11.1 The Work of Gregor Mendel

Key Questions

Where does an organism get its unique characteristics?

How are different forms of a gene distributed to offspring?

Vocabulary

genetics • fertilization • trait • hybrid • gene • allele • principle of dominance • segregation • gamete

Taking Notes

Two-Column Chart Before you read, draw a line down the center of a sheet of paper. On the left side, write the main ideas in this lesson. On the right side, note the details and examples that support each of those ideas.

THINK ABOUT IT What is an inheritance? To many people, it is money or property left to them by relatives who have passed away. That kind of inheritance matters, of course, but there is another kind that matters even more. It is something we each receive from our parents—a contribution that determines our blood type, the color of our hair, and so much more. Most people leave their money and property behind by writing a will. But what kind of inheritance makes a person's face round or their hair curly?

The Experiments of Gregor Mendel

Where does an organism get its unique characteristics?

Every living thing—plant or animal, microbe or human being—has a set of characteristics inherited from its parent or parents. Since the beginning of recorded history, people have wanted to understand how that inheritance is passed from generation to generation. The delivery of characteristics from parent to offspring is called heredity. The scientific study of heredity, known as **genetics,** is the key to understanding what makes each organism unique.

The modern science of genetics was founded by an Austrian monk named Gregor Mendel. Mendel, shown in **Figure 11–1,** was born in 1822 in what is now the Czech Republic. After becoming a priest, Mendel spent several years studying science and mathematics at the University of Vienna. He spent the next 14 years working in a monastery and teaching high school. In addition to his teaching duties, Mendel was in charge of the monastery garden. In this simple garden, he was to do the work that changed biology forever.

Mendel carried out his work with ordinary garden peas, partly because peas are small and easy to grow. A single pea plant can produce hundreds of offspring. Today we call peas a "model system." Scientists use model systems because they are convenient to study and may tell us how other organisms, including humans, actually function. By using peas, Mendel was able to carry out, in just one or two growing seasons, experiments that would have been impossible to do with humans and that would have taken decades—if not centuries—to do with pigs, horses, or other large animals.

FIGURE 11–1 Gregor Mendel

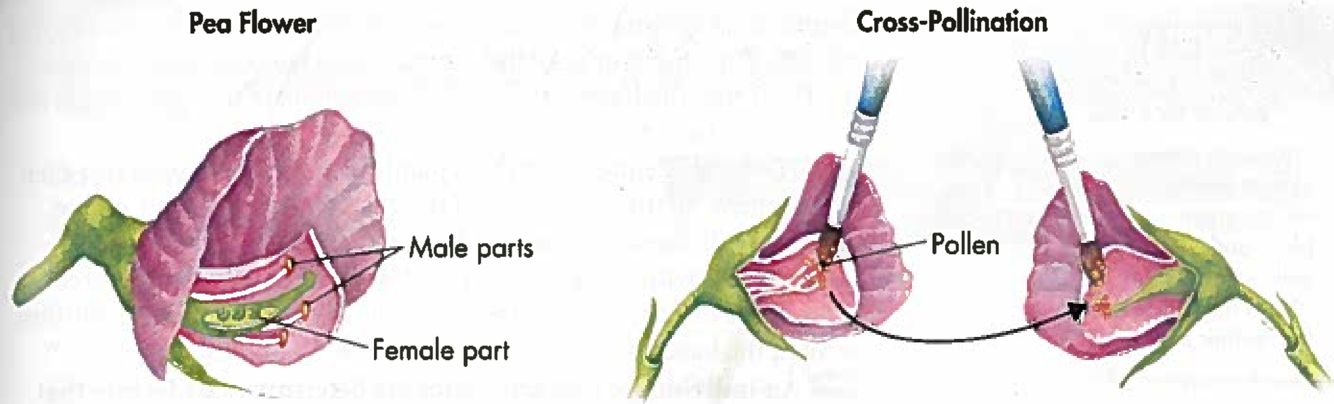

FIGURE 11–2 Cross-Pollination To cross-pollinate pea plants, Mendel cut off the male parts of one flower and then dusted the female part with pollen from another flower. **Apply Concepts** ***How did this procedure prevent self-pollination?***

The Role of Fertilization When Mendel began his experiments, he knew that the male part of each flower makes pollen, which contains the plant's male reproductive cells, called sperm. Similarly, Mendel knew that the female portion of each flower produces reproductive cells called eggs. During sexual reproduction, male and female reproductive cells join in a process known as **fertilization** to produce a new cell. In peas, this new cell develops into a tiny embryo encased within a seed.

Pea flowers are normally self-pollinating, which means that sperm cells fertilize egg cells from within the same flower. A plant grown from a seed produced by self-pollination inherits all of its characteristics from the single plant that bore it; it has a single parent.

Mendel's monastery garden had several stocks of pea plants. These plants were "true-breeding," meaning that they were self-pollinating, and would produce offspring identical to themselves. In other words, the traits of each successive generation would be the same. A **trait** is a specific characteristic, such as seed color or plant height, of an individual. Many traits vary from one individual to another. For instance, one stock of Mendel's seeds produced only tall plants, while another produced only short ones. One line produced only green seeds, another produced only yellow seeds.

To learn how these traits were determined, Mendel decided to "cross" his stocks of true-breeding plants—that is, he caused one plant to reproduce with another plant. To do this, he had to prevent self-pollination. He did so by cutting away the pollen-bearing male parts of a flower. He then dusted the pollen from a different plant onto the female part of that flower, as shown in **Figure 11–2.** This process, known as cross-pollination, produces a plant that has two different parents. Cross-pollination allowed Mendel to breed plants with traits different from those of their parents and then study the results.

Mendel studied seven different traits of pea plants. Each of these seven traits had two contrasting characteristics, such as green seed color or yellow seed color. Mendel crossed plants with each of the seven contrasting characteristics and then studied their offspring. The offspring of crosses between parents with different traits are called **hybrids.**

In Your Notebook *Explain, in your own words, what fertilization is.*

MYSTERY CLUE

Parakeets come in four colors: white, green, blue, and yellow. How many alleles might there be for feather color?

Genes and Alleles When doing genetic crosses, we call each original pair of plants the P, or parental, generation. Their offspring are called the F_1, or first filial, generation. (*Filius* and *filia* are the Latin words for "son" and "daughter.")

What were Mendel's F_1 hybrid plants like? To his surprise, for each trait studied, all the offspring had the characteristics of only one of its parents, as shown in **Figure 11–3.** In each cross, the nature of the other parent, with regard to each trait, seemed to have disappeared. From these results, Mendel drew two conclusions. His first conclusion formed the basis of our current understanding of inheritance. **An individual's characteristics are determined by factors that are passed from one parental generation to the next.** Today, scientists call the factors that are passed from parent to offspring **genes.**

Each of the traits Mendel studied was controlled by one gene that occurred in two contrasting varieties. These variations produced different expressions, or forms, of each trait. For example, the gene for plant height occurred in one form that produced tall plants and in another form that produced short plants. The different forms of a gene are called **alleles** (uh LEELZ).

Dominant and Recessive Traits Mendel's second conclusion is called the **principle of dominance.** This principle states that some alleles are dominant and others are recessive. An organism with at least one dominant allele for a particular form of a trait will exhibit that form of the trait. An organism with a recessive allele for a particular form of a trait will exhibit that form only when the dominant allele for the trait is not present. In Mendel's experiments, the allele for tall plants was dominant and the allele for short plants was recessive. Likewise, the allele for yellow seeds was dominant over the recessive allele for green seeds.

FIGURE 11–3 Mendel's F_1 Crosses When Mendel crossed plants with contrasting traits, the resulting hybrids had the traits of only one of the parents.

Mendel's Seven F_1 Crosses on Pea Plants

	Seed Shape	Seed Color	Seed Coat	Pod Shape	Pod Color	Flower Position	Plant Height
P	Round X Wrinkled	Yellow X Green	Gray X White	Smooth X Constricted	Green X Yellow	Axial X Terminal	Tall X Short
F_1	Round	Yellow	Gray	Smooth	Green	Axial	Tall

Quick Lab
GUIDED INQUIRY

Classroom Variation

1. Copy the data table into your notebook.
2. Write a prediction of whether the traits listed in the table will be evenly distributed or if there will be more dominant than recessive traits.
3. Examine your features, using a mirror if necessary. Determine which traits you have for features A–E.
4. Interview at least 14 other students to find out which traits they have. Tally the numbers. Record the totals in each column.

Trait Survey

Feature	Dominant Trait	Number	Recessive Trait	Number
A	Free ear lobes		Attached ear lobes	
B	Hair on fingers		No hair on fingers	
C	Widow's peak		No widow's peak	
D	Curly hair		Straight hair	
E	Cleft chin		Smooth chin	

Analyze and Conclude

1. Calculate Calculate the percentages of each trait in your total sample. How do these numbers compare to your prediction? MATH

2. Form a Hypothesis Why do you think recessive traits are more common in some cases?

In Your Notebook *Make a diagram that explains Mendel's principle of dominance.*

Segregation

How are different forms of a gene distributed to offspring?

Mendel didn't stop after one set of F_1 crosses, because he had another question: Had the recessive alleles simply disappeared, or were they still present in the new plants? To find out, he allowed all seven kinds of F_1 hybrids to self-pollinate. The offspring of an F_1 cross are called the F_2 (second filial) generation. In effect, Mendel crossed the F_1 generation with itself to produce the F_2 offspring, as shown in **Figure 11–4.**

The F_1 Cross When Mendel compared the F_2 plants, he made a remarkable discovery: The traits controlled by the recessive alleles reappeared in the second generation. Roughly one fourth of the F_2 plants showed the trait controlled by the recessive allele. Why, then, did the recessive alleles seem to disappear in the F_1 generation, only to reappear in the F_2 generation?

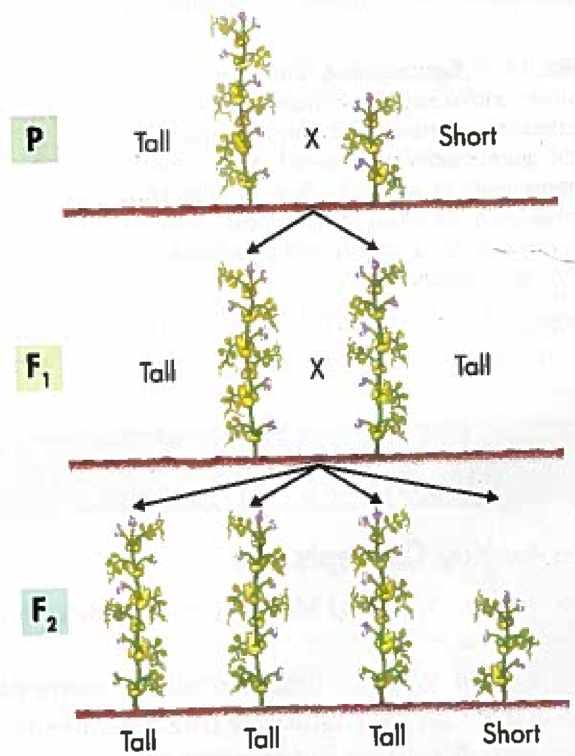

FIGURE 11–4 F_2 Cross When Mendel allowed the F_1 plants to reproduce by self-pollination, the traits controlled by recessive alleles reappeared in about one fourth of the F_2 plants in each cross. **Calculate** ***What proportion of the F_2 plants had a trait controlled by a dominant allele?*** MATH

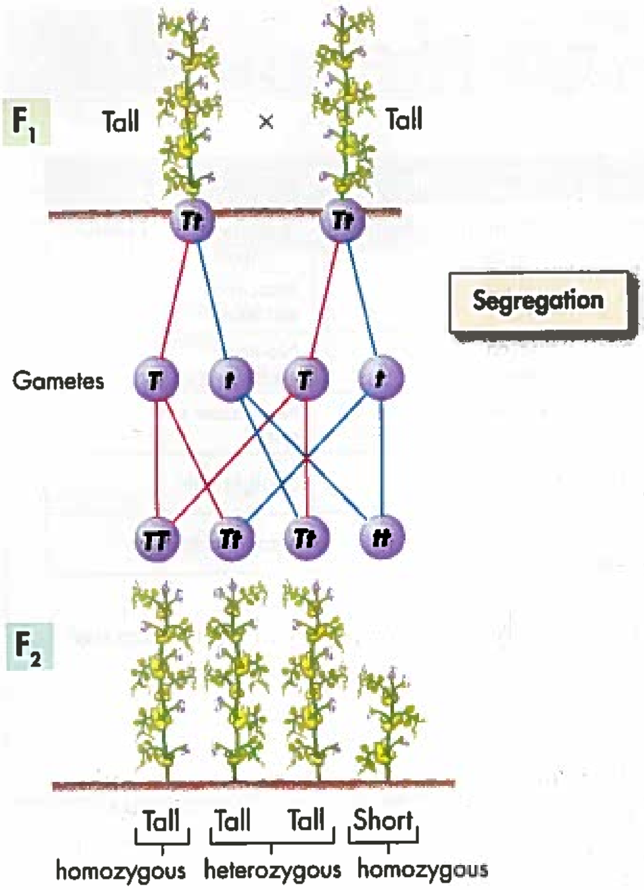

FIGURE 11–5 Segregation During gamete formation, alleles segregate from each other so that each gamete carries only a single copy of each gene. Each F_1 plant makes two types of gametes—those with the allele for tallness and those with the allele for shortness. The alleles are paired up again when gametes fuse during fertilization.

Explaining the F_1 Cross To begin with, Mendel assumed that a dominant allele had masked the corresponding recessive allele in the F_1 generation. However, the trait controlled by the recessive allele did show up in some of the F_2 plants. This reappearance indicated that, at some point, the allele for shortness had separated from the allele for tallness. How did this separation, or **segregation,** of alleles occur? Mendel suggested that the alleles for tallness and shortness in the F_1 plants must have segregated from each other during the formation of the sex cells, or **gametes** (GAM eetz). Did that suggestion make sense?

The Formation of Gametes Let's assume, as Mendel might have, that all the F_1 plants inherited an allele for tallness from the tall parent and one for shortness from the short parent. Because the allele for tallness is dominant, all the F_1 plants are tall. **During gamete formation, the alleles for each gene segregate from each other, so that each gamete carries only one allele for each gene.** Thus, each F_1 plant produces two kinds of gametes—those with the tall allele and those with the short allele.

Look at **Figure 11–5** to see how alleles separate during gamete formation and then pair up again in the F_2 generation. A capital letter represents a dominant allele. A lowercase letter represents a recessive allele. Now we can see why the recessive trait for height, *t*, reappeared in Mendel's F_2 generation. Each F_1 plant in Mendel's cross produced two kinds of gametes—those with the allele for tallness and those with the allele for shortness. Whenever a gamete that carried the *t* allele paired with the other gamete that carried the *t* allele to produce an F_2 plant, that plant was short. Every time one or both gametes of the pairing carried the *T* allele, a tall plant was produced. In other words, the F_2 generation had new combinations of alleles.

11.1 Assessment

Review Key Concepts

1. a. **Review** What did Mendel conclude determines biological inheritance?
   b. **Explain** What are dominant and recessive alleles?
   c. **Apply Concepts** Why were true-breeding pea plants important for Mendel's experiments?
2. a. **Review** What is segregation?
   b. **Explain** What happens to alleles between the P generation and the F_2 generation?
   c. **Infer** What evidence did Mendel use to explain how segregation occurs?

VISUAL THINKING

3. Use a diagram to explain Mendel's principles of dominance and segregation. Your diagram should show how alleles segregate during gamete formation.

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11.2 Applying Mendel's Principles

THINK ABOUT IT *Nothing in life is certain.* There's a great deal of wisdom in that old saying, and genetics is a fine example. If a parent carries two different alleles for a certain gene, we can't be sure which of those alleles will be inherited by any one of the parent's offspring. However, think carefully about the nature of inheritance and you'll see that even if we can't predict the exact future, we can do something almost as useful—we can figure out the odds.

Key Questions

How can we use probability to predict traits?

How do alleles segregate when more than one gene is involved?

What did Mendel contribute to our understanding of genetics?

Vocabulary

probability • homozygous • heterozygous • phenotype • genotype • Punnett square • independent assortment

Taking Notes

Preview Visuals Before you read, preview **Figure 11–7.** Try to infer the purpose of this diagram. As you read, compare your inference to the text. After you read, revise your statement if needed or write a new one about the diagram's purpose.

Probability and Punnett Squares

How can we use probability to predict traits?

Whenever Mendel performed a cross with pea plants, he carefully categorized and counted the offspring. Consequently, he had plenty of data to analyze. For example, whenever he crossed two plants that were hybrids for stem height (*Tt*), about three fourths of the resulting plants were tall and about one fourth were short.

Upon analyzing his data, Mendel realized that the principles of probability could be used to explain the results of his genetic crosses. **Probability** is a concept you may have learned about in math class. It is the likelihood that a particular event will occur. As an example, consider an ordinary event, such as flipping a coin. There are two possible outcomes of this event: The coin may land either heads up or tails up. The chance, or probability, of either outcome is equal. Therefore, the probability that a single coin flip will land heads up is 1 chance in 2. This amounts to 1/2, or 50 percent.

If you flip a coin three times in a row, what is the probability that it will land heads up every time? Each coin flip is an independent event with a 1/2 probability of landing heads up. Therefore, the probability of flipping three heads in a row is:

$$1/2 \times 1/2 \times 1/2 = 1/8$$

As you can see, you have 1 chance in 8 of flipping heads three times in a row. The multiplication of individual probabilities illustrates an important point: Past outcomes do not affect future ones. Just because you've flipped three heads in a row does not mean that you're more likely to have a coin land tails up on the next flip. The probability for that flip is still 1/2.

FIGURE 11–6 Probability Probability allows you to calculate the likelihood that a particular event will occur. The probability that the coin will land heads up is ½, or 50 percent.

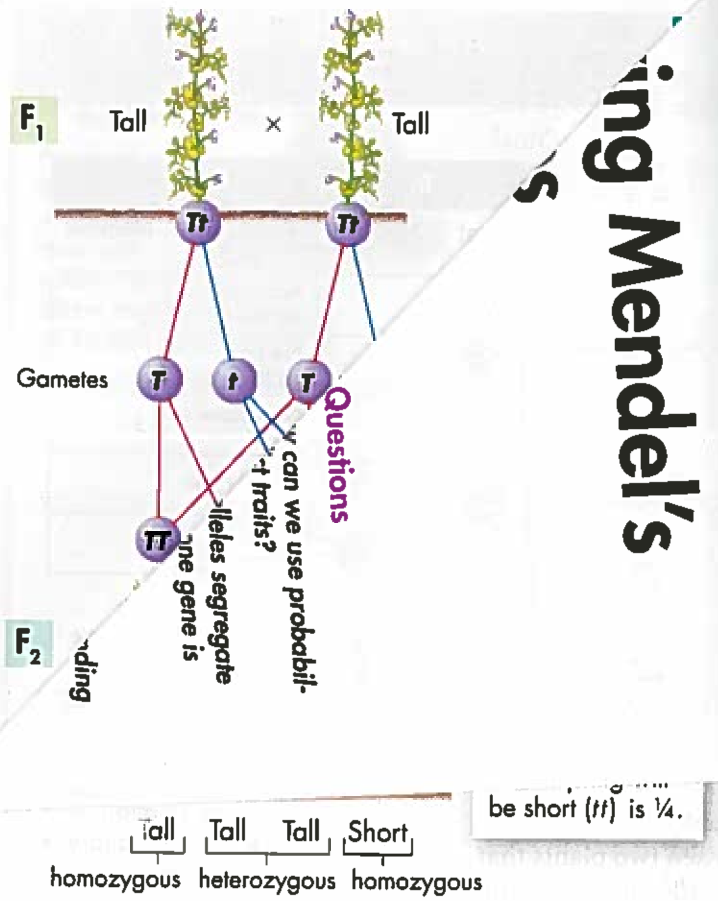


FIGURE 11–7 Segregation and Probability In this cross, the *TT* and *Tt* allele combinations produced three tall pea plants, while the *tt* allele combination produced one short plant. These quantities follow the laws of probability. **Predict** ***If you crossed a TT plant with a Tt plant, would the offspring be tall or short?***

…ng Segregation to Predict Outcomes …e way in which alleles segregate during …nete formation is every bit as random as …in flip. Therefore, the principles of prob-…ity can be used to predict the outcomes of …etic crosses.

…ook again at Mendel's F_1 cross, shown in …re 11–7. This cross produced a mixture of …nd short plants. Why were just 1/4 of the …ring short? Well, the F_1 plants were both …f each plant had one tall allele and one … allele (*Tt*), and if the alleles segregated as …del thought, then 1/2 of the gametes pro-…d by the plants would carry the short allele …t, the *t* allele is recessive. The only way to …ce a short (*tt*) plant is for two gametes, …arrying the *t* allele, to combine.

…ke the coin toss, each F_2 gamete has a one …, or 1/2, chance of carrying the *t* allele. … are two gametes, so the probability of …ametes carrying the *t* allele is 1/2 × 1/2 = 1/4. In other words, roughly one fourth of the F_2 offspring should be short, and the remaining three fourths should be tall. This predicted ratio—3 offspring exhibiting the dominant trait to 1 offspring exhibiting the recessive trait—showed up consistently in Mendel's experiments. For each of his seven crosses, about 3/4 of the plants showed the trait controlled by the dominant allele. About 1/4 showed the trait controlled by the recessive allele. Segregation did occur according to Mendel's model.

As you can see in the F_2 generation, not all organisms with the same characteristics have the same combinations of alleles. Both the *TT* and *Tt* allele combinations resulted in tall pea plants, but only one of these combinations contains identical alleles. Organisms that have two identical alleles for a particular gene—*TT* or *tt* in this example—are said to be **homozygous** (hoh moh ZY gus). Organisms that have two different alleles for the same gene—such as *Tt*—are **heterozygous** (het ur oh ZY gus).

Probabilities Predict Averages Probabilities predict the average outcome of a large number of events. If you flip a coin twice, you are likely to get one heads and one tails. However, you might also get two heads or two tails. To get the expected 50 : 50 ratio, you might have to flip the coin many times. The same is true of genetics.

The larger the number of offspring, the closer the results will be to the predicted values. If an F_2 generation contains just three or four offspring, it may not match Mendel's ratios. When an F_2 generation contains hundreds or thousands of individuals, the ratios usually come very close to matching predictions.

Genotype and Phenotype One of Mendel's most revolutionary insights followed directly from his observations of F_1 crosses: Every organism has a genetic makeup as well as a set of observable characteristics. All of the tall pea plants had the same **phenotype,** or physical traits. They did not, however, have the same **genotype,** or genetic makeup. Look again at **Figure 11–7** and you will find three different genotypes among the F_2 plants: *TT, Tt,* and *tt.* The genotype of an organism is inherited, whereas the phenotype is formed as a result of both the environment and the genotype. This means that two organisms may share the same phenotype but have different genotypes.

Using Punnett Squares One of the best ways to predict the outcome of a genetic cross is by drawing a simple diagram known as a **Punnett square.** **Punnett squares use mathematical probability to help predict the genotype and phenotype combinations in genetic crosses.** Constructing a Punnett square is fairly easy. You begin with a square. Then, following the principle of segregation, all possible combinations of alleles in the gametes produced by one parent are written along the top edge of the square. The other parent's alleles are then segregated along the left edge. Next, every possible genotype is written into the boxes within the square, just as they might appear in the F_2 generation. **Figure 11–8** on the next page shows step-by-step instructions for constructing Punnett squares.

In Your Notebook *In your own words, write definitions for the terms homozygous, heterozygous, phenotype, and genotype.*

BUILD Vocabulary

PREFIXES The prefix *pheno-* in **phenotype** comes from the Greek word *phainein,* meaning "to show." *Geno-,* the prefix in **genotype,** is derived from the Greek word *genus,* meaning "race, kind."

Quick Lab
GUIDED INQUIRY

How Are Dimples Inherited?

1. Write the last four digits of any telephone number. These four random digits represent the alleles of a gene that determines whether a person will have dimples. Odd digits represent the allele for the dominant trait of dimples. Even digits represent the allele for the recessive trait of no dimples.
2. Use the first two digits to represent a father's genotype. Use the symbols *D* and *d* to write his genotype as shown in the example.

Father's genotype is *dd* (2 even digits).

Mother's genotype is *Dd* (1 even digit and 1 odd digit).

46 | 38

3. Use the last two digits the same way to find the mother's genotype. Write her genotype.
4. Use **Figure 11–8** on the next page to construct a Punnett square for the cross of these parents. Then, using the Punnett square, determine the probability that their child will have dimples.
5. Determine the class average of the percent of children with dimples.

Analyze and Conclude

1. **Apply Concepts** How does the class average compare with the result of a cross of two heterozygous parents?
2. **Draw Conclusions** What percentage of the children will be expected to have dimples if one parent is homozygous for dimples (*DD*) and the other is heterozygous (*Dd*)?

VISUAL SUMMARY

HOW TO MAKE A PUNNETT SQUARE

FIGURE 11–8 By drawing a Punnett square, you can determine the allele combinations that might result from a genetic cross.

① Start With the Parents

One-Factor Cross

Write the genotypes of the two organisms that will serve as parents in a cross. In this example we will cross a male and female osprey, or fish eagle, that are heterozygous for large beaks. They each have genotypes of *Bb*.

Bb* and *Bb

Two-Factor Cross

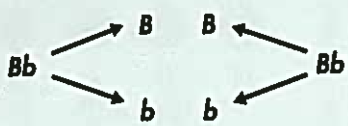
In this example we will cross two pea plants that are heterozygous for size (tall and short alleles) and pod color (green and yellow alleles). The genotypes of the two parents are *TtGg* and *TtGg*.

TtGg* and *TtGg

② Figure Out the Gametes

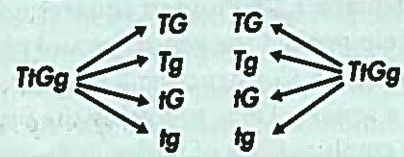
One-Factor Cross

Determine what alleles would be found in all of the possible gametes that each parent could produce.



Two-Factor Cross

Determine what alleles would be found in all of the possible gametes that each parent could produce.



③ Line Them Up

One-Factor Cross

Draw a table with enough squares for each pair of gametes from each parent. In this case, each parent can make two different types of gametes, *B* and *b*. Enter the genotypes of the gametes produced by both parents on the top and left sides of the table.

	B	b
B		
b		

Two-Factor Cross

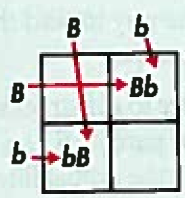
In this case, each parent can make 4 different types of gametes, so the table needs to be 4 rows by 4 columns, or 16 squares.

	TG	tG	Tg	tg
TG				
tG				
Tg				
tg				

④ Write Out the New Genotypes

One-Factor Cross

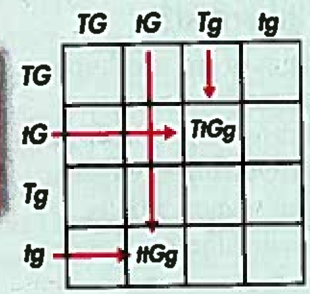
Fill in the table by combining the gametes' genotypes.



	B	b
B	BB	Bb
b	bB	bb

Two-Factor Cross

Fill in the table by combining the gametes' genotypes.



	TG	tG	Tg	tg
TG	TTGG	TtGG	TTGg	TtGg
tG	TtGG	ttGG	TtGg	ttGg
Tg	TTGg	TtGg	TTgg	Ttgg
tg	TtGg	ttGg	Ttgg	ttgg

⑤ Figure Out the Results

One-Factor Cross

Determine the genotype and phenotype of each offspring. Calculate the percentage of each. In this example, ¾ of the chicks will have large beaks, but only ½ will be heterozygous for this trait (*Bb*).

	B	b
B	BB	Bb
b	bB	bb

Two-Factor Cross

In this example, the color of the squares represents pod color. Alleles written in black indicate short plants, while alleles written in red indicate tall plants.

	TG	tG	Tg	tg
TG	TTGG	TtGG	TTGg	TtGg
tG	TtGG	ttGG	TtGg	ttGg
Tg	TTGg	TtGg	TTgg	Ttgg
tg	TtGg	ttGg	Ttgg	ttgg

Independent Assortment

How do alleles segregate when more than one gene is involved?

After showing that alleles segregate during the formation of gametes, Mendel wondered if the segregation of one pair of alleles affects another pair. For example, does the gene that determines the shape of a seed affect the gene for seed color? To find out, Mendel followed two different genes as they passed from one generation to the next. Because it involves two different genes, Mendel's experiment is known as a two-factor, or "dihybrid," cross. (Single-gene crosses are "monohybrid" crosses.)

The Two-Factor Cross: F_1 First, Mendel crossed true-breeding plants that produced only round yellow peas with plants that produced wrinkled green peas. The round yellow peas had the genotype *RRYY*, and the wrinkled green peas had the genotype *rryy*. All of the F_1 offspring produced round yellow peas. These results showed that the alleles for yellow and round peas are dominant. As the Punnett square in **Figure 11–9** shows, the genotype in each of these F_1 plants is *RrYy*. In other words, the F_1 plants were all heterozygous for both seed shape and seed color. This cross did not indicate whether genes assort, or segregate independently. However, it provided the hybrid plants needed to breed the F_2 generation.

The Two-Factor Cross: F_2 In the second part of this experiment, Mendel crossed the F_1 plants to produce F_2 offspring. Remember, each F_1 plant 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 F_2 plants produced 556 seeds. Mendel compared their variation. He observed that 315 of the seeds were round and yellow, while another 32 seeds were wrinkled and green—the two parental phenotypes. However, 209 seeds had combinations of phenotypes, and therefore combinations of alleles, that were not found in either parent. This clearly meant that the alleles for seed shape segregated independently of those for seed color. 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—even when they have the same parents.

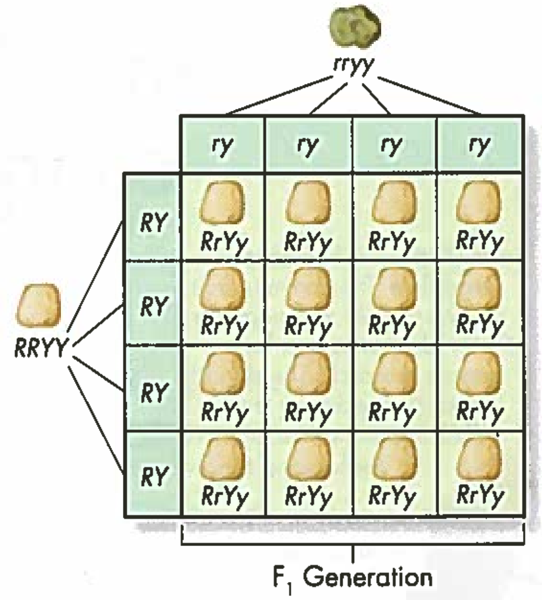


FIGURE 11–9 Two-Factor Cross: F_1 Mendel crossed plants that were homozygous dominant for round yellow peas with plants that were homozygous recessive for wrinkled green peas. All of the F_1 offspring were heterozygous dominant for round yellow peas. **Interpret Graphics** ***How is the genotype of the offspring different from that of the homozygous dominant parent?***

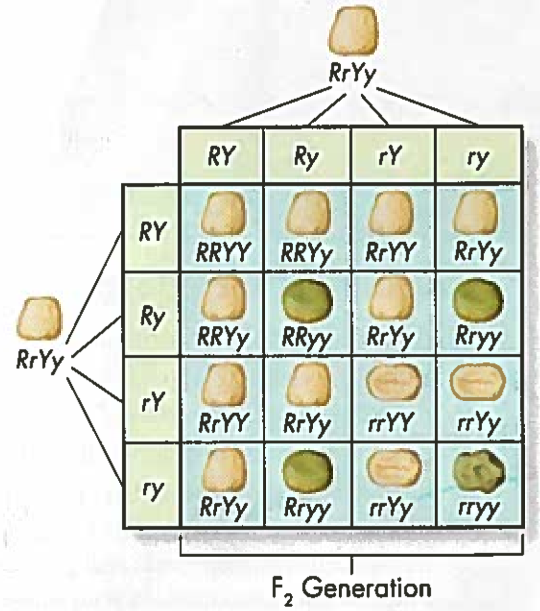


FIGURE 11–10 Two-Factor Cross: F_2 When Mendel crossed F_1 plants that were heterozygous dominant for round yellow peas, he found that the alleles segregated independently to produce the F_2 generation.

A Summary of Mendel's Principles

What did Mendel contribute to our understanding of genetics?

As you have seen, Mendel's principles of segregation and independent assortment can be observed through one- and two-factor crosses. **Mendel's principles of heredity, observed through patterns of inheritance, form the basis of modern genetics.** These principles are as follows:

- The inheritance of biological characteristics is determined by individual units called genes, which are passed from parents to offspring.
- Where two or more forms (alleles) of the gene for a single trait exist, some alleles 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 segregate from each other when gametes are formed.
- Alleles for different genes usually segregate independently of each other.

Mendel's principles don't apply only to plants. At the beginning of the 1900s, the American geneticist Thomas Hunt Morgan wanted to use a model organism of another kind to advance the study of genetics. 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 11–11.** *Drosophila* can produce plenty of offspring—a single pair can produce as many as 100 progeny. Before long, Morgan and other biologists had tested all of Mendel's principles and learned that they applied to flies and other organisms as well. In fact, Mendel's basic principles 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.

FIGURE 11–11 A Model Organism The common fruit fly, *Drosophila melanogaster,* is an ideal organism for genetic research. These fruit flies are poised on a lemon.

11.2 Assessment

Review Key Concepts

1. a. Review What is probability?

b. Use Models How are Punnett squares used to predict the outcomes of genetic crosses?

2. a. Review What is independent assortment?

b. Calculate An F_1 plant that is homozygous for shortness is crossed with a heterozygous F_1 plant. What is the probability that a seed from the cross will produce a tall plant? Use a Punnett square to explain your answer and to compare the probable genetic variations in the F_2 plants. MATH

3. a. Review How did Gregor Mendel contribute to our understanding of inherited traits?

b. Apply Concepts Why is the fruit fly an ideal organism for genetic research?

Apply the Big idea

Information and Heredity

4. Suppose you are an avid gardener. One day, you come across a plant with beautiful lavender flowers. Knowing that the plant is self-pollinating, you harvest its seeds and plant them. Of the 106 plants that grow from these seeds, 31 have white flowers. Using a Punnett square, draw conclusions about the nature of the allele for lavender flowers.

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11.3 Other Patterns of Inheritance

THINK ABOUT IT Mendel's principles offer a tidy set of rules with which to predict various patterns of inheritance. Unfortunately, biology is not a tidy science. There are exceptions to every rule, and exceptions to the exceptions. What happens if one allele is not completely dominant over another? What if a gene has several alleles?

Key Questions

What are some exceptions to Mendel's principles?

Does the environment have a role in how genes determine traits?

Vocabulary

incomplete dominance • codominance • multiple allele • polygenic trait

Taking Notes

Outline Make an outline using the green and blue headings. As you read, write bulleted notes below each heading to summarize its topic.

Beyond Dominant and Recessive Alleles

What are some exceptions to Mendel's principles?

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 inheritance. 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. Mendel's principles alone cannot predict traits that are controlled by multiple alleles or multiple genes.

Incomplete Dominance A cross between two four o'clock (*Mirabilis*) plants shows a common exception to Mendel's principles. **Some alleles are neither dominant nor recessive.** As shown in **Figure 11–12,** the F_1 generation produced by a cross between red-flowered (*RR*) and white-flowered (*WW*) *Mirabilis* plants consists of pink-colored flowers (*RW*). 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 lies somewhere between the two homozygous phenotypes.

Codominance A similar situation arises from **codominance,** in which the phenotypes produced by both alleles are clearly expressed. 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 "erminette," 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 in chickens. Many human genes, including one for a protein that controls cholesterol levels in the blood, show codominance, too. People with the heterozygous form of this gene produce two different forms of the protein, each with a different effect on cholesterol levels.

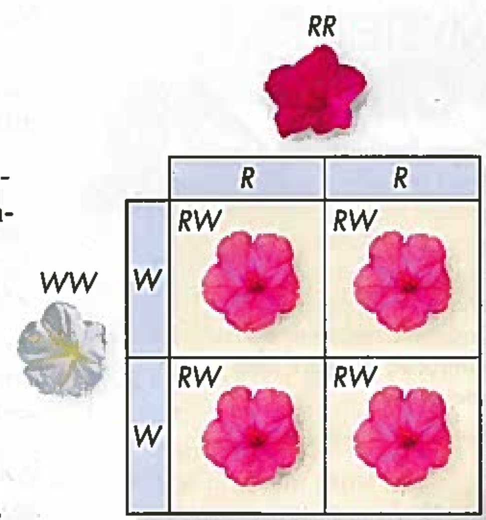


FIGURE 11–12 Incomplete Dominance In four o'clock plants, the alleles for red and white flowers show incomplete dominance. Heterozygous (*RW*) plants have pink flowers—a mix of red and white coloring.

Analyzing Data

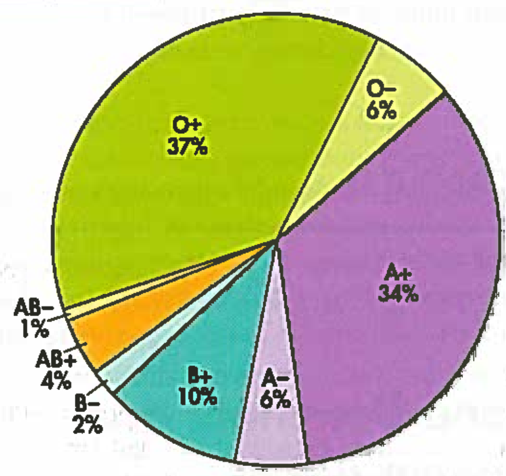
Human Blood Types

Red blood cells carry antigens, molecules that can trigger an immune reaction, on their surfaces. Human blood type A carries an A antigen, type B has a B antigen, type AB has both antigens, and type O carries neither antigen. The gene for these antigens has three alleles; A, B, and O.

For a transfusion to succeed, it must not introduce a new antigen into the body of the recipient. So, a person with type A blood may receive type O, but not vice versa.

Another gene controls a second type of antigen, known as Rh factor. Rh^+ individuals carry this antigen, while Rh^- ones don't. This chart of the U.S. population shows the percentage of each blood type.

Blood Groups in the U.S. Population



1. **Interpret Graphs** Which blood type makes up the greatest percentage of the U.S. population?
2. **Calculate** What percentage of the total U.S. population has a positive Rh factor? What percentage has a negative Rh factor?
3. **Infer** Which blood type can be used for transfusion into the largest percentage of individuals? Which type has the smallest percentage of possible donors available?
4. **Predict** Could a person with O^+ blood have two parents with O^- blood? Could that person have a daughter with AB^+ blood? Explain your answers.

MYSTERY CLUE

Green feathers don't actually contain green pigments. Rather, they contain a mixture of blue and yellow pigments. Could feather color be controlled by more than one gene?

Multiple Alleles So far, our examples have described genes for which there are only two alleles, such as *a* and *A*. In nature, such genes are the exception rather than the rule. **Many genes exist in several different forms and are therefore said to have multiple alleles.** A gene with more than two alleles is said to have **multiple alleles.** An individual, of course, usually has only two copies of each gene, but many different alleles are often found within 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 coat colors. 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.** *Polygenic* means "many genes." For example, at least three genes are involved in making the reddish-brown pigment in the eyes of fruit flies. Polygenic traits often show a wide range of phenotypes. The variety of skin color in humans comes about partly because more than four different genes probably control this trait.

In Your Notebook *In your own words, describe multiple alleles and polygenic traits. How are they similar? How are they different?*

Genes and the Environment

Does the environment have a role in how genes determine traits?

The characteristics of any organism—whether plant, fruit fly, or human being—are not determined solely by the genes that organism inherits. Genes provide a plan for development, but how that plan unfolds also depends on the environment. In other words, the phenotype of an organism is only partly determined by its genotype.

Consider the western white butterfly, *Pontia occidentalis*, shown in **Figure 11–13.** It is found throughout western North America. Butterfly enthusiasts had noted for years that western whites hatching in the summer (right) had different color patterns on their wings than those hatching in the spring (left). Scientific studies showed the reason—butterflies hatching in the shorter days of springtime had greater levels of pigment in their wings, making their markings appear darker than those hatching in the longer days of summer. In other words, the environment in which the butterflies develop influences the expression of their genes for wing coloration. **Environmental conditions can affect gene expression and influence genetically determined traits.** An individual's actual phenotype is determined by its environment as well as its genes.

In the case of the western white butterfly, these changes in wing pigmentation are particularly important. In order to fly effectively, the body temperature of the butterfly must be 28°C–40°C (about 84°F–104°F). Since the spring months are cooler in the west, greater pigmentation helps them reach the body temperature needed for flight. Similarly, in the hot summer months, less pigmentation enables the moths to avoid overheating.

Environmental Temperature and Butterfly Needs		
Temp. Needed for Flight	**Average Spring Temp.**	**Average Summer Temp.**
28–40°C	26.5°C	34.8°C

FIGURE 11–13 Temperature and Wing Color Western white butterflies that hatch in the spring have darker wing patterns than those that hatch in summer. The dark wing color helps increase their body heat. This trait is important because the butterflies need to reach a certain temperature in order to fly. **Calculate** ***What is the difference between the minimum temperature these butterflies need to fly and the average spring temperature? Would the same calculation apply to butterflies developing in the summer?*** MATH

11.3 Assessment

Review Key Concepts

1. a. **Review** What does *incomplete dominance* mean? Give an example.
   b. **Design an Experiment** Design an experiment to determine whether the pink flowers of petunia plants result from incomplete dominance.
2. a. **Review** Describe two inheritance patterns besides simple dominance.
   b. **Compare and Contrast** What is the difference between incomplete dominance and codominance?

PRACTICE PROBLEM

3. 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.

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11.4 Meiosis

THINK ABOUT IT As geneticists in the early 1900s applied Mendel's principles, they wondered where genes might be located. They expected genes to be carried on structures inside the cell, but *which* structures? What cellular processes could account for segregation and independent assortment, as Mendel had described?

Key Questions

How many sets of genes do multicellular organisms inherit?

What events occur during each phase of meiosis?

How is meiosis different from mitosis?

How can two alleles from different genes be inherited together?

Vocabulary

homologous • diploid • haploid • meiosis • tetrad • crossing-over • zygote

Taking Notes

Compare/Contrast Table Before you read, make a compare/contrast table to show the differences between mitosis and meiosis. As you read, complete the table.

Chromosome Number

How many sets of genes do multicellular organisms inherit?

To hold true, Mendel's principles require at least two events to occur. First, an organism with two parents must inherit a single copy of every gene from each parent. Second, when that organism produces gametes, those two sets of genes must be separated so that each gamete contains just one set of genes. As it turns out, chromosomes—those strands of DNA and protein inside the cell nucleus—are the carriers of genes. The genes are located in specific positions on chromosomes.

Diploid Cells Consider the fruit fly that Morgan used, *Drosophila*. A body cell in an adult fruit fly has eight chromosomes, as shown in **Figure 11–14.** Four of the chromosomes come from its male parent, and four come from its female parent. These two sets of chromosomes are **homologous** (hoh MAHL uh gus), meaning that each of the four chromosomes 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,** meaning "two sets." **The diploid cells of most adult organisms contain two complete sets of inherited chromosomes and two complete sets of genes.** The diploid number of chromosomes is sometimes represented by the symbol 2N. Thus, for *Drosophila,* the diploid number is 8, which can be written as $2N = 8$, where N represents the single set of chromosomes found in a sperm or egg cell.

Haploid Cells Some cells contain only a single set of chromosomes, and therefore a single set of genes. Such cells are **haploid,** meaning "one set." The gametes of sexually reproducing organisms, including fruit flies and peas, are haploid. For *Drosophila* gametes, the haploid number is 4, which can be written as $N = 4$.

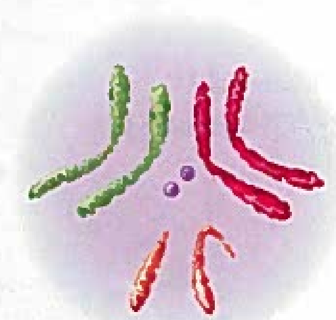
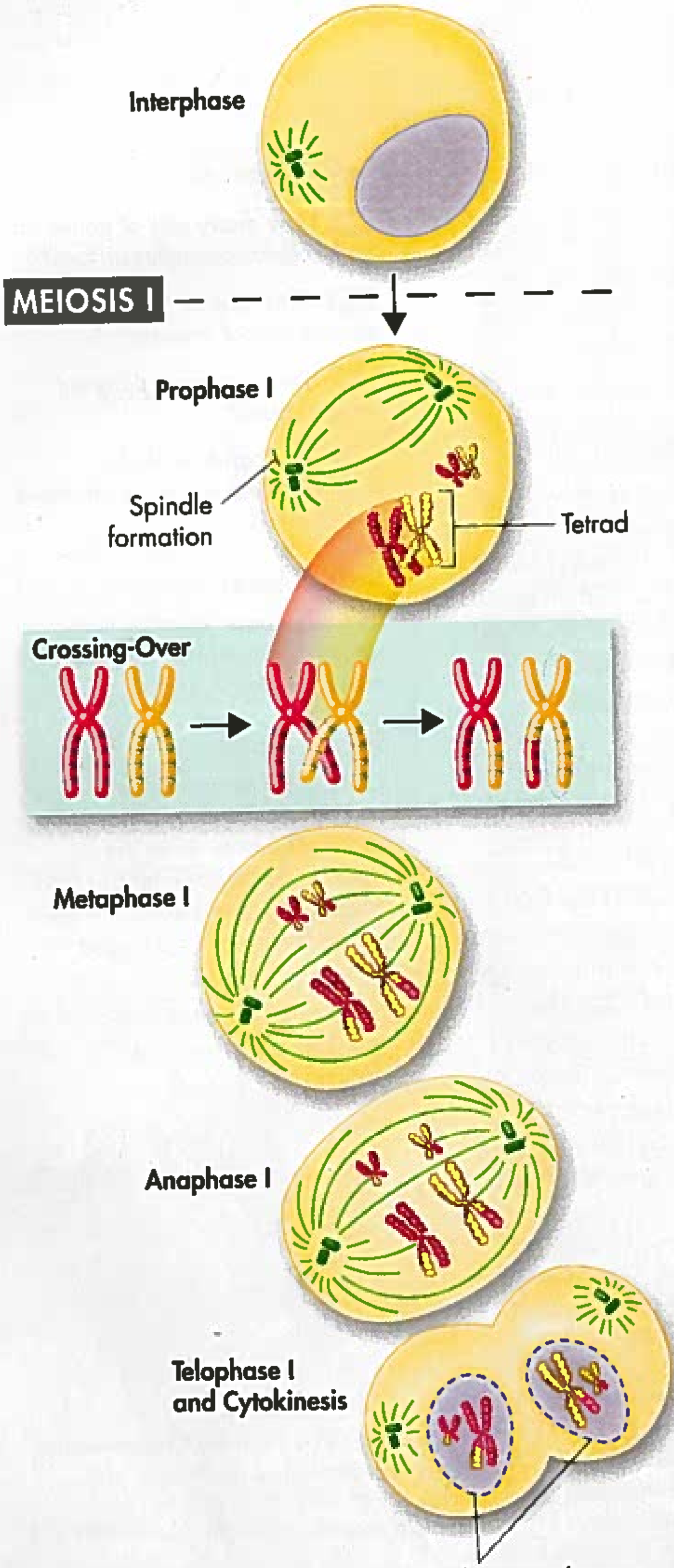


FIGURE 11–14 Fruit Fly Chromosomes These chromosomes are from a fruit fly. Each of the fruit fly's body cells is diploid, containing eight chromosomes.

FIGURE 11–15 Meiosis I During meiosis I, a diploid cell undergoes a series of events that results in the production of two daughter cells. Neither daughter cell has the same sets of chromosomes that the original diploid cell had. **Interpret Graphics** ***How does crossing-over affect the alleles on a chromosome?***



Phases of Meiosis

What events occur during each 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 in which the number of chromosomes per cell is cut in half through the separation of homologous chromosomes in a diploid cell. Meiosis usually involves two distinct divisions, called meiosis I and meiosis II. By the end of meiosis II, the diploid cell becomes four haploid cells. Let's see how meiosis takes place in a cell that has a diploid number of 4 (2N = 4).

Meiosis I Just prior to meiosis I, the cell undergoes a round of chromosome replication during interphase. As in mitosis, which was discussed in Chapter 10, each replicated chromosome consists of two identical chromatids joined at the center. Follow the sequence in **Figure 11–15** as you read about meiosis I.

▶ ***Prophase I*** After interphase I, the cell begins to divide, and the chromosomes pair up. **In prophase I of meiosis, each replicated chromosome pairs with its corresponding homologous chromosome.** This pairing forms a structure called a **tetrad,** which contains four chromatids. As the homologous chromosomes form tetrads, they undergo a process called **crossing-over.** First, the chromatids of the homologous chromosomes cross over one another. Then, the crossed sections of the chromatids—which contain alleles—are exchanged. Crossing-over therefore produces new combinations of alleles in the cell.

▶ ***Metaphase I and Anaphase I*** As prophase I ends, a spindle forms and attaches to each tetrad. **During metaphase I of meiosis, paired homologous chromosomes line up across the center of the cell.** As the cell moves into anaphase I, the homologous pairs of chromosomes separate. **During anaphase I, spindle fibers pull each homologous chromosome pair toward opposite ends of the cell.**

▶ ***Telophase I and Cytokinesis*** When anaphase I is complete, the separated chromosomes cluster at opposite ends of the cell. **The next phase is telophase I, in which a nuclear membrane forms around each cluster of chromosomes. Cytokinesis follows telophase I, forming two new cells.**

Meiosis I results in two cells, called daughter cells. Each cell has four chromatids, as it would after mitosis. However, because each pair of homologous chromosomes was separated, neither daughter cell 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 now enter a second meiotic division. Unlike the first division, neither cell goes through a round of chromosome replication before entering meiosis II.

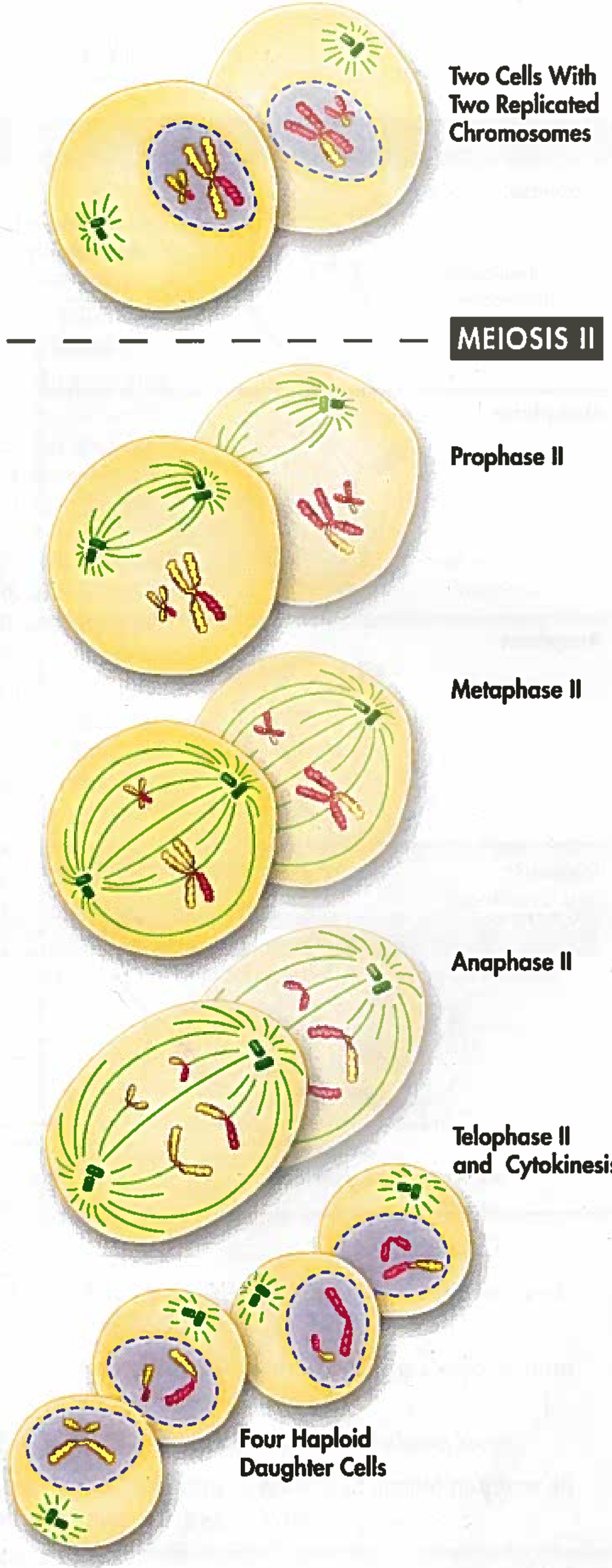
▶ ***Prophase II*** **As the cells enter prophase II, their chromosomes—each consisting of two chromatids—become visible.** The chromosomes do not pair to form tetrads, because the homologous pairs were already separated during meiosis I.

▶ ***Metaphase II, Anaphase II, Telophase II, and Cytokinesis*** During metaphase of meiosis II, chromosomes line up in the center of each cell. As the cell enters anaphase, the paired chromatids separate. **The final four phases of meiosis II are similar to those in meiosis I. However, the result is four haploid daughter cells.** In the example shown here, each of the four daughter cells produced in meiosis II receive two chromatids. These four daughter cells now contain the haploid number (N)—just two chromosomes each.

Gametes to Zygotes The haploid cells produced by meiosis II are the gametes that are so important to heredity. In male animals, these gametes 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. The female gamete is called an egg in animals and an egg cell in some plants. Fertilization generates new combinations of alleles in a **zygote** (ZY goht). The zygote undergoes cell division by mitosis and eventually forms a new organism.

In Your Notebook *Describe the difference between meiosis I and meiosis II. How are the end results different?*

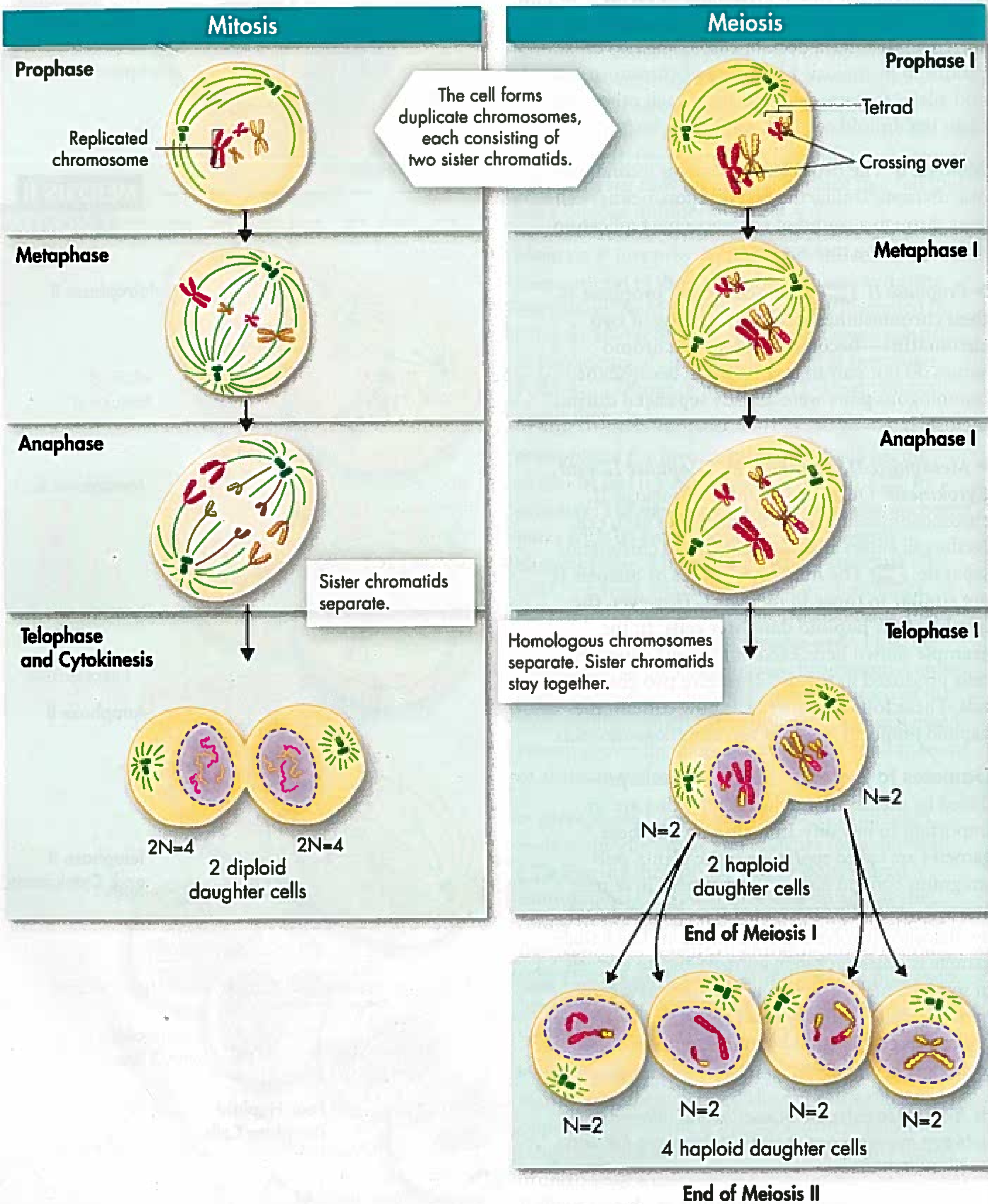
FIGURE 11–16 Meiosis II The second meiotic division, called meiosis II, produces four haploid daughter cells.



VISUAL SUMMARY

COMPARING MITOSIS AND MEIOSIS

FIGURE 11–17 Mitosis and meiosis both ensure that cells inherit genetic information. Both processes begin after interphase, when chromosome replication occurs. However, the two processes differ in the separation of chromosomes, the number of cells produced, and the number of chromosomes each cell contains.



Comparing Meiosis and Mitosis

How is meiosis different from mitosis?

The words *mitosis* and *meiosis* may sound similar, but the two processes are very different, as you can see in **Figure 11–17.** Mitosis is a form of asexual reproduction, whereas meiosis is an early step in sexual reproduction. There are three other ways in which these two processes differ.

Replication and Separation of Genetic Material Mitosis and meiosis are both preceded by a complete copying, or replication, of the genetic material of chromosomes. However, the next steps differ dramatically. **In mitosis, when the two sets of genetic material separate, each daughter cell receives one complete set of chromosomes. In meiosis, homologous chromosomes line up and then move to separate daughter cells.** As a result, the two alleles for each gene are segregated, and end up in different cells. The sorting and recombination of genes in meiosis result in a greater variety of possible gene combinations than could result from mitosis.

Changes in Chromosome Number **Mitosis does not normally change the chromosome number of the original cell. This is not the case for meiosis, which reduces the chromosome number by half.** A diploid cell that enters mitosis with eight chromosomes will divide to produce two diploid daughter cells, each of which also has eight chromosomes. On the other hand, a diploid cell that enters meiosis with eight chromosomes will pass through two meiotic divisions to produce four haploid gamete cells, each with only four chromosomes.

Analyzing Data

Calculating Haploid and Diploid Numbers

Haploid and diploid numbers are designated by the algebraic notations N and 2N, respectively. Either number can be calculated when the other is known. For example, if the haploid number (N) is 3, the diploid number (2N) is 2 × 3, or 6. If the diploid number (2N) is 12, the haploid number (N) is 12/2, or 6.

The table shows haploid or diploid numbers of a variety of organisms. Copy the table into your notebook and complete it. Then, use the table to answer the questions that follow.

Trait Survey

Organism	Haploid Number	Diploid Number
Amoeba	N=25	
Chimpanzee	N=24	
Earthworm	N=18	
Fern		2N=1010
Hamster	N=22	
Honeybee		2N=56
Human		2N=46
Onion		2N=16

1. **Calculate** What are the haploid numbers for the fern and onion plants? MATH
2. **Interpret Data** In the table, which organisms' diploid numbers are closest to that of a human?
3. **Apply Concepts** Why is a diploid number always even?
4. **Evaluate** Which organism's haploid and diploid numbers do you find the most surprising? Why?

Number of Cell Divisions Mitosis is a single cell division, resulting in the production of two identical daughter cells. On the other hand, meiosis requires two rounds of cell division, and, in most organisms, produces a total of four daughter cells. **Mitosis results in the production of two genetically identical diploid cells, whereas meiosis produces four genetically different haploid cells.**

Gene Linkage and Gene Maps

How can two alleles from different genes be inherited together?

If you think carefully about Mendel's principle of independent assortment in relation to meiosis, one question might bother you. Genes that are located on different chromosomes assort independently, but what about genes that are located on the same chromosome? Wouldn't they generally be inherited together?

Gene Linkage The answer to this question, as Thomas Hunt Morgan first realized in 1910, is yes. Morgan's research on fruit flies led him to the principle of gene 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, Morgan used a fly with reddish-orange eyes and miniature wings in a series of test crosses. His results showed that the genes for those two traits were almost always inherited together. Only rarely did the genes separate 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. As it turns out, *Drosophila* has four linkage groups and four pairs of chromosomes.

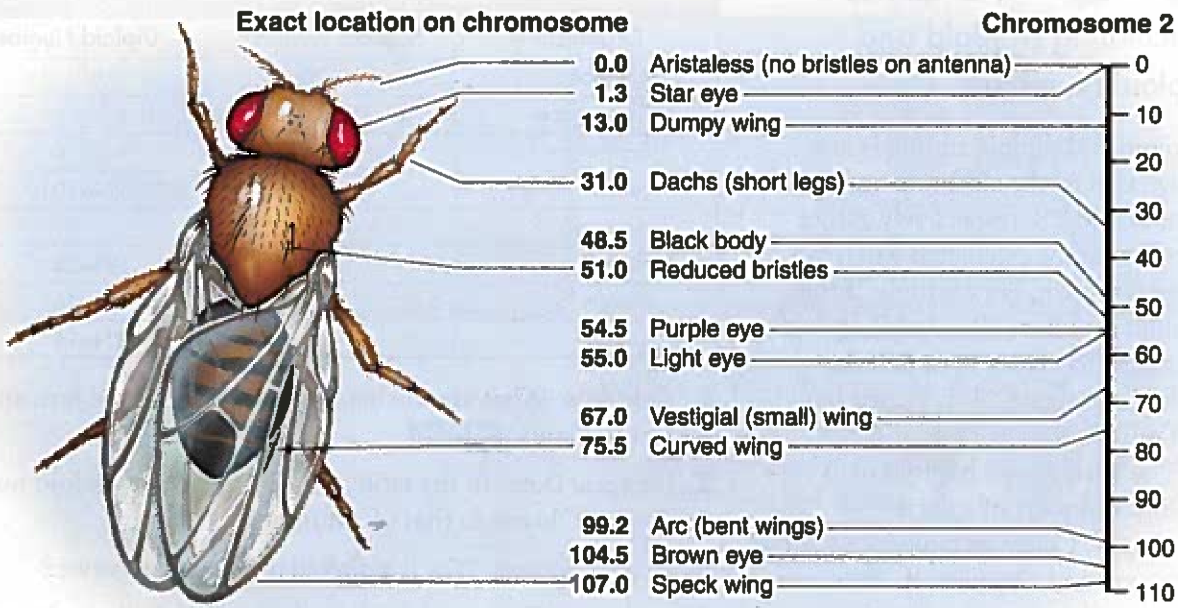


FIGURE 11–18 Gene Map This gene map shows the location of a variety of genes on chromosome 2 of the fruit fly. The genes are named after the problems that abnormal alleles cause, *not* after the normal structures. **Interpret Graphics** ***Where on the chromosome is the "purple eye" gene located?***

Morgan's findings 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. **Alleles of different genes tend to be inherited together from one generation to the next when those genes are located on the same chromosome.**

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

Gene Mapping In 1911, a Columbia University student was working part time in Morgan's lab. This student, Alfred Sturtevant, wondered if the frequency of crossing-over between genes during meiosis might be a clue to the genes' locations. Sturtevant reasoned that the farther apart two genes were on a chromosome, the more likely it would be that crossing-over would occur between them. If two genes are close together, then crossovers between them should be rare. If two genes are far apart, then crossovers between them should be more common. By this reasoning, he could use the frequency of crossing-over between genes to determine their distances from each other.

Sturtevant gathered up several notebooks of lab data and took them back to his room. The next morning, he presented Morgan with a gene map showing the relative locations of each known gene on one of the *Drosophila* chromosomes. Sturtevant's method has been used to construct gene maps, like the one in **Figure 11–18**, ever since this discovery.

MYSTERY CLUE

White is the least common color found in parakeets. What does this fact suggest about the genotypes of both green parents?

11.4 Assessment

Review Key Concepts

1. a. **Review** Describe the main results of meiosis.
   b. **Calculate** In human cells, 2N = 46. How many chromosomes would you expect to find in a sperm cell? How many would you expect to find in an egg cell? MATH
2. a. **Review** Write a summary of each phase of meiosis.
   b. **Use Analogies** Compare the chromosomes of a diploid cell to a collection of shoes in a closet. How are they similar? What would make the shoe collection comparable to the chromosomes of a haploid cell?
3. a. **Review** What are the principle differences between mitosis and meiosis?
   b. **Apply Concepts** Is there any difference between sister chromatids and homologous pairs of chromosomes? Explain.
4. a. **Review** How does the principle of independent assortment apply to chromosomes?
   b. **Infer** If two genes are on the same chromosome but usually assort independently, what does that tell you about how close together they are?

Apply the Big idea

Information and Heredity

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

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