis forms the tetrads. They line up at the midway between the two poles of the cell to form the metaphase plate. There is equal chance of a microtubule fiber to encounter a maternally or a paternally inherited chromosome. Orientation of each tetrad is independent of the orientation of other tetrads.
d. Prophase I of meiosis forms the tetrads. They line up at the midway between the two poles of the cell to form the metaphase plate. There is a chance of microtubule fiber to encounter maternally inherited chromosome. Orientation of each tetrad is independent of the orientation of other tetrads.

16. Which of the following distinguishes metaphase I from metaphase II?

a. Metaphase I occurs when chromosomes appear in homologous pairs on the spindle. Metaphase II has a single line of chromosomes on the spindle. A Pair of chromosomes is pulled apart and migrate towards pole in anaphase I, while in anaphase II sister chromatids separate. Telophase I reconstitutes the nucleus and loosen the chromosomes, while telophase II mimics telophase I.

b. Prophase I condenses the chromosomes and eliminates the nuclear membrane. The microtubules arrange in a spindle. Prophase II mimics prophase I. Metaphase I occurs when chromosomes appear in homologous pairs on the spindle. Metaphase II has a single line of chromosomes on the spindle. Pairs of chromosomes are pulled apart and migrate towards the poles during anaphase I, while in anaphase II sister chromatids separate. Telophase I reconstitutes the nucleus and condenses the chromosomes, while telophase II mimics telophase I.

c. Prophase I condense the chromosomes and add nuclear membrane. The microtubules arrange in a spindle. Prophase II mimics prophase I. Metaphase I occurs when chromosomes appear in homologous pairs on the spindle. Metaphase II has a single line of chromosomes on the spindle. Pair of chromosomes are pulled apart and migrate towards the poles in anaphase I, while in anaphase II sister chromatids separate. Telophase I reconstitutes the nucleus and loosens the chromosomes, while telophase II mimics telophase I.

d. Prophase I condenses the chromosomes and eliminates the nuclear membrane. The microtubules arrange in a spindle. Prophase II mimics prophase I. Metaphase I occurs when chromosomes appear in homologous pairs on the spindle. During Metaphase II, the chromosomes line up in a double line across the spindle. Each pair of chromosomes is pulled apart and migrate towards the poles in anaphase I, while in anaphase II sister chromatids separate. Telophase I reconstitutes the nucleus and loosen the chromosomes, while telophase II mimics telophase I.

17. Though the stages of meiosis have the same names as the stages of mitosis, they exhibit fundamental differences. What are the main differences between the two processes?

a. Meiosis differs from mitosis in that the number of chromosomes is halved and genetic variation is introduced in meiosis, but not in mitosis.

b. Meiosis differs from mitosis in that the number of chromosomes is halved and genetic variation is reduced in meiosis, but not in mitosis.

c. Metaphase and telophase portions of meiosis and mitosis are the same. Meiosis and mitosis are also the same, except for the number of chromosomes. Anaphase I and anaphase are different.

d. Prophase and telophase portions of meiosis and mitosis are the same. Meiosis II and mitosis are also the same and have the same number of chromosomes. Anaphase I and anaphase are different.

18. Explain how the orientation of homologous chromosomes during metaphase I of meiosis contributes to greater variation in gametes.

a. The random alignment of homologous chromosomes at the metaphase plate ensures the random destination of the chromosomes in the daughter cells.

b. Because homologous chromosomes dissociate from the spindle fibers during metaphase I, they move randomly to the daughter cells.

c. The homologous chromosomes are paired tightly during metaphase I and undergo crossover as the synaptonemal complex forms a lattice around them.

d. Recombination of maternal and paternal chromosomes occurs in metaphase I because the homologous chromosomes are not connected at their centromeres.

19. Explain how the Red Queen’s catchphrase, “It takes all the running you can do to stay in the same place,” describes co-evolution between competing species.

a. When a sexually reproducing species and an asexually reproducing species compete for the same resources, they both "run [evolve] in the same place" because the increased genetic variation in the sexually reproducing species balances the loss in energy it uses to find and attract mates.

b. When one species gains an advantage with a favorable variation, selection increases on another species with which it competes. This species must also develop an advantage or it will be outcompeted. The two species "run [evolve] to stay in the same place."

c. When one species develops a mutation that decreases its ability to survive, a competing species will become better able to survive even though it has not changed in any way. In effect, this species "runs [evolves] to stay in the same place."

d. When two asexually reproducing species encounter rapid environmental change, the species that is also able to reproduce sexually will outcompete the other. This way it can "run [evolve] to stay in the same place."

20. Which three processes lead to variation among offspring that have the same two parents?

a. genetic recombination, fertilization, meiosis

b. crossing over, random chromosome assortment, genetic recombination

c. meiosis, crossing over, genetic recombination

d. fertilization, crossing over, random chromosome assortment

21. Compare the three main types of life cycles in multicellular organisms and give an example of an organism that employs each.

a. In a diploid dominant cycle, the multicellular diploid stage is present, as in humans. Haploid dominant life cycles have a multicellular haploid stage, as in fungi. In alternation of generations, both haploid dominant and diploid dominant stages alternate, as in plants.

b. In a diploid dominant cycle, the unicellular diploid stage is present, as in humans. In a haploid dominant life cycle, a unicellular haploid stage is present, as in fungi. In alternation of generations both haploid dominant and diploid dominant stages alternate, as in plants.

c. In a diploid dominant cycle, a multicellular haploid stage is present, as in humans. In a haploid dominant life cycle, a multicellular diploid stage is present, as in fungi. In alternation of generations, both haploid dominant and diploid dominant stages alternate, as in plants.

d. In a diploid dominant cycle, a multicellular diploid stage is present, as in algae. In a haploid dominant life cycle, a multicellular haploid stage is present, as in plants. In alternation of generations, both haploid dominant and diploid dominant stages alternate, as in fungi.

TEST PREP FOR AP® COURSES

22. Reproductive cells in most species are different from the cells that make up the rest of the organism. What are the "body" cells called and how are they different from the reproductive cells?

a. Body cells are called gametes and they have half the number of chromosomes found in reproductive cells.

b. Body cells are called somatic cells and have the same number of chromosomes as reproductive cells.

c. Body cells are called somatic cells and have double the number of chromosomes found in reproductive cells.

d. Body cells are called gametes and have double the number of chromosomes found in reproductive cells.

23. Spores are structures produced by some plants and all fungi. Which is true about them?

a. Spores are haploid reproductive cells that can produce haploid organisms through mitosis.

b. Spores are haploid precursors to gametes that give rise to gametes when environmental conditions are favorable.

c. Spores are haploid reproductive cells that can produce diploid cells without fertilization.

d. Spores are haploid cells formed only during asexual reproduction and so are not formed by meiosis.

24. In prophase I, the homologous chromosomes are paired up and linked together. What binds the chromosomes together and maintains their alignment?

a. cohesin proteins

b. tetrads

c. the centromere

d. synaptonemal complex

25. One of the ways that sexual reproduction enhances the diversity of offspring from the same parents is through a process called crossing over. What entities does this occur between during prophase I?

a. sister chromatids
b. tetrads
c. non-homologous chromosomes
d. non-sister chromatids of homologous chromosomes

26. There are three sources of genetic variation in sexual reproduction. Which is not considered random?

a. All are random.
b. Crossing over
c. Egg and sperm fertilization
d. Tetrad alignment on the meiotic spindle.

27. Which one of the three types of life cycles of sexually reproducing organisms does not have a multicellular haploid stage?

a. alternation of generations
b. diploid-dominant
c. haploid-dominant
d. They all have a multicellular haploid stage in their life cycles.

28. How are spores produced in haploid-dominant and alternation of generation life cycles?

a. by gametophytes
b. by germ cells
c. through mitosis
d. through meiosis

29. What is one thing that is true of haploid-dominant life cycles but not of alternation of generation life cycles?

a. meiosis
b. (+) and (−) mating types
c. spores
d. a free-living haploid stage

SCIENCE PRACTICE CHALLENGE QUESTIONS

30. Meiosis involves processes that are common to all eukaryotes, involving the same or similar genes. **Evaluate** the support for the theory of evolution provided by this evidence and, additionally, by the absence of any alternative process.

31. Meiotic phases of yeast cells were observed microscopically with fluorescent markers (Nachman et al., Cell, 131(3), 2007) to determine the time intervals of meiosis I and meiosis II. The data are displayed in the following figure:

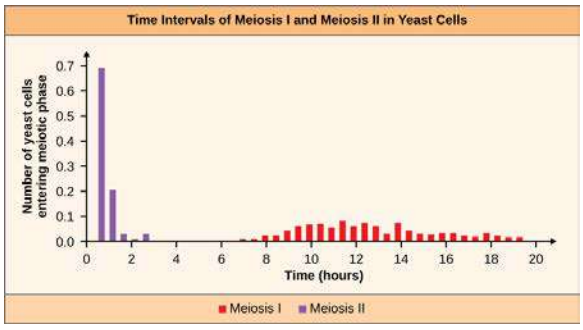


Figure 11.11

The duration of meiosis I is measured relative to the transfer of spores to the growth medium. The duration of meiosis II is measured relative to the emergence from meiosis I. On the *y-axis*, the fraction of cells observed to enter each phase are shown, where the sampling has been made in increments of 0.5 hours.

A. Qualitatively **compare** the mean and standard deviation for these two distributions.

B. The gene Ime1 is transcribed at the start of meiosis I in response to nitrogen starvation. This activates Ime2 that interacts with Ime1. If, during meiosis I, the cells are supplied with nitrogen, meiosis is halted. Based on these data, **justify the claim** that this interaction provides a negative feedback loop.

C. **Explain** the advantage provided to the population and the risk to individual cells of the timing of meiosis displayed in the graph above.

32. Construct an explanation as to how DNA is transmitted to the next generation via meiosis followed by fertilization.

33. In eukaryotes, sexual reproduction involves the recombination of heritable information from both parents via meiosis followed by fertilization. Meiosis reduces the number of chromosomes from diploid (2n) to haploid (1n) during the production of gametes. Meiosis begins with the duplication of DNA, producing four strands of DNA in two pairs of homologous chromosomes: 2(2n) becomes 4(n), that is, four haploid cells, where n is the number of strands of DNA in a chromosome.

A. **Construct** an explanation of the importance of random, independent assortment to genetic variation by **creating a diagram** that represents homologous chromosomes during prophase I without crossover and the possible arrangements of these chromosomes during metaphase I:

- without recombination during prophase I

- with recombination involving two chiasmata

B. An alternative would be to bypass the initial duplication of DNA: 2n becomes 2(n), that is, a diploid cell becomes two haploid cells. **Predict** the effect that this would have on genetic variation.