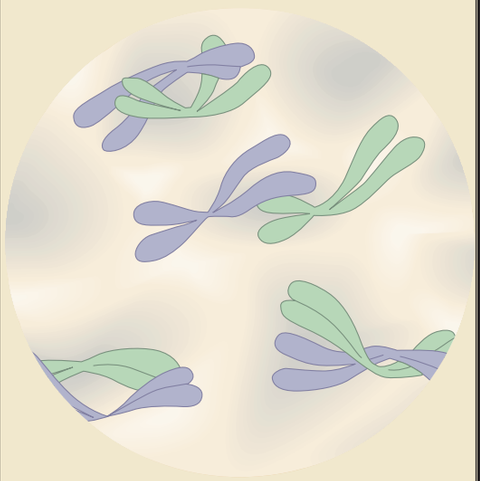
9 Meiosis
Sex-Cell Formation



CHAPTER 9

Chapter Outline

Key Concepts	Applications
Know the steps in meiosis.	• To explain what happens when a sex cell is made. • Be able to diagram the stages of meiosis. • Explain how meiosis differs from mitosis. • Understand the genetic advantage to sexual reproduction. • Explain how one person can make many different types of sex cells.
Know how meiosis normally occurs.	• Know how certain genetic abnormalities occur.
Understand how gametes are formed and unite at fertilization.	• Understand why brothers and sisters of the same birthparents can be so different.
Understand the difference between meiosis and mitosis.	• Explain the difference between sexual and asexual reproduction.

9.1 Sexual Reproduction

The most successful kinds of plants and animals are those that have developed a method of shuffling and exchanging genetic information. This usually involves organisms that have two sets of genetic data, one inherited from each parent. **Sexual reproduction** is the formation of a new individual by the union of two sex cells. Before sexual reproduction can occur, the two sets of genetic information must be reduced to one set. This is somewhat similar to shuffling a deck of cards and dealing out hands; the shuffling and dealing assure that each hand will be different. An organism with two sets of chromosomes can produce many combinations of chromosomes when it produces sex cells, just as many different hands can be dealt from one pack of cards. When one of these sex cells unites with another, a new organism containing two sets of genetic information is formed. This new organism's genetic information might very well have survival advantages over the information found in either parent; this is the value of sexual reproduction.

In chapter 8, we discussed the cell cycle and pointed out that it is a continuous process, without a beginning or an end. The process of mitosis followed by growth is important in the life cycle of any organism. Thus, the *cell cycle* is part of an organism's *life cycle* (figure 9.1).

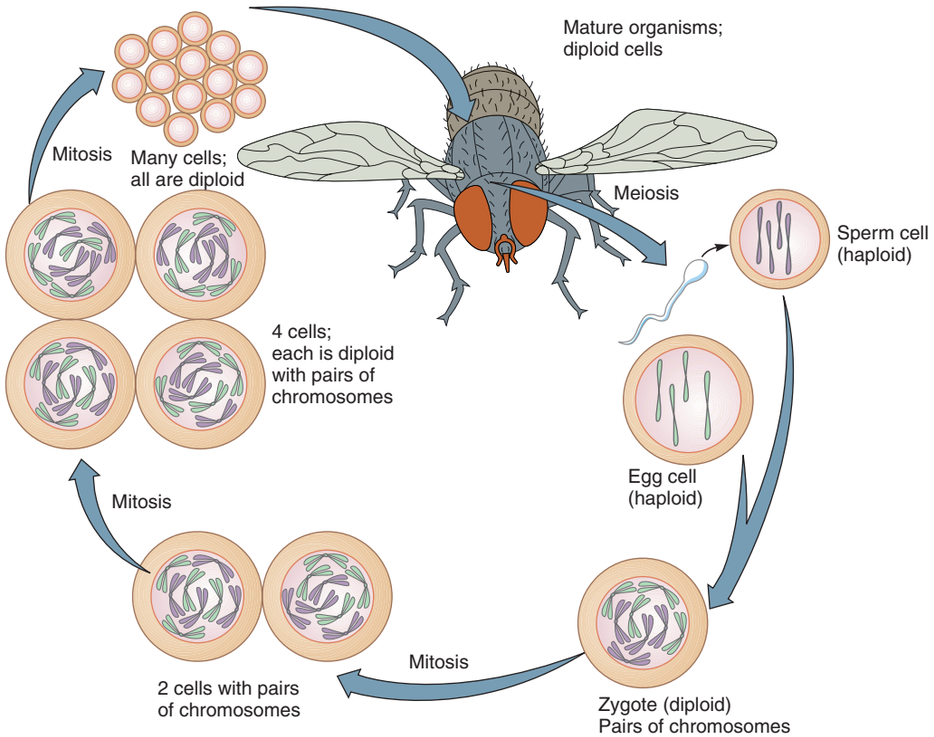
The sex cells produced by male organisms are called **sperm,** and those produced by females are called **eggs.** A general term sometimes used to refer to either eggs or sperm is **gamete** (sex cell). The cellular process that is responsible for generating gametes is called **gametogenesis.** The uniting of an egg and sperm (gametes) is known as **fertilization.**

In many organisms the **zygote,** which results from the union of an egg and a sperm, divides repeatedly by mitosis to form the complete organism. Notice in figure 9.1 that the zygote and its descendants have two sets of chromosomes. However, the male gamete and the female gamete each contain only one set of chromosomes. These sex cells are said to be **haploid.** The haploid number of chromosomes is noted as *n*. A zygote contains two sets and is said to be **diploid.** The diploid number of chromosomes is noted as $2n$ ($n + n = 2n$). Diploid cells have two sets of chromosomes, one set from each parent. Remember, a chromosome is composed of two chromatids, each containing double-stranded DNA. These two chromatids are attached to each other at a point called the *centromere*. In a diploid nucleus, the chromosomes occur as **homologous chromosomes**—a pair of chromosomes in a diploid cell that contain similar genes throughout their length. One of the chromosomes of a homologous pair was donated by the father, the other by the mother (figure 9.2). Different species of organisms vary in the number of chromosomes they contain. Table 9.1 lists several different organisms and their haploid and diploid chromosome numbers.

It is necessary for organisms that reproduce sexually to form gametes having only one set of chromosomes. If

Figure 9.1

Life Cycle
The cells of this adult fruit fly have eight chromosomes in their nuclei. In preparation for sexual reproduction, the number of chromosomes must be reduced by half so that fertilization will result in the original number of eight chromosomes in the new individual. The offspring will grow and produce new cells by mitosis.



gametes contained two sets of chromosomes, the zygote resulting from their union would have four sets of chromosomes. The number of chromosomes would continue to double with each new generation, which could result in the extinction of the species. However, this does not usually happen; the number of chromosomes remains constant generation after generation. Because cell division by mitosis and cytokinesis results in cells that have the same number of chromosomes as the parent cell, two questions arise: how are sperm and egg cells formed, and how do they get only half the chromosomes of the diploid cell? The answers lie in the process of **meiosis,** the specialized pair of cell divisions that reduce the chromosome number from diploid ($2n$) to haploid (n). One of the major functions of meiosis is to produce cells that have one set of genetic information. Therefore, when fertilization occurs, the zygote will have two sets of chromosomes, as did each parent.

Not every cell goes through the process of meiosis. Only specialized organs are capable of producing haploid cells (figure 9.3). In animals, the organs in which meiosis occurs are called **gonads.** The female gonads that produce eggs are called **ovaries.** The male gonads that produce sperm are called **testes.** Organs that produce gametes are also found in algae and plants. Some of these are very simple. In algae such as *Spirogyra,* individual cells become specialized for gamete production. In plants, the structures are very complex. In flowering plants, the **pistil** produces eggs or ova, and the **anther** produces pollen, which contains sperm.

To illustrate meiosis in this chapter, we have chosen to show a cell that has only eight chromosomes (figure 9.4). (In reality, humans have 46 chromosomes, or 23 pairs.) The haploid number of chromosomes in this cell is four, and these haploid cells contain only one complete set of four chromosomes. You can see that there are eight chromosomes in this cell—four from the mother and four from the father. A closer look at figure 9.4 shows you that there are only four types of chromosomes, but two of each type:

1. Long chromosomes consisting of chromatids attached at centromeres near the center
2. Long chromosomes consisting of chromatids attached near one end
3. Short chromosomes consisting of chromatids attached near one end
4. Short chromosomes consisting of chromatids attached near the center

We can talk about the number of chromosomes in two ways. We can say that our hypothetical diploid cell has eight replicated chromosomes, or we can say that it has four pairs of homologous chromosomes.

Haploid cells, on the other hand, do not have homologous chromosomes. They have one of each type of chromosome. The whole point of meiosis is to distribute the chromosomes and the genes they carry so that each daughter cell gets one member of each homologous pair. In this way, each daughter cell gets one complete set of genetic information.

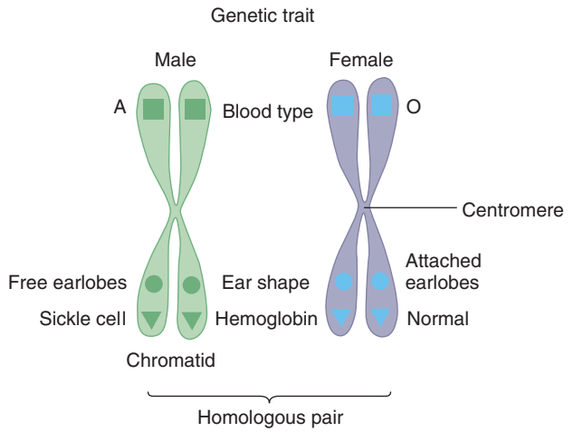


Figure 9.2

A Pair of Homologous Chromosomes
A pair of chromosomes of similar size and shape that have genes for the same traits are said to be homologous. Notice that the genes may not be identical but code for the same type of information. Homologous chromosomes are of the same length, have the same types of genes in the same sequence, and have their centromeres in the same location—one came from the male parent and the other was contributed by the female parent.

Table 9.1

CHROMOSOME NUMBERS

Organism	Haploid Number	Diploid Number
Mosquito	3	6
Fruit fly	4	8
Housefly	6	12
Toad	18	36
Cat	19	38
Human	23	46
Hedgehog	23	46
Chimpanzee	24	48
Horse	32	64
Dog	39	78
Onion	8	16
Kidney bean	11	22
Rice	12	24
Tomato	12	24
Potato	24	48
Tobacco	24	48
Cotton	26	52

9.2 The Mechanics of Meiosis: Meiosis I

Meiosis is preceded by an interphase stage during which DNA replication occurs. In a sequence of events called *meiosis I,* members of homologous pairs of chromosomes divide into two complete sets. This is sometimes called a **reduction division,** a type of cell division in which daughter cells get only half the chromosomes from the parent cell. The division begins with replicated chromosomes composed of two chromatids. The sequence of events in meiosis I is artificially divided into four phases: prophase I, metaphase I, anaphase I, and telophase I.

Prophase I

During prophase I, the cell is preparing itself for division (figure 9.5). The chromatin material coils and thickens into chromosomes, the nucleoli disappear, the nuclear membrane is disassembled, and the spindle begins to form. The spindle is formed in animals when the centrioles move to the poles. There are no centrioles in plant cells, but the spindle does form. However, there is an important difference between the prophase stage of mitosis and prophase I of meiosis. During prophase I, homologous chromosomes recognize one another by their centromeres, move through the cell toward one another, and come to lie next to each other in a process

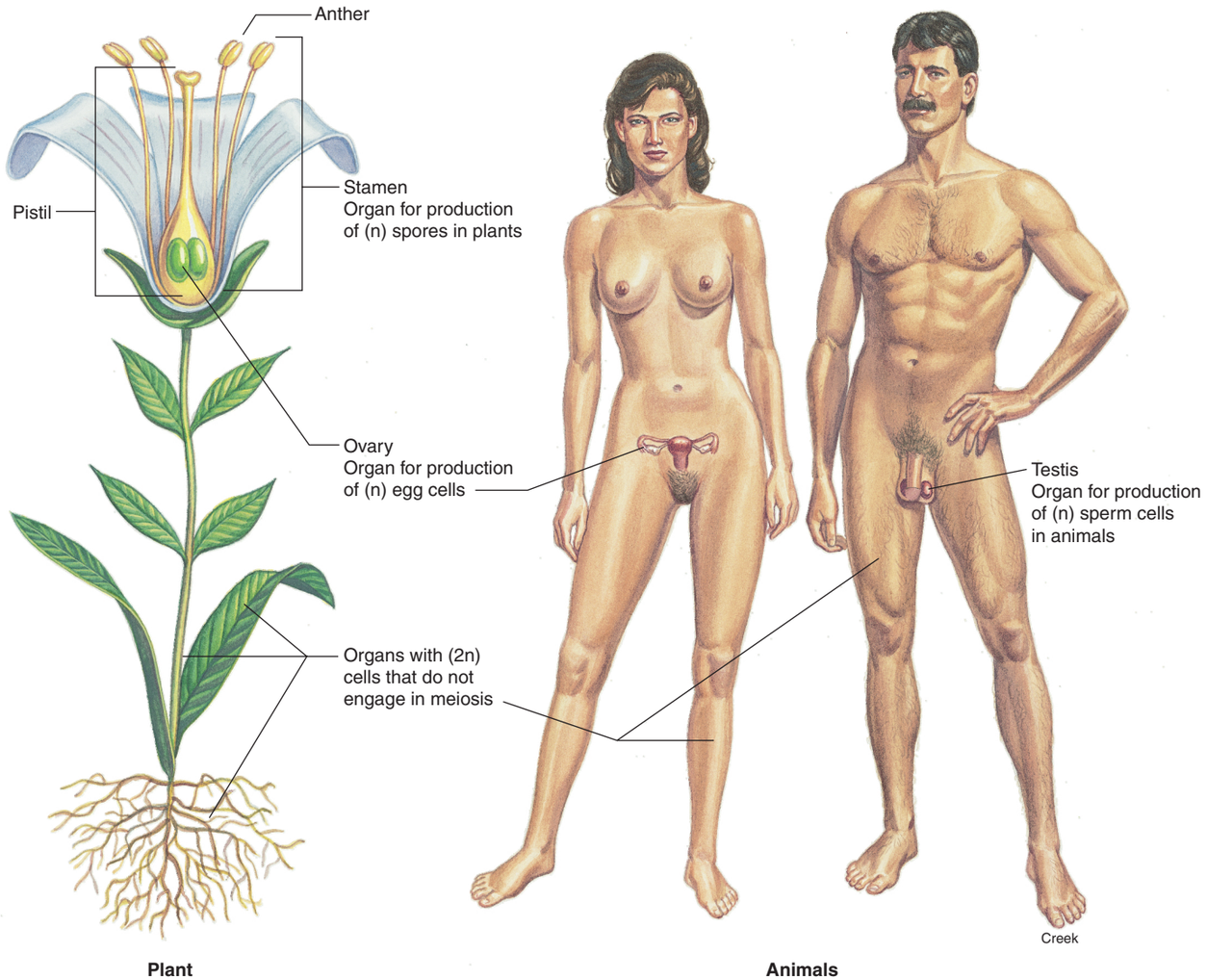


Figure 9.3

Haploid and Diploid Cells
Both plants and animals produce cells with a haploid number of chromosomes. The male anther in plants and the testes in animals produce haploid male cells, sperm. In both plants and animals, the ovaries produce haploid female cells, eggs.

called **synapsis.** While the chromosomes are synapsed, a unique event called *crossing-over* may occur. **Crossing-over** is the exchange of equivalent sections of DNA on homologous chromosomes. We will fit crossing-over into the whole picture of meiosis later.

Metaphase I

The synapsed pair of homologous chromosomes now move into position on the equatorial plane of the cell. In this stage, the centromere of each chromosome attaches to the spindle.

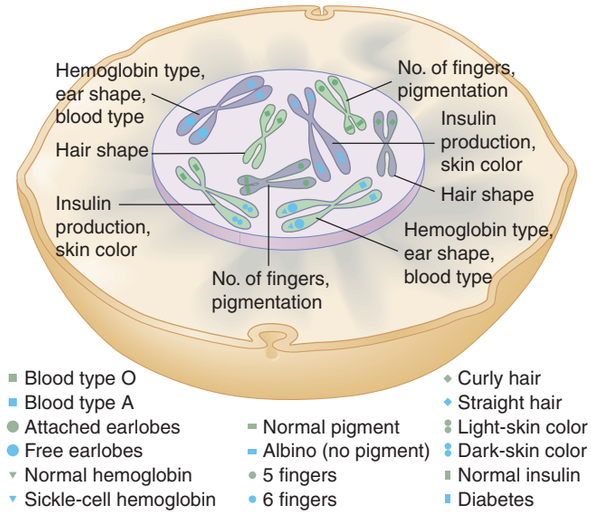


Figure 9.4

Chromosomes in a Cell
In this diagram of a cell, the eight chromosomes are scattered in the nucleus. Even though they are not arranged in pairs, note that there are four pairs of replicated (each pair consisting of one green and one purple chromosome) homologous chromosomes. Check to be certain you can pair them up using the list of characteristics.

The synapsed homologous chromosomes move to the equator of the cell as single units. How they are arranged on the equator (which one is on the left and which one is on the right) is determined by chance (figure 9.6). In the cell in figure 9.6, three green chromosomes from the father and one purple chromosome from the mother are lined up on the left. Similarly, one green chromosome from the father and three purple chromosomes from the mother are on the right. They could have aligned themselves in several other ways. For instance, they could have lined up as shown in figure 9.6.

Anaphase I

Anaphase I is the stage during which homologous chromosomes separate (figure 9.7). During this stage, the chromosome number is *reduced from diploid to haploid.* The two members of each pair of homologous chromosomes move away from each other toward opposite poles. The centromeres do not

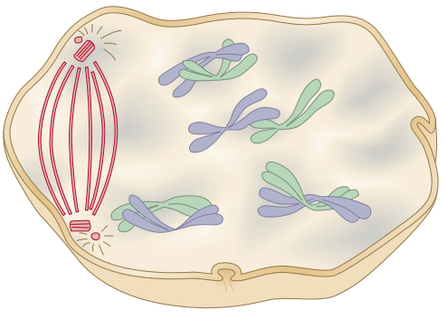


Figure 9.5

Prophase I
During prophase I, the cell is preparing for division. A unique event that occurs in prophase I is the synapsis of the chromosomes. Notice that the nuclear membrane is no longer apparent and that the paired homologs are free to move about the cell.

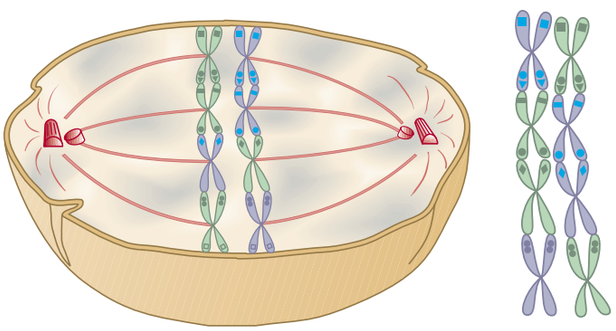


Figure 9.6

Metaphase I
Notice that the homologous chromosome pairs are arranged on the equatorial plane in the synapsed condition. The cell shows one way the chromosomes could be lined up. A second possible arrangement is shown to the right of the cell. How many other ways can you diagram metaphase I?

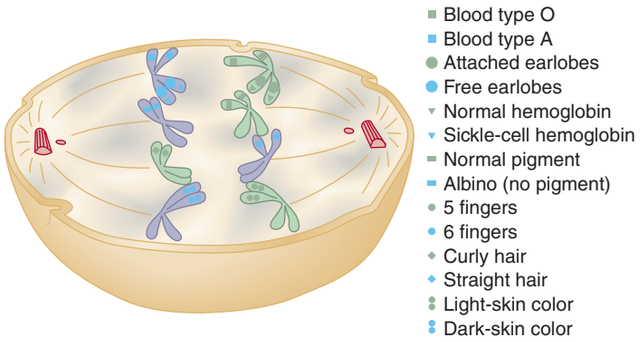


Figure 9.7

Anaphase I
During this phase, one member of each homologous pair is segregated from the other member of the pair. Notice that the centromeres of the chromosomes do not replicate.

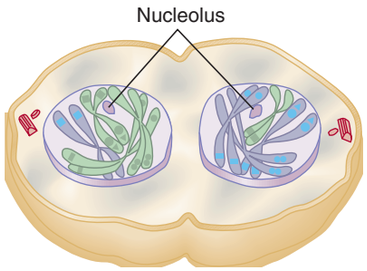
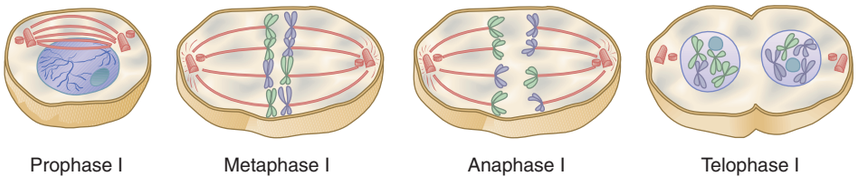


Figure 9.8

Telophase I
What activities would you expect during the telophase stage of cell division? What term is used to describe the fact that the cytoplasm is beginning to split the parent cell into two daughter cells?

Figure 9.9

Meiosis I
The stages in meiosis I result in reduction division. This reduces the number of chromosomes in the parental cell from the diploid number to the haploid number in each of the two daughter cells.



replicate during this phase. The direction each takes is determined by how each pair was originally arranged on the spindle. Each chromosome is independently attached to a spindle fiber at its centromere. Unlike the anaphase stage of mitosis, *the centromeres that hold the chromatids together do not divide during anaphase I of meiosis (the chromosomes are still in their replicated form)*. Each chromosome still consists of two chromatids. Because the homologous chromosomes and the genes they carry are being separated from one another, this process is called **segregation.** The way in which a single pair of homologous chromosomes segregates does not influence how other pairs of homologous chromosomes segregate. That is, each pair segregates independently of other pairs. This is known as **independent assortment** of chromosomes.

Telophase I

Telophase I consists of changes that return the cell to an interphaselike condition (figure 9.8). The chromosomes uncoil and become long, thin threads, the nuclear membrane re-forms around them, and nucleoli reappear. During this activity, cytokinesis divides the cytoplasm into two separate cells.

Because of meiosis I, the total number of chromosomes is divided equally, and each daughter cell has one member of each homologous chromosome pair. This means that the genetic data each cell receives is one-half the total, but each cell continues to have a complete set of the genetic information. Each individual chromosome is still composed of two chromatids joined at the centromere, and the chromosome number is reduced from diploid ($2n$) to haploid (n). In the cell we have been using as our example, the number of chromosomes is reduced from eight to four. The four pairs of chromosomes have been distributed to the two daughter cells. Depending on the type of cell, there may be a time following telophase I when a cell engages in normal metabolic activity that corresponds to an interphase stage. *However, the chromosomes do not replicate before the cell enters meiosis II.* Figure 9.9 shows the events in meiosis I.

9.3 The Mechanics of Meiosis: Meiosis II

Meiosis II includes four phases: prophase II, metaphase II, anaphase II, and telophase II. The two daughter cells formed during meiosis I continue through meiosis II so that, usually, four cells result from the two divisions.

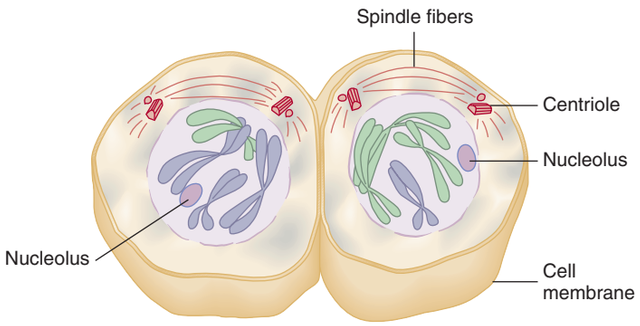


Figure 9.10

Prophase II
The two daughter cells are preparing for the second division of meiosis. Study this diagram carefully. Can you list the events of this stage?

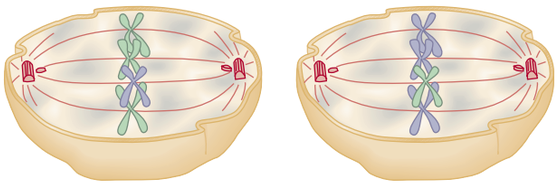


Figure 9.11

Metaphase II
During metaphase II, each chromosome lines up on the equatorial plane. Each chromosome is composed of two chromatids (a replicated chromosome) joined at a centromere. How does metaphase II of meiosis compare to metaphase I of meiosis?

Prophase II

Prophase II is similar to prophase in mitosis; the nuclear membrane is disassembled, nucleoli disappear, and the spindle apparatus begins to form. However, it differs from prophase I because these cells are haploid, not diploid (figure 9.10). Also, synapsis, crossing-over, segregation, and independent assortment do not occur during meiosis II.

Metaphase II

The metaphase II stage is typical of any metaphase stage because the chromosomes attach by their centromeres to the spindle at the equatorial plane of the cell. Because pairs of chromosomes are no longer together in the same cell, each chromosome moves as a separate unit (figure 9.11).

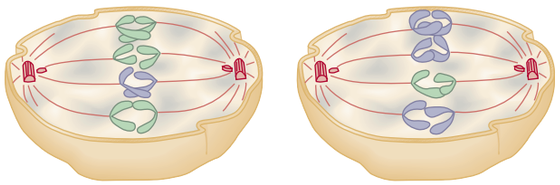


Figure 9.12

Anaphase II
Anaphase II is very similar to the anaphase of mitosis. The centromere of each chromosome divides and one chromatid separates from the other. As soon as this happens, we no longer refer to them as chromatids; we now call each strand of nucleoprotein a chromosome.

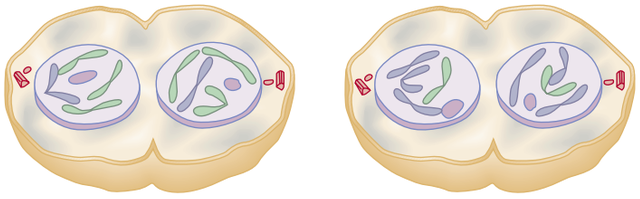


Figure 9.13

Telophase II
During the telophase II stage, what events would you expect?

Anaphase II

Anaphase II differs from anaphase I because during anaphase II the centromere of each chromosome divides, and the chromatids, now called *daughter chromosomes*, move to the poles as in mitosis (figure 9.12). Remember, there are no paired homologs in this stage; therefore, segregation and independent assortment cannot occur.

Telophase II

During telophase II, the cell returns to a nondividing condition. As cytokinesis occurs, new nuclear membranes form, chromosomes uncoil, nucleoli re-form, and the spindles disappear (figure 9.13). This stage is followed by differentiation; the four cells mature into gametes—either sperm or eggs. The events of meiosis II are summarized in figure 9.14.

In many organisms, egg cells are produced in such a manner that three of the four cells resulting from meiosis in a female disintegrate. However, because the one that survives is randomly chosen, the likelihood of any one particular combination of genes being formed is not affected. The whole point of learning the mechanism of meiosis is to see how variation happens (table 9.2).

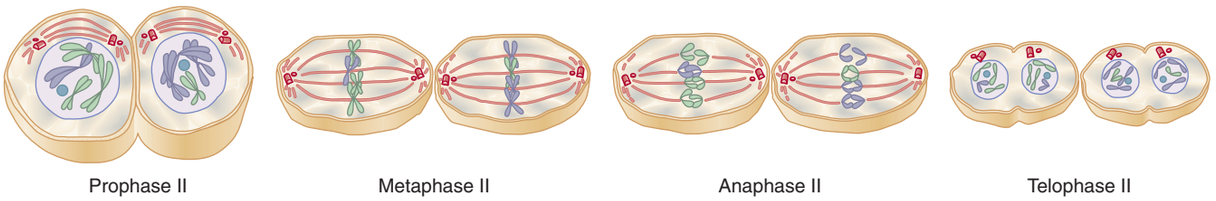
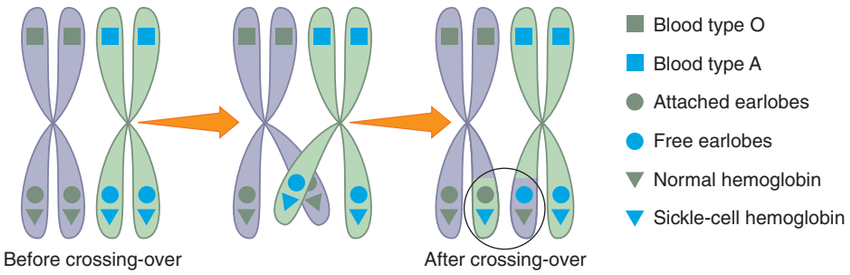


Figure 9.14

Meiosis II
During meiosis II, the centromere of each chromosome replicates and each chromosome divides into separate chromatids. Four haploid cells are produced, each having one chromatid of each kind.

Figure 9.15

Synapsis and Crossing-Over
While pairs of homologous chromosomes are in synapsis, one part of one chromatid can break off and be exchanged for an equivalent part of its homologous chromatid. List the new combination of genes on each chromatid that has resulted from the crossing-over.



9.4 Sources of Variation

The formation of a haploid cell by meiosis and the combination of two haploid cells to form a diploid cell by sexual reproduction results in variety in the offspring. Five factors influence genetic variation in offspring: mutations, crossing-over, segregation, independent assortment, and fertilization.

Mutation

Several types of mutations were discussed in chapter 7: point mutations and chromosomal mutations. In point mutations, a change in a DNA nucleotide results in the production of a different protein. In chromosomal mutations, genes are rearranged. By causing the production of different proteins, both types of mutations increase variation. The second source of variation is crossing-over.

Crossing-Over

Crossing-over occurs during meiosis I while homologous chromosomes are synapsed. Crossing-over is the exchange of a part of a chromatid from one homologous chromosome with an equivalent part of a chromatid from the other homologous chromosome. This exchange results in a new gene combination. Remember that a chromosome is a double strand of DNA. To break a chromosome, bonds between sugars and phosphates are broken. This is done at the same spot on both chromatids, and the two pieces switch places. After switching places, the two pieces of DNA are bonded together by re-forming the bonds between the sugar and the phosphate molecules.

Examine figure 9.15 carefully to note precisely what occurs during crossing-over. This figure shows a pair of homologous chromosomes close to each other. Notice that each gene occupies a specific place on the chromosome. This is the *locus,* a place on a chromosome where a gene is located. Homologous chromosomes contain an identical order of genes. For the sake of simplicity, only a few loci are labeled on the chromosomes used as examples. Actually, the chromosomes contain hundreds or possibly thousands of genes.

What does crossing-over have to do with the possible kinds of cells that result from meiosis? Consider figure 9.16. Notice that without crossing-over, only two kinds of genetically different gametes result. Two of the four gametes have one type of chromosome, whereas the other two have the other type of chromosome. With crossing-over, four genetically different gametes are formed. With just one crossover, we double the number of kinds of gametes possible from meiosis. Because crossing-over can occur at almost any point along the length of the chromosome, great variation is possible. In fact, crossing-over can occur at a number of different points on the same chromosome; that is, there can be more than one crossover per chromosome pair (figure 9.17).

Crossing-over helps explain why a child can show a mixture of family characteristics (figure 9.18). If the violet chromosome was the chromosome that a mother received from her mother, the child could receive some genetic information not only from the mother's mother, but also from the

Table 9.2

REVIEW OF THE STAGES OF MEIOSIS

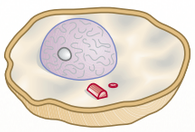
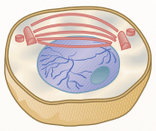
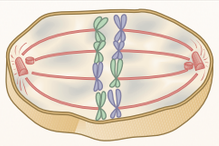
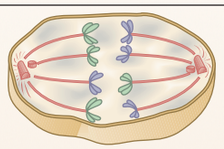
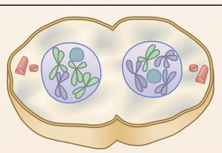
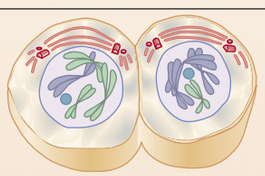
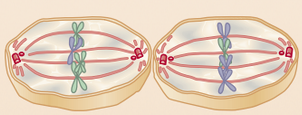
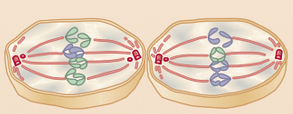
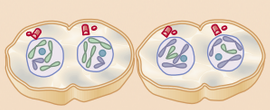
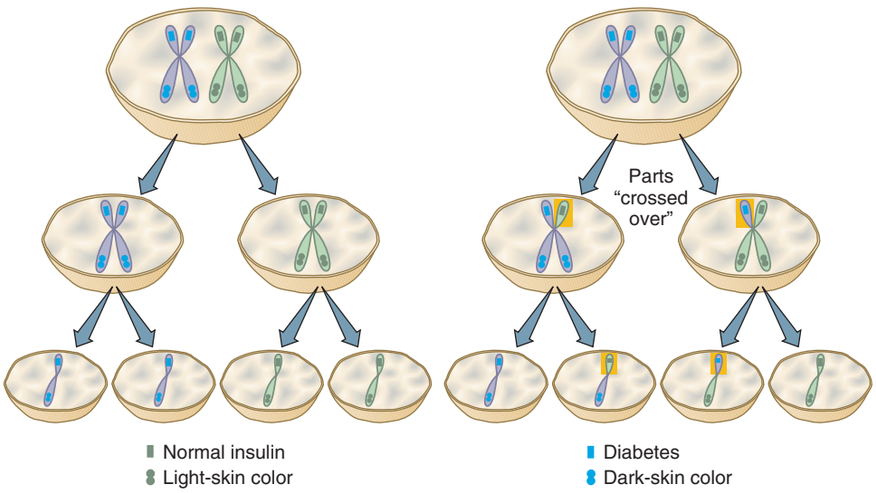
Interphase		As the diploid ($2n$) cell moves from G_0 into meiosis, the chromosomes replicate during the S phase of interphase.
Prophase I		The replicated chromatin begins to coil into recognizable chromosomes and the homologues synapse; chromatids may cross over; the nuclear membrane and nucleoli fragment; centrioles move to form the cell's poles; spindle fibers are formed.
Metaphase I		Synapsed homologous chromosomes align as pairs along the equatorial plane and attach to the spindle fibers at their centromeres; each pair positions itself independently of all others.
Anaphase I		Homologous pairs of chromosomes separate from one another as they move toward the poles of the cell.
Telophase I		The two newly forming daughter cells are now haploid (n) since each only contains one of each pair of homologous chromosomes; the nuclear membranes and nucleoli re-form; spindle fibers fragment; the chromosomes unwind and change from chromosomes (composed of two chromatids) to chromatin.
Prophase II		Each of the two haploid (n) daughter cells from meiosis I undergoes chromatin coiling to form chromosomes composed of two chromatids; the nuclear membrane fragments; centrioles move to form the cell's poles; spindle fibers form.
Metaphase II		Chromosomes move to the equator of the cell and attach to the spindle fibers at the centromeres.
Anaphase II		Centromeres complete DNA replication allowing the chromatids to separate toward the poles.
Telophase II		Four haploid (n) cells are formed from the division of the two meiosis I cells; the nuclear membranes and nucleoli re-form; spindle fibers fragment; the chromosomes unwind and change from chromosomes to chromatin; these cells become the sex cells (egg or sperm) of higher organisms.

Figure 9.16

Variations Resulting from Crossing-Over
The cells on the left resulted from meiosis without crossing-over; those on the right had one crossover. Compare the results of meiosis in both cases.



mother's father. When crossing-over occurs during the meiotic process, pieces of genetic material are exchanged between the chromosomes. This means that genes that were originally on the same chromosome become separated. They are moved to their synapsed homologue, and therefore into different gametes. The closer two genes are to each other on a chromosome (i.e., the more closely they are *linked*), the more likely they will stay together and not be separated during crossing-over. Thus, there is a high probability that they will be inherited together. The farther apart two genes are, the more likely it is that they will be separated during crossing-over. This fact enables biologists to construct chromosome maps (How Science Works 9.1).

Segregation

After crossing-over has taken place, segregation occurs. This involves the separation and movement of homologous chromosomes to the poles. Let's say a person has a normal form of the gene for insulin production on one chromosome and an abnormal form of this gene on the other. Such a person

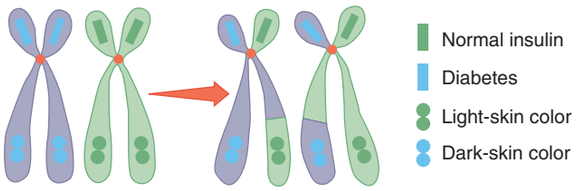


Figure 9.17

Multiple Crossovers
Crossing-over can occur several times between the chromatids of one pair of homologous chromosomes. List the new combinations of genes on each chromatid that have resulted from the crossing-over.

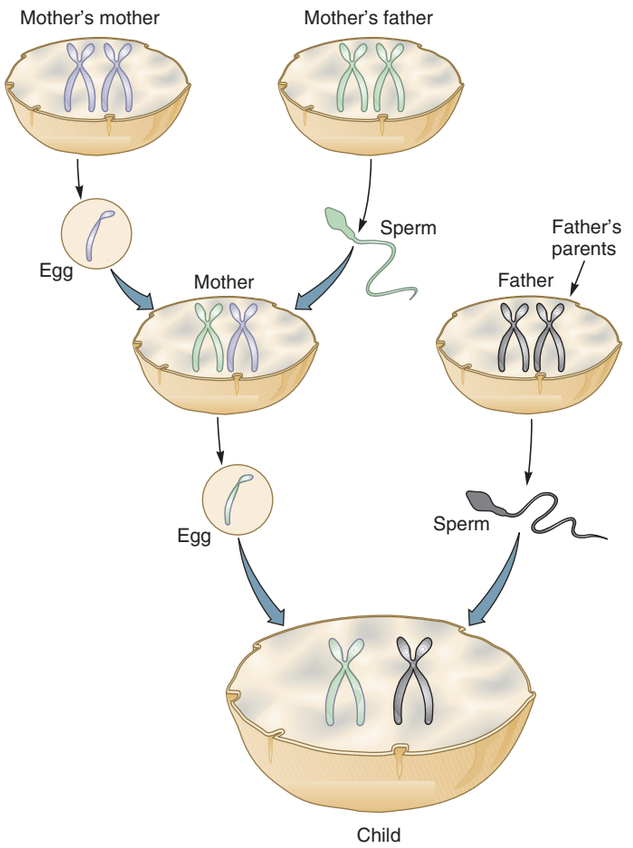


Figure 9.18

Mixing of Genetic Information Through Several Generations
The mother of this child has information from both of her parents. The child receives a mixture of this information from the mother. Note that only the maternal line has been traced in this diagram. Can you imagine how many more combinations would result after including the paternal heritage?

HOW SCIENCE WORKS 9.1

The Human Genome Project

The Human Genome Project was first proposed in 1986 by the U.S. Department of Energy (DOE), and cosponsored soon after by the National Institutes of Health (NIH). These agencies were the main research agencies within the U.S. government responsible for developing and planning the project. Later, a private U.S. corporation, Celera Genomics, joined the effort as a competitor. It is one of the most ambitious projects ever undertaken in the biological sciences. The goal was nothing less than the complete characterization of the genetic makeup of humans. The project was completed early in 2001 when the complete nucleotide sequence of all 23 pairs of human chromosomes was determined. With this in hand, scientists will now be able to produce a map of each of the chromosomes that will show the names and places of all our genes. This international project involving about 100 laboratories worldwide required only 16 years to complete. Work began in many of these labs in 1990. Powerful computers are used to store and share the enormous amount of information derived from the analyses of human DNA. To get an idea of the size of this project, consider this: A human Y chromosome (one of the smallest of the human chromosomes) is estimated to be composed of 28 million nitrogenous bases. The larger X chromosome may be composed of 160 million nitrogenous base pairs!

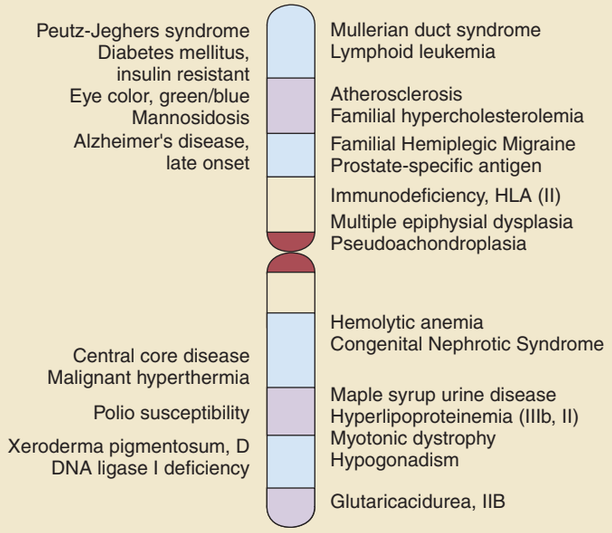
Two kinds of work progressed simultaneously. First, *physical maps* were constructed by determining the location of specific "markers" (known sequences of bases) and their closeness to genes (see figure). A kind of chromosome map already exists that pictures patterns of colored bands on chromosomes, a result of chromosome-staining procedures. Using these banded chromosomes, the markers were then related to these colored bands on a specific region of a chromosome. Work is continuing on the Human Genome Project to identify the location of specific genes. Each year a more complete picture is revealed.

The second kind of work was for labs to determine the exact order of nitrogenous bases of the DNA for each chromosome. Techniques exist for determining base sequences, but it is a time-consuming job to sort out the several million bases that may be found in any one chromosome. Coming from behind with new, speedier techniques, Celera Genomics was able to catch up to NIH labs and completed their sequencing at almost the same time. The benefit of having these two organizations as competitors is that when finished they could compare and contrast results. Amazingly, the discrepancies between their findings were declared insignificant. It was originally estimated, for example, that there were between 100,000 and 140,000 genes in the human genome. However, when the results were compared the evidence from both organizations indicated that there are only 30,000 to 40,000 genes. Knowing this information provides insights into the evolution of humans and the mutation rates of males verses females. This will make future efforts to work with the genome through bioengineering much easier.

When the physical maps are finally completed for all of the human genes, it will be possible to examine a person's DNA and identify genetic abnormalities. This could be extremely useful in diagnosing diseases and providing genetic counseling to those considering having children. This kind of information would also create possibilities for new gene therapies. Once it is known where an abnormal gene is located and how it differs in base sequence from the normal DNA sequence, steps could be taken to correct the abnormality. However, there is also a concern that, as knowledge of our genetic makeup becomes easier to determine, some people may attempt to use this information for profit or political power. This is a real concern because some health insurance companies refuse to insure people with "preexisting conditions" or those at "genetic risk" for certain abnormalities. They fail to realize that between 5 and 50 such "conditions" or mutations are normally found in each individual. Refusing to provide coverage would save these companies the expense of future medical bills incurred by "less-than-perfect" people. Another fear is that attempts may be made to "breed out" certain genes and people from the human population in order to create a "perfect race."

Here are some other intriguing findings from the human genome and the genome identification projects of other organisms:

- Human genes are not scattered at random among the human chromosomes. "Forests" or "clusters" of genes are found on certain chromosomes separated by "deserts" of genes. For example, chromosomes 17 and 19 are forested with thousands of genes while chromosome 18 has many fewer genes.
- Rice appears to have about 50,000 genes.
- Roundworms have about 26,000 genes.
- Fruits flies contain an estimated 13,600 genes.
- Yeast cells have about 6,241 genes.
- There are numerous and virtually identical genes found in many organisms that appear to be very distantly related—for example, mice, humans, and yeasts.
- Genes jump around (transposons) within the chromosomes more than scientists ever thought.
- The mutation rate of male humans is about twice that of females.
- Humans are about 99.9% identical at the DNA level! Scientists believe that there is virtually no basis for race since there is much greater variation within a so-called race than there is between the so-called races.



Genes Known to Be on Human Chromosome Number 19
The gene map shows the appropriate positions of several genes known to be on human chromosome number 19.

would produce enough insulin to be healthy and would not be diabetic. When this pair of chromosomes segregates during anaphase I, one daughter cell receives a chromosome with a normal gene for insulin production and the second daughter cell receives a chromosome with an abnormal gene for diabetes. The process of segregation causes genes to be separated from one another so that they have an equal chance of being transmitted to the next generation. If the mate also has one normal gene for insulin production and one abnormal for diabetes, that person also produces two kinds of gametes.

Both of the parents have normal insulin production. If one or both of them contributed a gene for normal insulin production during fertilization, the offspring would produce enough insulin to be healthy. However if, by chance, both parents contributed the gamete with the abnormal gene for diabetes, the child would be a diabetic. Thus, parents may produce offspring with traits different from their own. In this variation, no new genes are created; they are simply redistributed in a fashion that allows for the combination of genes in the offspring to be different from the parents' gene combinations. This will be explored in greater detail in chapter 10.

Independent Assortment

So far in discussing variety, we have dealt with only one pair of chromosomes, which allows two varieties of gametes. Now let's consider how variation increases when we add a second pair of chromosomes (figure 9.19).

In figure 9.19, chromosomes carrying insulin-production information always separate from each other. The second pair of chromosomes with the information for the number of fingers also separates. Because the pole to which a chromosome moves is a chance event, half the time the chromosomes divide so that insulin production and six-fingeredness move in one direction, whereas diabetes and five-fingeredness move in the opposite direction. Half the time, insulin production and five-fingeredness go together and diabetes and six-fingeredness go to the other pole. With four chromosomes (two pairs), four kinds of gametes are possible (figure 9.20). With three pairs of homologous chromosomes, there are eight possible kinds of cells with respect to chromosome combinations resulting from meiosis. See if you can list them. The number of possible chromosomal combinations of gametes is found by the expression 2^n, where n equals the number of pairs of chromosomes. With three pairs of chromosomes, n equals 3, and so $2^n = 2^3 = 2 \times 2 \times 2 = 8$. With 23 pairs of chromosomes, as in the human cell, $2^n = 2^{23} = 8{,}388{,}608$. More than 8 million kinds of sperm cells or egg cells are possible from a single human parent organism. This number is actually smaller than the maximum variety that could be produced because it only takes into consideration the variety generated as a result of independent assortment. This huge variation is possible because each pair of homologous chromosomes assorts independently of the other pairs of homologous chromosomes (independent assortment). In addition to this variation, crossing-over creates new gene combinations, and mutation can cause the formation of new genes, thereby increasing this number greatly.

Fertilization

Because of the large number of possible gametes resulting from independent assortment, segregation, mutation, and crossing-over, an incredibly large number of types of offspring can result. Because human males can produce millions

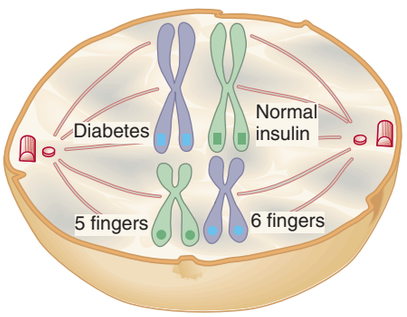


Figure 9.19

The Independent Orientation of Homologous Chromosome Pairs
The orientation of one pair of chromosomes on the equatorial plane does not affect the orientation of a second pair of chromosomes. This results in increased variety in the haploid cells.

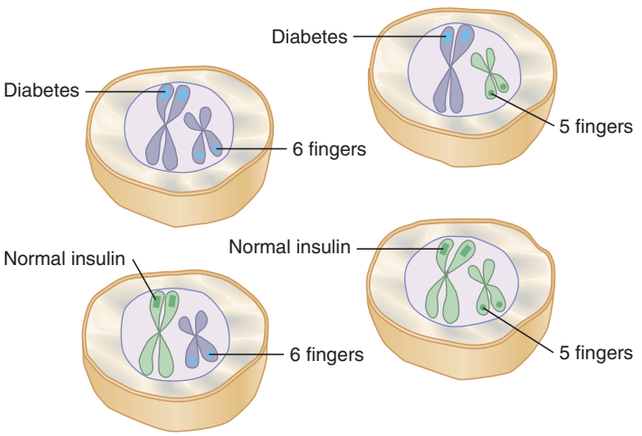


Figure 9.20

Variation Resulting from Independent Assortment
When a cell has two pairs of homologous chromosomes, four kinds of haploid cells can result from independent assortment. How many kinds of haploid cells could result if the parental cell had three pairs? Four pairs?

of genetically different sperm and females can produce millions of genetically different eggs, the number of kinds of offspring possible is infinite for all practical purposes. With the possible exception of identical twins, every human that has ever been born is genetically unique (refer to chapter 21).

9.5 Nondisjunction and Chromosomal Abnormalities

In the normal process of meiosis, diploid cells have their number of chromosomes reduced to haploid. This involves segregating homologous chromosomes into separate cells during the first meiotic division. Occasionally, a pair of homologous chromosomes does not segregate properly during gametogenesis and both chromosomes of a pair end up in the same gamete. This kind of division is known as **nondisjunction** (figure 9.21). As you can see in this figure, two cells are missing a chromosome and the genes that were carried on it. This usually results in the death of the cells. The other cells have a double dose of one chromosome. Apparently, the genes of an organism are balanced against one another. A double dose of some genes and a single dose of others results in abnormalities that may lead to the death of the cell. Some of these abnormal cells, however, do live and develop into sperm or eggs. If one of these abnormal sperm or eggs unites with a normal gamete, the offspring will have an abnormal number of chromosomes. There will be three of one of the kinds of chromosomes instead of the normal two, a condition referred to as **trisomy.** Should the other cell survive and become involved in fertilization, it will only have one of the pair of homologous chromosomes, a condition referred to as **monosomy.** All the cells that develop by mitosis from such zygotes will be either trisomic or monosomic.

It is possible to examine cells and count chromosomes. Among the easiest cells to view are white blood cells. They are dropped onto a microscope slide so that the cells are broken open and the chromosomes are separated. Photographs are taken of chromosomes from cells in the metaphase stage of mitosis. The chromosomes in the pictures can then be cut and arranged for comparison to known samples (figure 9.22). This picture of an individual's chromosomal makeup is referred to as that person's *karyotype*.

One example of the effects of nondisjunction is the condition known as **Down syndrome.** If a gamete with two number 21 chromosomes has been fertilized by another

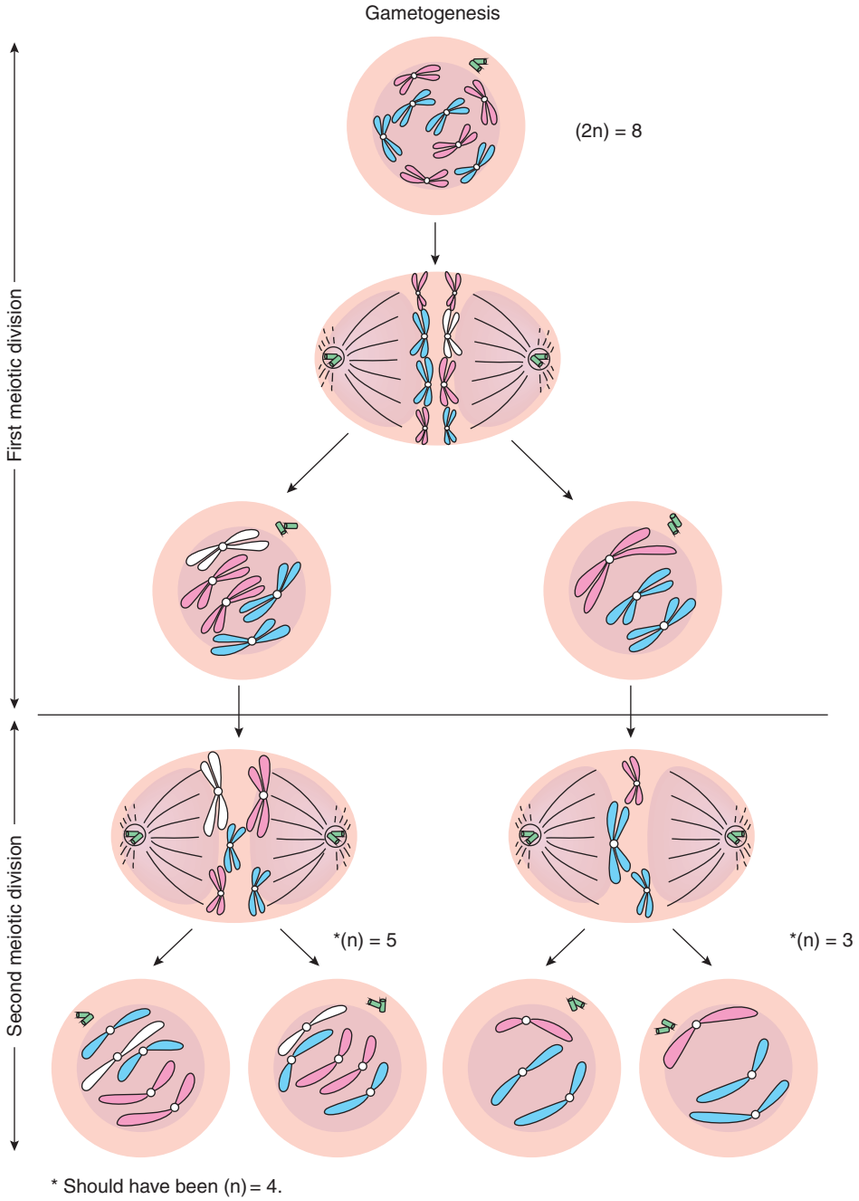
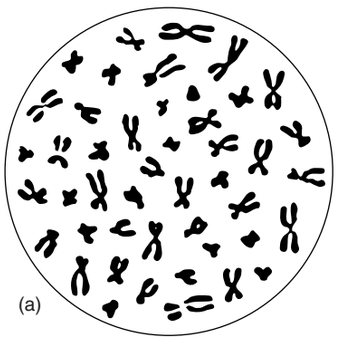


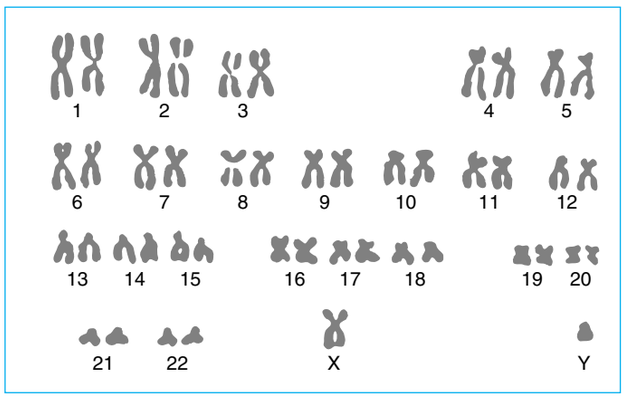
Figure 9.21

Nondisjunction During Gametogenesis
When a pair of homologous chromosomes fails to separate properly during meiosis I, gametogenesis results in gametes that have an abnormal number of chromosomes. Notice that two of the highlighted cells have an additional chromosome, whereas the other two are deficient by that same chromosome.

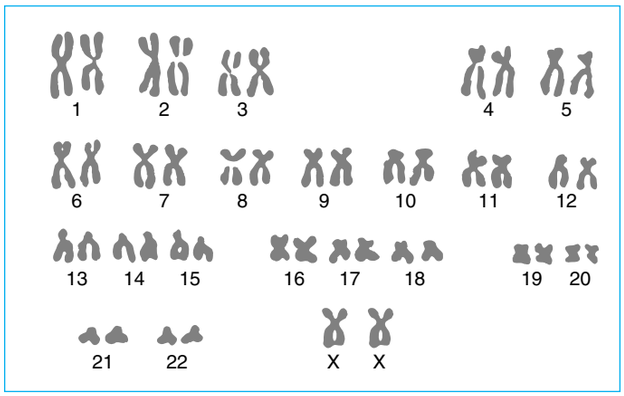
Figure 9.22

Human Male and Female Chromosomes
The randomly arranged chromosomes shown in the circle simulate metaphase cells spattered onto a microscope slide (*a*). Those in parts (*b*) and (*c*) have been arranged into homologous pairs. Part (*b*) shows a male karyotype with an X and Y chromosome and (*c*) shows a female karyotype with two X chromosomes.


(a)



(b)



(c)

containing the typical one copy of chromosome number 21, the resulting zygote would have 47 chromosomes (e.g., 24 from the female plus 23 from the male parent) (figure 9.23). The child who developed from this fertilization would have 47 chromosomes in every cell of his or her body as a result of mitosis, and thus would have the symptoms characteristic of Down syndrome. These may include thickened eyelids, some mental impairment, and faulty speech (figure 9.24). Premature aging is probably the most significant impact of this genetic disease. On the other hand, a child born with only one chromosome 21 rarely survives.

It was thought that the mother's age at childbirth played an important part in the occurrence of trisomies such as Down syndrome. In women, gametogenesis begins early in life, but cells destined to become eggs are put on hold during meiosis I (see chapter 21). Beginning at puberty and ending at menopause, one of these cells completes meiosis I monthly. This means that cells released for fertilization later in life are older than those released earlier in life. Therefore, it was believed that the chances of abnormalities such as nondisjunction increase as the age of the mother increases. However, the evidence no longer supports this age-egg link. Currently, the increase in frequency of trisomies with age has been correlated with a decrease in the activity of a woman's

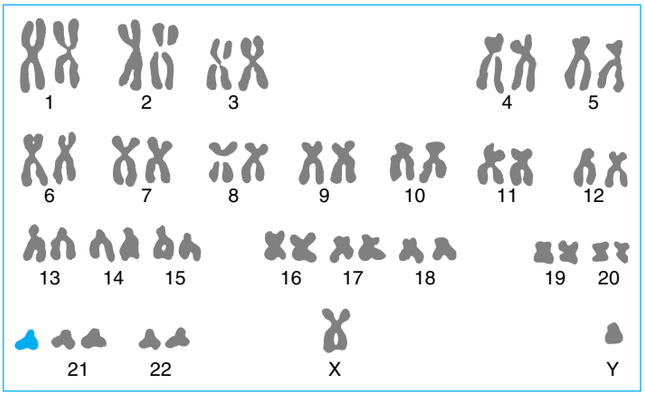


Figure 9.23

Chromosomes from an Individual Displaying Down Syndrome
Notice that each pair of chromosomes has been numbered and that the person from whom these chromosomes were taken has an extra chromosome number 21. The person with this trisomic condition could display a variety of physical characteristics, including slightly slanted eyes, flattened facial features, a large tongue, and a tendency toward short stature and fingers. Most individuals also display mental retardation.

Figure 9.24

Down Syndrome
Every cell in a Downic child's body has one extra chromosome. With special care, planning, and training, people with this syndrome can lead happy, productive lives.

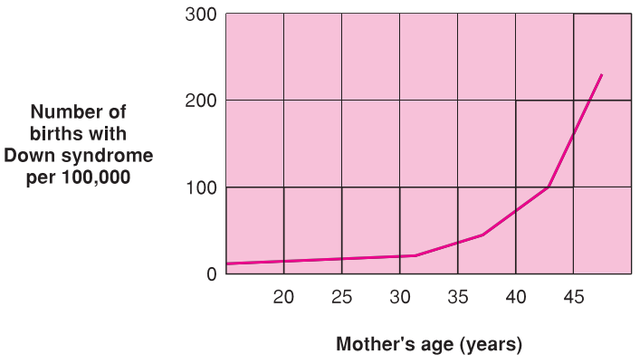


Figure 9.25

Down Syndrome as a Function of a Mother's Age
Notice that as the age of the female increases, the frequency of Downic children increases only slightly until the age of approximately 37. From that point on, the rate increases drastically. This increase may be because older women experience fewer miscarriages of abnormal embryos.

immune system. As she ages, her immune system is less likely to recognize the difference between an abnormal and a normal embryo. This means that she is more likely to carry an abnormal fetus to full term.

Figure 9.25 illustrates the frequency of occurrence of Down syndrome at different ages in women. Notice that the frequency increases very rapidly after age 37. For this reason, many physicians encourage couples to have their children in their early to mid-twenties and not in their late thirties or early forties. Physicians normally encourage older women who are pregnant to have the cells of their fetus checked to see if they have the normal chromosome number. It is important to know that the male parent can also contribute the extra chromosome 21. However, it appears that this occurs less than 30% of the time.

Sometimes a portion of chromosome 14 may be cut out and joined to chromosome 21. The transfer of a piece of one nonhomologous chromosome to another is called a chromosomal **translocation.** A person with this 14/21 translocation is monosomic and has only 45 chromosomes; one 14 and one 21 are missing and replaced by the translocated 14/21. Statistically, about 15% of the children of carrier mothers inherit the 14/21 chromosome and have Down syndrome. Fewer of the children born to fathers with the 14/21 translocation inherit the abnormal chromosome and are Downic.

Whenever an individual is born with a chromosomal abnormality such as a monosomic or a trisomic condition, it is recommended that both parents have a karyotype in an attempt to identify the possible source of the problem. This is not to fix blame but to provide information on the likelihood that a next pregnancy would also result in a child with a chromosomal abnormality. Other examples of trisomy are described in chapter 21, Human Reproduction, Sex, and Sexuality.

9.6 Chromosomes and Sex Determination

You already know that there are several different kinds of chromosomes, that each chromosome carries genes unique to it, and that these genes are found at specific places. Furthermore, diploid organisms have homologous pairs of chromosomes. Sexual characteristics are determined by genes in the same manner as other types of characteristics. In many organisms, sex-determining genes are located on specific chromosomes known as **sex chromosomes.** All other chromosomes not involved in determining the sex of an individual are known as **autosomes.** In humans and all other mammals, and in some other organisms (e.g., fruit flies), the sex of an individual is determined by the presence of a certain chromosome combination. The genes that determine maleness are located on a small chromosome known as the *Y chromosome*. This Y chromosome behaves as if it and another larger chromosome, known as the *X chromosome,* were homologs. Males have one X and one Y chromosome. Females have two X chromosomes. Some animals have their sex determined in a completely different way. In bees, for example, the females are diploid and the males are haploid. Other plants and animals have still other chromosomal mechanisms for determining their sex (Outlooks 9.1).

9.7 A Comparison of Mitosis and Meiosis

Some of the similarities and differences between mitosis and meiosis were pointed out earlier in this chapter. Study table 9.3 to familiarize yourself with the differences between these two processes.

OUTLOOKS 9.1

The Birds and the Bees . . . and the Alligators

The determination of the sex of an individual depends on the kind of organism you are! For example, in humans, the physical features that result in maleness are triggered by a gene on the Y chromosome. Lack of a Y chromosome results in an individual that is female. In other organisms, sex may be determined by other combinations of chromosomes or environmental factors.

Organism	Sex Determination
Birds	Chromosomally determined: XY individuals are female.
Bees	Males (the drones) are haploid and females (workers or queens) are diploid.
Certain species of alligators, turtles, and lizards	Egg incubation temperatures cause hormonal changes in the developing embryo; higher incubation temperatures cause the developing brain to shift sex in favor of the individual becoming a female. (Placing a drop of the hormone estrogen on the developing egg also causes the embryo to become female!)
Boat shell snails	Males can become females but will remain male if they mate and remain in one spot.
Shrimp, orchids, and some tropical fish	Males convert to females; on occasion females convert to males, probably to maximize breeding.
African reed frog	Females convert to males, probably to maximize breeding.

Table 9.3

A COMPARISON OF MITOSIS AND MEIOSIS

Mitosis	Meiosis
1. One division completes the process.	1. Two divisions are required to complete the process.
2. Chromosomes do not synapse.	2. Homologous chromosomes synapse in prophase I.
3. Homologous chromosomes do not cross over.	3. Homologous chromosomes do cross over.
4. Centromeres divide in anaphase.	4. Centromeres divide in anaphase II, but not in anaphase I.
5. Daughter cells have the same number of chromosomes as the parent cell ($2n \rightarrow 2n$ or $n \rightarrow n$).	5. Daughter cells have half the number of chormosomes as the parent cell ($2n \rightarrow n$).
6. Daughter cells have the same genetic information as the parent cell.	6. Daughter cells are genetically different from the parent cell.
7. Results in growth, replacement of worn-out cells, and repair of damage.	7. Results in sex cells.

SUMMARY

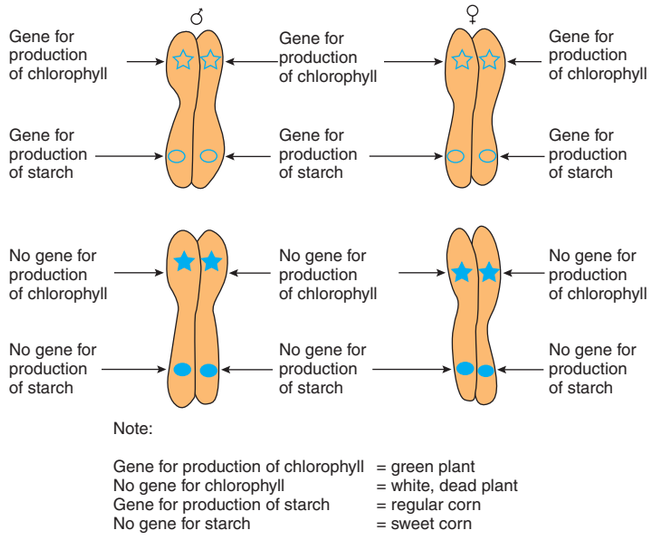
Meiosis is a specialized process of cell division resulting in the production of four cells, each of which has the haploid number of chromosomes. The total process involves two sequential divisions during which one diploid cell reduces to four haploid cells. Because the chromosomes act as carriers for genetic information, genes separate into different sets during meiosis. Crossing-over and segregation allow hidden characteristics to be displayed, whereas independent assortment allows characteristics donated by the mother and the father to be mixed in new combinations.

Together, crossing-over, segregation, and independent assortment ensure that all sex cells are unique. Therefore when any two cells unite to form a zygote, the zygote will also be one of a kind. The sex of many kinds of organisms is determined by specific chromosome combinations. In humans, females have two X chromosomes; males have an X and a Y chromosome.

THINKING CRITICALLY

Assume that corn plants have a diploid number of only 2. In the following figure, the male plant's chromosomes are diagrammed on the left, and those of the female are diagrammed on the right.

Diagram sex-cell formation in the male and female plant. How many variations in sex cells can occur and what are they? What variations can occur in the production of chlorophyll and starch in the descendants of these parent plants?



CONCEPT MAP TERMINOLOGY

Construct a concept map to show relationships among the following concepts.

age
Down syndrome
meiosis I
nondisjunction
reduction division
segregation
synapsis
trisomy

KEY TERMS

anther
autosomes
crossing-over
diploid
Down syndrome
egg
fertilization
gamete
gametogenesis
gonad
haploid
homologous chromosomes
independent assortment
meiosis
monosomy
nondisjunction
ovaries
pistil
reduction division (also meiosis)
segregation
sex chromosomes
sexual reproduction
sperm
synapsis
testes
translocation
trisomy
zygote

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Topics	Questions	Media Resources
9.1 Sexual Reproduction	1. How do haploid cells differ from diploid cells? 2. Why is meiosis necessary in organisms that reproduce sexually? 3. Define the terms *zygote, fertilization,* and *homologous chromosomes.* 4. Diagram fertilization as it would occur between a sperm and an egg with the haploid number of 3.	**Quick Overview** • Importance of haploid sex cells **Key Points** • Sexual reproduction **Animations and Review** • Evolution of sex
9.2 The Mechanics of Meiosis: Meiosis I	5. Diagram the metaphase I stage of a cell with the diploid number of 8. 6. What is unique about prophase I?	**Quick Overview** • Reduction of ploidy **Key Points** • The mechanics of meiosis: Meiosis I **Labeling Exercises** • Meiosis I
9.3 The Mechanics of Meiosis: Meiosis II		**Quick Overview** • Similar to mitosis **Key Points** • The mechanics of meiosis: Meiosis II **Animations and Review** • Meiosis

(*continued*)

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Topics	Questions	Media Resources
9.3 The Mechanics of Meiosis: Meiosis II (*continued*)		**Interactive Concept Maps** • Meiosis I and meiosis II **Experience This!** • Models of meiosis
9.4 Sources of Variation	7. How much variation as a result of independent assortment can occur in cells with the following number of diploid numbers: 2, 4, 6, 8, and 22? 8. What are the major sources of variation in the process of meiosis?	**Quick Overview** • Creating new combinations of alleles **Key Points** • Sources of variation **Animations and Review** • Recombination
9.5 Nondisjunction and Chromosomal Abnormalities		**Quick Overview** • Problems with chromosome migration **Key Points** • Nondisjunction and chromosomal abnormalities **Animations and Review** • Introduction • Abnormal chromosomes **Interactive Concept Maps** • Text concept map **Human Explorations** • Exploring meiosis: Down syndrome
9.6 Chromosomes and Sex Determination		**Quick Overview** • Autosomes and sex chromosomes **Animations and Review** • Sex chromosomes • Concept quiz **Key Points** • Chromosomes and sex determination
9.7 A Comparison of Mitosis and Meiosis	9. Can a haploid cell undergo meiosis? 10. List three differences between mitosis and meiosis.	**Quick Overview** • Understand similarities and differences. **Key Points** • A comparison of mitosis and meiosis **Animations and Review** • Review of cell division • Concept quiz **Interactive Concept Maps** • Mitosis vs. meiosis **Review Questions** • Meiosis: Sex-cell formation