

▲ **Figure 11-13** The common fruit fly is a popular organism for genetic research. **Inferring** Why are fruit flies easier to use for genetic research than large animals, such as dogs?

Applying Mendel's Principles

Mendel's principles don't apply only to plants. At the beginning of the 1900s, the American geneticist Thomas Hunt Morgan decided to look for a model organism to advance the study of genetics. He wanted an animal that was small, easy to keep in the laboratory, and able to produce large numbers of offspring in a short period of time. He decided to work on a tiny insect that kept showing up, uninvited, in his laboratory. The insect was the common fruit fly, *Drosophila melanogaster*, shown in **Figure 11-13**.

Morgan grew the flies in small milk bottles stoppered with cotton gauze. *Drosophila* was an ideal organism for genetics because it could produce plenty of offspring, and it did so quickly. A single pair of flies could produce as many as 100 offspring. Before long, Morgan and other biologists had tested every one of Mendel's principles and learned that they applied not just to pea plants but to other organisms as well.

Mendel's principles also apply to humans. The basic principles of Mendelian genetics can be used to study the inheritance of human traits and to calculate the probability of certain traits appearing in the next generation. You will learn more about human genetics in Chapter 14.

Genetics and the Environment

The characteristics of any organism, whether bacterium, fruit fly, or human being, are not determined solely by the genes it inherits. Rather, characteristics are determined by interaction between genes and the environment. For example, genes may affect a sunflower plant's height and the color of its flowers. However, these same characteristics are also influenced by climate, soil conditions, and the availability of water. Genes provide a plan for development, but how that plan unfolds also depends on the environment.

11-3 Section Assessment

1. **Key Concept** Explain what *independent assortment* means.
2. **Key Concept** Describe two inheritance patterns besides simple dominance.
3. What is the difference between incomplete dominance and codominance?
4. Why are fruit flies an ideal organism for genetic research?

5. **Critical Thinking Comparing and Contrasting** A geneticist studying coat color in animals crosses a male rabbit having the genotype CC with a female having genotype Cc^{ch}. The geneticist then crosses a cc^{ch} male with a Cc^{ch} female. In which of the two crosses are the offspring more likely to show greater genetic variation? Use Punnett squares to explain your answer.

Sharpen Your Skills

Problem Solving

Construct a genetics problem to be given as an assignment to a classmate. The problem must test incomplete dominance, codominance, multiple alleles, or polygenic traits. Your problem must have an answer key that includes all of your work.

11-4 Meiosis

Gregor Mendel did not know where the genes he had discovered were located in the cell. Fortunately, his predictions of how genes should behave were so specific that it was not long before biologists were certain they had found them. Genes are located on chromosomes in the cell nucleus.

Mendel's principles of genetics require at least two things. First, each organism must inherit a single copy of every gene from each of its "parents." Second, when an organism produces its own gametes, those two sets of genes must be separated from each other so that each gamete contains just one set of genes. This means that when gametes are formed, there must be a process that separates the two sets of genes so that each gamete ends up with just one set. Although Mendel didn't know it, gametes are formed through exactly such a process.

Chromosome Number

As an example of how this process works, let's consider the fruit fly, *Drosophila*. A body cell in an adult fruit fly has 8 chromosomes, as shown in **Figure 11-14**. Four of the chromosomes came from the fruit fly's male parent, and 4 came from its female parent. These two sets of chromosomes are **homologous** (hoh-MAHL-uh-guhs), meaning that each of the 4 chromosomes that came from the male parent has a corresponding chromosome from the female parent.

A cell that contains both sets of homologous chromosomes is said to be **diploid**, which means "two sets." The number of chromosomes in a diploid cell is sometimes represented by the symbol 2N. Thus for *Drosophila*, the diploid number is 8, which can be written 2N = 8. Diploid cells contain two complete sets of chromosomes and two complete sets of genes. This agrees with Mendel's idea that the cells of an adult organism contain two copies of each gene.

By contrast, the gametes of sexually reproducing organisms, including fruit flies and peas, contain only a single set of chromosomes, and therefore only a single set of genes. Such cells are said to be **haploid**, which means "one set." For *Drosophila*, this can be written as N = 4, meaning that the haploid number is 4.

Phases of Meiosis

How are haploid (N) gamete cells produced from diploid (2N) cells? That's where **meiosis** (my-OH-sis) comes in. **Meiosis is a process of reduction division in which the number of chromosomes per cell is cut in half through the separation of homologous chromosomes in a diploid cell.**

Guide for Reading

Key Concepts

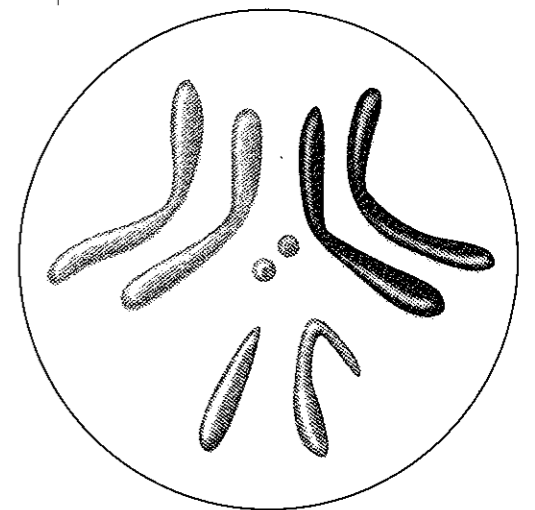
- What happens during the process of meiosis?
- How is meiosis different from mitosis?

Vocabulary

homologous
diploid
haploid
meiosis
tetrad
crossing-over

Reading Strategy:

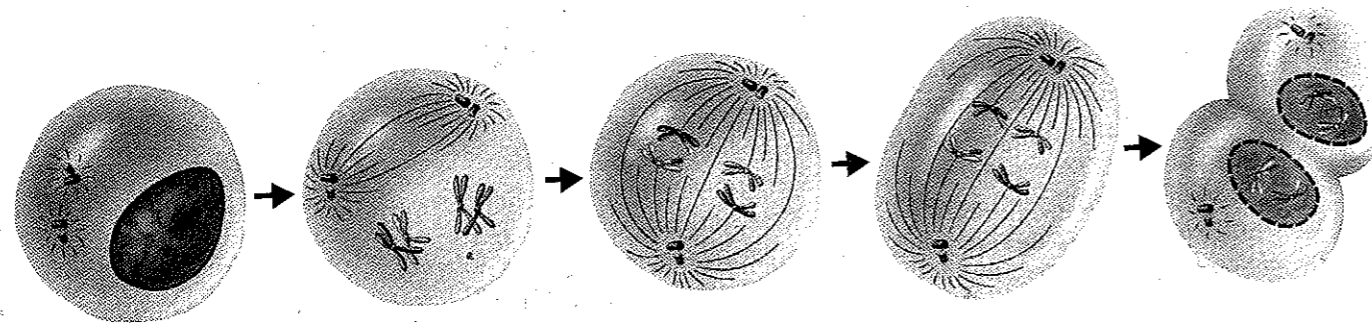
Using Visuals Before you read, preview **Figure 11-15**. As you read, note what happens at each stage of meiosis.



► **Figure 11-14** These chromosomes are from a fruit fly. Each of the fruit fly's body cells has 8 chromosomes.

MEIOSIS

Figure 11-15 During meiosis, the number of chromosomes per cell is cut in half through the separation of the homologous chromosomes. The result of meiosis is 4 haploid cells that are genetically different from one another and from the original cell.



Interphase I

Cells undergo a round of DNA replication, forming duplicate chromosomes.

MEIOSIS I

Prophase I

Each chromosome pairs with its corresponding homologous chromosome to form a tetrad.

Metaphase I

Spindle fibers attach to the chromosomes.

Anaphase I

The fibers pull the homologous chromosomes toward opposite ends of the cell.

Telophase I and Cytokinesis

Nuclear membranes form. The cell separates into two cells.

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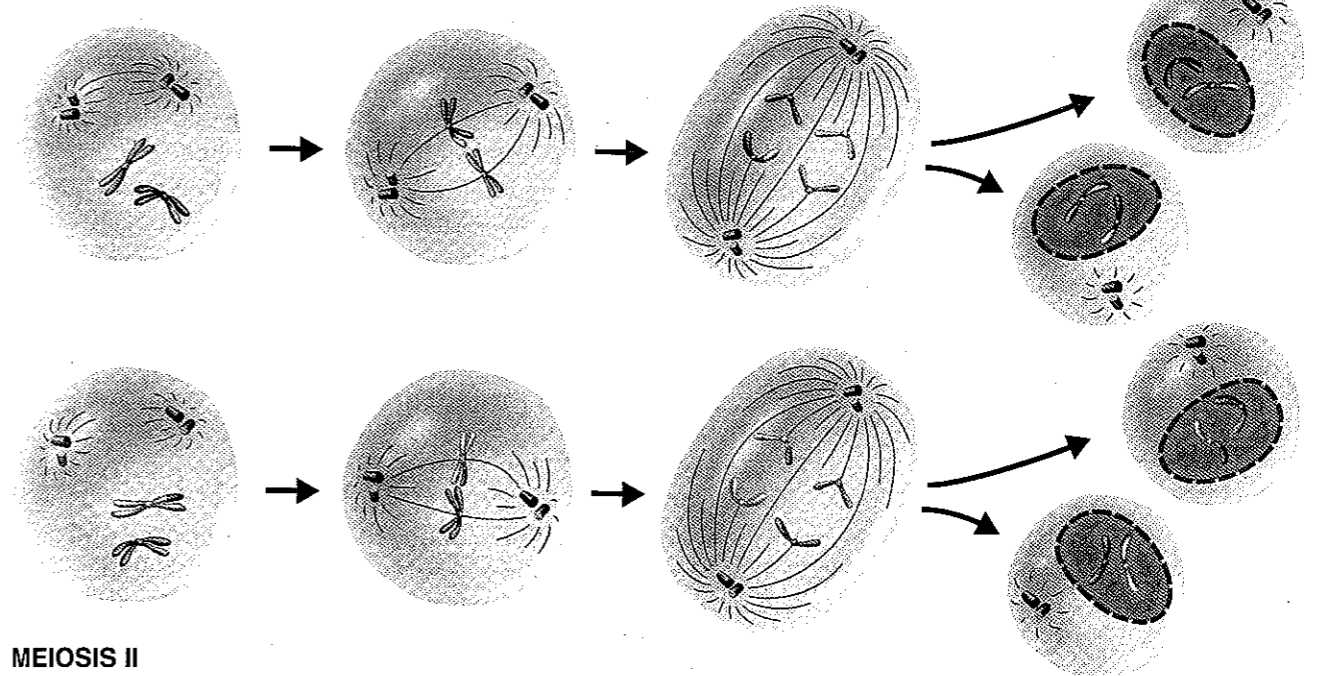
Meiosis usually involves two distinct divisions, called meiosis I and meiosis II. By the end of meiosis II, the diploid cell that entered meiosis has become 4 haploid cells. **Figure 11-15** shows meiosis in an organism that has a diploid number of 4 ($2N = 4$).

Meiosis I Prior to meiosis I, each chromosome is replicated. The cells then begin to divide in a way that looks similar to mitosis. In mitosis, the 4 chromosomes line up individually in the center of the cell. The 2 chromatids that make up each chromosome then separate from each other.

In prophase of meiosis I, however, each chromosome pairs with its corresponding homologous chromosome to form a structure called a **tetrad**. There are 4 chromatids in a tetrad. This pairing of homologous chromosomes is the key to understanding meiosis.

As homologous chromosomes pair up and form tetrads in meiosis I, they exchange portions of their chromatids in a process called **crossing-over**. Crossing-over, shown in **Figure 11-16**, results in the exchange of alleles between homologous chromosomes and produces new combinations of alleles.

What happens next? The homologous chromosomes separate, and two new cells are formed. Although each cell now has 4 chromatids (as it would after mitosis), something is different.



MEIOSIS II

Prophase II

Meiosis I results in two haploid (N) daughter cells, each with half the number of chromosomes as the original cell.

Metaphase II

The chromosomes line up in a similar way to the metaphase stage of mitosis.

Anaphase II

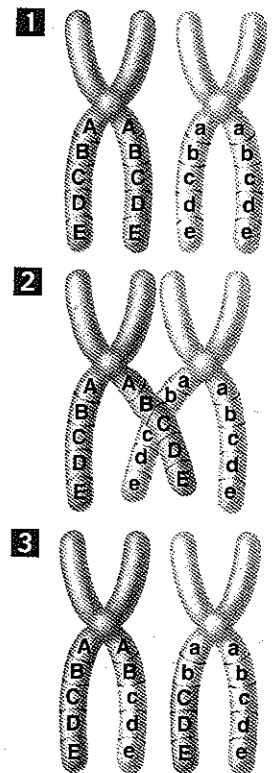
The sister chromatids separate and move toward opposite ends of the cell.

Telophase II and Cytokinesis

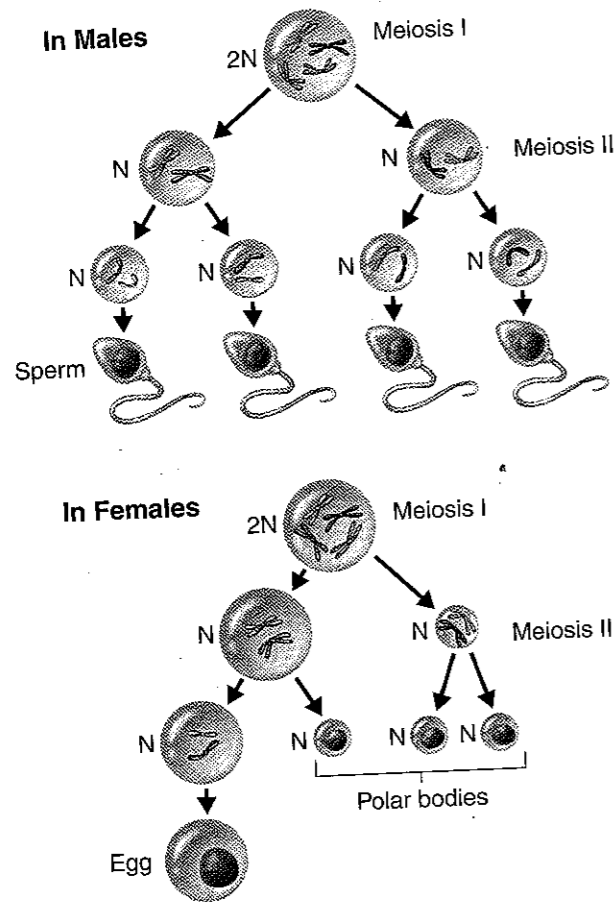
Meiosis II results in four haploid (N) daughter cells.

Because each pair of homologous chromosomes was separated, neither of the daughter cells has the two complete sets of chromosomes that it would have in a diploid cell. Those two sets have been shuffled and sorted almost like a deck of cards. The two cells produced by meiosis I have sets of chromosomes and alleles that are different from each other and from the diploid cell that entered meiosis I.

Meiosis II The two cells produced by meiosis I now enter a second meiotic division. Unlike the first division, neither cell goes through a round of chromosome replication before entering meiosis II. Each of the cell's chromosomes has 2 chromatids. During metaphase II of meiosis, chromosomes line up in the center of each cell. In anaphase II, the paired chromatids separate. In this example, each of the four daughter cells produced in meiosis II receives 2 chromatids. Those four daughter cells now contain the haploid number (N)—just 2 chromosomes each.



► **Figure 11-16** Crossing-over occurs during meiosis. (1) Homologous chromosomes form a tetrad. (2) Chromatids cross over one another. (3) The crossed sections of the chromatids are exchanged. **Interpreting Graphics** How does crossing-over affect the alleles on a chromatid?



▲ **Figure 11-17** Meiosis produces four genetically different haploid cells. In males, meiosis results in four equal-sized gametes called sperm. In females, only one large egg cell results from meiosis. The other three cells, called polar bodies, usually are not involved in reproduction.

Gamete Formation

In male animals, the haploid gametes produced by meiosis are called sperm. In some plants, pollen grains contain haploid sperm cells. In female animals, generally only one of the cells produced by meiosis is involved in reproduction. This female gamete is called an egg in animals and an egg cell in some plants.

In many female animals, the cell divisions at the end of meiosis I and meiosis II are uneven, so that a single cell, which becomes an egg, receives most of the cytoplasm, as shown in **Figure 11-17**. The other three cells produced in the female during meiosis are known as polar bodies and usually do not participate in reproduction.

Comparing Mitosis and Meiosis

In a way, it's too bad that the words *mitosis* and *meiosis* sound so much like each other, because the two processes are very different. **Mitosis results in the production of two genetically identical diploid cells, whereas meiosis produces four genetically different haploid cells.**

A diploid cell that divides by mitosis gives rise to two diploid (2N) daughter cells. The daughter cells have sets of chromosomes and alleles that are identical to each other and to the original parent cell. Mitosis allows an organism's body to grow and replace cells. In asexual reproduction, a new organism is produced by mitosis of the cell or cells of the parent organism.

Meiosis, on the other hand, begins with a diploid cell but produces four haploid (N) cells. These cells are genetically different from the diploid cell and from one another. Meiosis is how sexually reproducing organisms produce gametes. In contrast, asexual reproduction involves only mitosis.

11-5 Linkage and Gene Maps

If you thought carefully about Mendel's principle of independent assortment as you analyzed meiosis, one question might have been bothering you. It's easy to see how genes located on different chromosomes assort independently, but what about genes located on the same chromosome? Wouldn't they generally be inherited together?

Gene Linkage

The answer to these questions, as Thomas Hunt Morgan first realized in 1910, is yes. Morgan's research on fruit flies led him to the principle of linkage. After identifying more than 50 *Drosophila* genes, Morgan discovered that many of them appeared to be "linked" together in ways that, at first glance, seemed to violate the principle of independent assortment. For example, a fly with reddish-orange eyes and miniature wings, like the one shown in **Figure 11-18**, was used in a series of crosses. The results showed that the genes for those traits were almost always inherited together and only rarely became separated from each other.

Morgan and his associates observed so many genes that were inherited together that before long they could group all of the fly's genes into four linkage groups. The linkage groups assorted independently, but all of the genes in one group were inherited together. *Drosophila* has four linkage groups. It also has four pairs of chromosomes, which led to two remarkable conclusions. First, each chromosome is actually a group of linked genes. Second, Mendel's principle of independent assortment still holds true. **It is the chromosomes, however, that assort independently, not individual genes.**

How did Mendel manage to miss gene linkage? By luck, or by design, six of the seven genes he studied are on different chromosomes. The two genes that are found on the same chromosome are so far apart that they also assort independently.

Gene Maps

If two genes are found on the same chromosome, does this mean that they are linked forever? Not at all. Crossing-over during meiosis sometimes separates genes that had been on the same chromosome onto homologous chromosomes. Crossover events occasionally separate and exchange linked genes and produce new combinations of alleles. This is important because it helps to generate genetic diversity.

Guide for Reading

- Key Concept**
- What structures actually assort independently?

Vocabulary
gene map

Reading Strategy:
Predicting Before you read, preview **Figure 11-19**. Predict how a diagram like this one can be used to determine how likely genes are to assort independently. As you read, note whether or not your prediction was correct.

▼ **Figure 11-18** The genes for this fruit fly's reddish-orange eyes and miniature wings are almost always inherited together. The reason for this is that the genes are close together on a single chromosome. **It is the chromosomes that assort independently, not individual genes.**

11-4 Section Assessment

1. **Key Concept** Describe the main results of meiosis.
2. **Key Concept** What are the principal differences between mitosis and meiosis?
3. What do the terms *diploid* and *haploid* mean?
4. What is crossing-over?

5. **Critical Thinking Applying Concepts** In human cells, $2N = 46$. How many chromosomes would you expect to find in a sperm cell? In an egg cell? In a white blood cell? Explain.

Connecting Concepts

Sexual and Asexual Reproduction

In asexual reproduction, mitosis occurs, but not meiosis. Which type of reproduction—sexual or asexual—results in offspring with greater genetic variation? Explain your answer.