After showing that alleles segregate during the formation of gametes, Mendel wondered if they did so independently. In other words, does the segregation of one pair of alleles affect the segregation of another pair of alleles? For example, does the gene that determines whether a seed is round or wrinkled in shape have anything to do with the gene for seed color? Must a round seed also be yellow?

**Independent Assortment**

To answer these questions, Mendel performed an experiment to follow two different genes as they passed from one generation to the next. Mendel’s experiment is known as a two-factor cross.

**The Two-Factor Cross:** F₁

First, Mendel crossed true-breeding plants that produced only round yellow peas (genotype **RRYY**) with plants that produced wrinkled green peas (genotype **rryy**). All of the F₁ offspring produced round yellow peas. This shows that the alleles for yellow and round peas are dominant over the alleles for green and wrinkled peas. A Punnett square for this cross, shown in Figure 11–9, shows that the genotype of each of these F₁ plants is **RrYy**. This cross does not indicate whether genes assort, or segregate, independently. However, it provides the hybrid plants needed for the next cross—the cross of F₁ plants to produce the F₂ generation.

**Figure 11–9** Mendel crossed plants that were homozygous dominant for round yellow peas with plants that were homozygous recessive for wrinkled green peas. All of the F₁ offspring produced round yellow peas. This shows that the alleles for yellow and round peas are dominant over the alleles for green and wrinkled peas. A Punnett square for this cross, shown in Figure 11–9, shows that the genotype of each of these F₁ plants is **RrYy**. This cross does not indicate whether genes assort, or segregate, independently. However, it provides the hybrid plants needed for the next cross—the cross of F₁ plants to produce the F₂ generation.

**Interpreting Graphics** How is the genotype of the offspring different from that of the homozygous dominant parent?

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**Vocabulary Preview**

Explain that the prefix poly- means “more than one.” Ask: What do you think a polygenic trait is? (A trait controlled by more than one gene)

**Reading Strategy: Finding Main Ideas** Before you read, draw a line down the center of a sheet of paper. On the left side, write down the main topics of the section. On the right side, note supporting details and examples.

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**Guide for Reading**

**Key Concepts**
- What is the principle of independent assortment?
- What inheritance patterns exist aside from simple dominance?

**Vocabulary**
- Independent assortment
- Incomplete dominance
- Codominance
- Multiple alleles
- Polygenic traits

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**FOCUS**

**Objectives**

11.3.1 Explain the principle of independent assortment.
11.3.2 Describe the inheritance patterns that exist aside from simple dominance.
11.3.3 Explain how Mendel’s principles apply to all organisms.

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**INSTRUCT**

**Independent Assortment**

**Build Science Skills**

**Applying Concepts** Give students F₁ corn cobs produced in a dihybrid cross between homozygous purple, starchy (PPSS) and yellow, sweet parents (ppss). Ask: Which traits are controlled by dominant alleles? (Purple and starchy) Then, have students construct a Punnett square to show all the possible gametes and offspring from the cross. (Punnett squares should look similar to the one in Figure 11–9. Possible gametes for the ppss parent are **ps**. Those for the PPSS parent are **PS**. All offspring will be heterozygous, PpSs.)

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**SECTION RESOURCES**

**Print:**
- Laboratory Manual A, Chapter 11 Lab
- Laboratory Manual B, Chapter 11 Lab
- Teaching Resources, Lesson Plan 11–3, Adapted Section Summary 11–3, Adapted Worksheets 11–3, Section Summary 11–3, Worksheets 11–3, Section Review 11–3
- Reading and Study Workbook A, Section 11–3
- Adapted Reading and Study Workbook B, Section 11–3

**Technology:**
- iText, Section 11–3
- Transparencies Plus, Section 11–3
- Lab Simulations CD-ROM, Mendelian Inheritance
The Two-Factor Cross: F₂
Mendel knew that the F₁ plants had genotypes of RrYy. In other words, the F₁ plants were all heterozygous for both the seed shape and seed color genes. How would the alleles segregate when the F₂ plants were crossed to each other to produce an F₂ generation? Remember that each plant in the F₁ generation was formed by the fusion of a gamete carrying the dominant RY alleles with another gamete carrying the recessive ry alleles. Did this mean that the two dominant alleles would always stay together? Or would they “segregate independently,” so that any combination of alleles was possible?

In Mendel’s experiment, the F₂ plants produced 556 seeds. Mendel compared the variation in the seeds. He observed that 315 seeds were round and yellow and another 32 were wrinkled and green, the two parental phenotypes. However, 209 of the seeds had combinations of phenotypes—and therefore combinations of alleles—not found in either parent. This clearly meant that the alleles for seed shape segregated independently of those for seed color—a principle known as independent assortment. Put another way, genes that segregate independently—such as the genes for seed shape and seed color in pea plants—do not influence each other’s inheritance. Mendel’s experimental results were very close to the 9 : 3 : 3 : 1 ratio that the Punnett square shown in Figure 11–10 predicts. Mendel had discovered the principle of independent assortment. The principle of independent assortment states that genes for different traits can segregate independently during the formation of gametes. Independent assortment helps account for the many genetic variations observed in plants, animals, and other organisms.

Problem Solving

Producing True-Breeding Seeds
Suppose you work for a company that specializes in ornamental flowers. One spring, you find an ornamental plant with beautiful lavender flowers. Knowing that these plants are self-pollinating, you harvest seeds from it. You plant the seeds the following season. Of the 106 test plants, 31 have white flowers. Is there a way to develop seeds that produce only lavender flowers?

Defining the Problem
Describe the problem that must be solved to make the lavender-flowered plants a commercial success.

Organizing Information
The first lavender flower produced offspring with both lavender and white flowers when allowed to self-pollinate. Use your knowledge of Mendelian genetics, including Punnett squares, to draw conclusions about the nature of the allele for these lavender flowers.

Creating a Solution
Write a description of how you would produce seeds guaranteed to produce 100 percent lavender plants. A single plant can produce as many as 1000 seeds.

Presenting Your Plan
Prepare a step-by-step outline of your plan, including the materials and steps. Present your plan to your class.

Answer to . . .

Introduction to Genetics 271
A Summary of Mendel’s Principles

Mendel’s principles form the basis of the modern science of genetics. These principles can be summarized as follows:

- The inheritance of biological characteristics is determined by individual units known as genes. Genes are passed from parents to their offspring.
- In cases in which two or more forms (alleles) of the gene for a single trait exist, some forms of the gene may be dominant and others may be recessive.
- In most sexually reproducing organisms, each adult has two copies of each gene—one from each parent. These genes are segregated from each other when gametes are formed.
- Some alleles are neither dominant nor recessive, and many traits are controlled by multiple alleles or multiple genes.

Beyond Dominant and Recessive Alleles

Despite the importance of Mendel’s work, there are important exceptions to most of his principles. For example, not all genes show simple patterns of dominant and recessive alleles. In most organisms, genetics is more complicated, because the majority of genes have more than two alleles. In addition, many important traits are controlled by more than one gene. Some alleles are neither dominant nor recessive, and many traits are controlled by multiple alleles or multiple genes.

Incomplete Dominance

A cross between two four o’clock (Mirabilis) plants shows one of these complications. The F1 generation produced by a cross between red-flowered (RR) and white-flowered (WW) plants consists of pink-colored flowers (RW), as shown in Figure 11–11. Which allele is dominant in this case? Neither one. Cases in which one allele is not completely dominant over another are called incomplete dominance. In incomplete dominance, the heterozygous phenotype is somewhere in between the two homozygous phenotypes.

Codominance

A similar situation is codominance, in which both alleles contribute to the phenotype. For example, in certain varieties of chicken, the allele for black feathers is codominant with the allele for white feathers. Heterozygous chickens have a color described as “ermine,” speckled with black and white feathers. Unlike the blending of red and white colors in heterozygous four o’clocks, black and white colors appear separately. Many human genes show codominance, too, including one for a protein that controls cholesterol levels in the blood. People with the heterozygous form of the gene produce two different forms of the protein, each with a different effect on cholesterol levels.

Testing to identify F1 genotypes

Mendel was very thorough in his methodology, so it really comes as no surprise that he devised a method to test his hypotheses in various ways. One method he used, which is used frequently by geneticists today, has come to be known as the testcross. A testcross is used to identify the genotype of F1 hybrids. For this cross, F1 hybrids are crossed back to the parent with the trait controlled by the recessive allele. When Mendel used a testcross for his F1 offspring, he expected to observe approximately equal numbers of offspring with the traits controlled by the dominant and recessive alleles. That is what he observed. Today, a testcross is used to determine whether an individual with the phenotype controlled by the dominant allele is heterozygous or homozygous. If the individual is homozygous, none of the offspring will have the phenotype controlled by the recessive allele.
Explain that coat colors, as shown in Figure 11–12, come about partly because more than four different genes contribute to the different alleles. Different combinations of alleles result in the four colors you see here. For example, the wide range of skin color in humans comes about partly because more than four different genes contribute to the different alleles. Different combinations of alleles result in the four colors you see here.

Multiple Alleles Many genes have more than two alleles and are therefore said to have multiple alleles. This does not mean that an individual can have more than two alleles. It only means that more than two possible alleles exist in a population. One of the best-known examples is coat color in rabbits. A rabbit’s coat color is determined by a single gene that has at least four different alleles. The four known alleles display a pattern of simple dominance that can produce four possible coat colors, as shown in Figure 11–12. Many other genes have multiple alleles, including the human genes for blood type.

Polygenic Traits Many traits are produced by the interaction of several genes. Traits controlled by two or more genes are said to be polygenic traits, which means “having many genes.” For example, at least three genes are involved in making the reddish-brown pigment in the eyes of fruit flies. Different combinations of alleles for these genes produce very different eye colors. Polygenic traits often show a wide range of phenotypes. For example, the wide range of skin color in humans comes about partly because more than four different genes probably control this trait.

Address Misconceptions
Students might try to apply the ideas of simple dominance to other types of gene expression. Give students many different examples of incomplete dominance, codominance, multiple alleles, and polygenic traits. Collect pictures for students to compare the various phenotypes.

Use Visuals
Figure 11–12 Explain that coat color in rabbits does show a pattern of simple dominance among four alleles. Have students study the phenotypes of the rabbits in the figure. Challenge them to arrange the alleles for coat color in order from the most dominant to the least dominant. (C>Cc>c>c) Then, have students make up genetic crosses for coat color in rabbits and exchange them with partners. Partners should solve the problems using Punnett squares.
Chapter 11

They are small, easy to keep in the laboratory, and produce large numbers of offspring in a short period of time.

In incomplete dominance, two alleles combine their effects to produce a single in-between phenotype, such as pink flowers from red and white parents. In codominance, each allele is expressed separately, as when erminette chickens have both black and white feathers.

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. The geneticist then crosses a Cc male with a Cc female. In which of the two crosses are the offspring more likely to show greater genetic variation? Use Punnett squares to explain your answer.

**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. **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. The geneticist then crosses a Cc male with a Cc female. In which of the two crosses are the offspring more likely to show greater genetic variation? Use Punnett squares to explain your answer.

If your class subscribes to the iText, use it to review the Key Concepts in Section 11–3.