11 OBSERVING PATTERNS IN INHERITED TRAITS

In Pursuit of a Better Rose

Researchers at Texas A&M and Clemson universities are breathing new life into *rose breeding*. People have been practicing this form of artificial selection for thousands of years. Starting with small, simple, five-petaled wild roses, they patiently cross-bred plants and in time were rewarded with a profusion of petals, fabulous fragrances, exquisite colors, and other compelling traits. Today, rose fanciers in thirty-six countries all over the world claim membership in the World Federation of Rose Societies. In any given year, people from all walks of life buy billions of dollars' worth of rosebuds and blooms. On Valentine's Day in the United States alone, 110 million cut roses are offered as symbols of love and romance. Roses are now big business.

Fossils in Colorado tell us that roses have been around for at least 40 million years. When rose breeding started, the ancestral stock had a diploid chromosome number two sets of seven chromosomes. A great variety of cultivars now have four, seven, fourteen, even twenty-one sets of chromosomes! Within those chromosomes are genes that specify the size, number, and shape of petals and thorns, genes that deal with floral scents and colors, and genes that dictate whether plants bloom once or all year long. Other genes influence resistance to diseases and pests.

Unlike many wild roses, most of the cultivated varieties are susceptible to black spot, powdery mildew, and other

diseases (Figure 11.1). The fungus that causes black spot is notably active in rainy, humid regions; the one that causes powdery mildew thrives in greenhouses. Fungicides work against pathogenic fungi, but they are costly, and many kinds also kill beneficial microorganisms.

Possibly a safer approach would be to cross-breed a wild plant known to have disease resistance with a plant known to be susceptible. However, traditional breeding practices are hit-or-miss, and they are tedious. Breeders have to wait for plants to form seeds, then plant the seeds, then observe whether any or all plants of the new generation, and the next, and the one after that show disease resistance.

Enter the new researchers. They are working to make genetic maps for all seven of the rose chromosomes. Just as road maps pinpoint cities along a highway, genetic maps can pinpoint where genes that influence specific traits are located along the length of chromosomes. By pinpointing a gene that influences a desired trait, breeders will be able to speed up their artificial selection practices.

For example, remember those radioisotopes described in Chapter 2? Researchers use them to make a DNA probe, a bit of radioactive DNA. They use it to test offspring from a cross for a specific DNA region—say, one near a gene that affects disease resistance. If the probe does not bind to the DNA of offspring, a breeder can assume the new plant has



Figure 11.1 One representative of a long history of artificial selection. Like most of the modern cultivars and unlike many wild roses, this one is vulnerable to black spot, a disease that results in the telltale destruction of leaves. Researchers are working to develop faster, more efficient ways to breed roses that have disease resistance and other desired traits.



IMPACTS, ISSUES



not inherited the resistance gene and can try a new cross. Such *marker-assisted selection* is useful when several genes control a trait, as for disease resistance. A plant lineage that inherits all the genes may be the least vulnerable to attack.

In time, the maps being pieced together at Texas A&M, Clemson, and elsewhere will become consolidated into a permanent genetic map for roses. Its information will be retrieved for breeding programs. It also will be put to use for actual transfers of desirable genes into roses by way of biotechnology and genetic engineering. But these are cutting-edge topics that will not make much sense without in-depth knowledge of the structure and function of DNA, genes, and their protein products. We reserve them for later chapters in this unit. For now, start with something you already know about—the chromosomes and alleles introduced in the preceding chapter. This will be enough for you to follow the classical breeding practices that gave us our first glimpses of the principles of inheritance.



WHERE MODERN GENETICS STARTED

Gregor Mendel gathered the first experimental evidence of the genetic basis of inheritance: Each gene has a specific location on a chromosome. Organisms that have a diploid chromosome number have *pairs* of genes, at equivalent locations on pairs of homologous chromosomes. Alleles that are nonidentical may affect a trait differently. One allele is often dominant, in that its effect on a trait masks the effect of a recessive allele paired with it. Section 11.1

INSIGHTS FROM MONOHYBRID EXPERIMENTS

Some experiments yielded evidence of gene segregation: When one chromosome is separated from its homologous partner during meiosis, their pairs of alleles also separate and end up in different gametes. Section 11.2

INSIGHTS FROM DIHYBRID EXPERIMENTS

Other experiments yielded evidence of independent assortment: During meiosis, each pair of homologous chromosomes is sorted out for distribution into one gamete or another independently of how all of the other pairs of homologous chromosomes are assorted. Section 11.3

VARIATIONS IN GENE EXPRESSION

Not all traits have clearly dominant or recessive forms. One allele of a pair may be fully or partially dominant over its partner or codominant with it. Two or more gene pairs often influence the same trait, and some single genes influence many traits. The environment introduces more variation in gene expression. Sections 11.4–11.7

How Would You Vote?

The federal government helps support some agricultural extension programs that offer homeowners advice on gardens and ornamental plants. Do you consider this to be an appropriate use of government resources? See BiologyNow for details, then vote online.



Before starting this chapter, review the definitions of genes, alleles, and diploid versus haploid chromosome numbers (Sections 10.1 and 10.2). As you read, you may wish to refer to the earlier introduction to natural selection (1.4) and to the visual road map for the stages of meiosis (10.3). You will be considering experimental evidence of two major topics that were introduced earlier—the effects that crossing over and metaphase I alignments have on inheritance (10.4).



.1 Mendel, Pea Plants, and Inheritance Patterns

LINKS TO SECTIONS 1.4, 10.1 We turn now to recurring inheritance patterns among humans and other sexually reproducing species. You already know meiosis halves the parental chromosome number, which is restored at fertilization. Here the story picks up with some observable outcomes of these events.

More than a century ago, people wondered about the basis of inheritance. Most had an idea that two parents contribute hereditary material to offspring, but few even suspected that it is organized in units, or genes.



Figure 11.3 *Animated!* Garden pea plant (*Pisum sativum*), which can self-fertilize or cross-fertilize. Experimenters can control the transfer of its hereditary material from one flower to another.

Rather, according to the prevailing view, hereditary material was fluid, with the fluids from both parents blending at fertilization like milk into coffee.

The idea of "blending inheritance" failed to explain the obvious. For example, many children who differ in eye color or hair color have the same two parents. If parental fluids blended, then the eye or hair color of children should be a blend of the parental colors. If neither parent had freckles, freckled children would never pop up. A white mare bred with a black stallion should consistently give birth to gray offspring, but as horse breeders knew, this was not always the case. Blending inheritance could scarcely explain much of the obvious variation in traits that people could see with their own eyes.

Even Charles Darwin accepted the blending notion until he and his cousin conducted experiments that disproved it. According to Darwin's theory of natural selection, individuals of a population show variation in traits. Over the generations, variations that help an individual survive and reproduce show up among more and more offspring, and less helpful variations become less frequent and might even disappear. Thus blending inheritance *seemed* to support the theory of natural selection. As it turned out, the idea of discrete units of information—genes—explain it better.

Even before Darwin presented his theory, someone was gathering evidence that eventually would help support it. A monk, Gregor Mendel (Figure 11.2), had already guessed that sperm and eggs carry distinct units of information about heritable traits. After he analyzed specific traits of pea plants, one generation after another, he found indirect but *observable* evidence of how parents transmit genes to offspring.

MENDEL'S EXPERIMENTAL APPROACH

Mendel spent most of his adult life in Brno, a city near Vienna that is now part of the Czech Republic. Yet he was not a man of narrow interests who accidentally stumbled onto dazzling principles.

Mendel's monastery was close to European capitals that were centers of scientific inquiry. Having been raised on a farm, he was keenly aware of agricultural principles and their applications. He kept abreast of literature on breeding experiments. He belonged to an agricultural society and won awards for developing improved varieties of vegetables and fruits. Shortly after entering the monastery, Mendel took courses in mathematics, physics, and botany at the University of Vienna. Few scholars of his time showed interest in both plant breeding *and* mathematics.

- A pair of homologous chromosomes, each in the unduplicated state (most often, one from a male parent and its partner from a female parent).
- b A <u>gene locus</u> (plural, loci), the location for a specific gene on a chromosome. <u>Alleles</u> are at corresponding loci on a pair of homologous chromosomes.
- **c** A pair of alleles may be identical or nonidentical. They are represented in the text by letters such as *D* or *d*.
- d Three *pairs of genes* (at three loci on this pair of homologous chromosomes); same thing as three pairs of alleles.

Figure 11.4 *Animated!* A few genetic terms. Garden peas and other species with a diploid chromosome number have pairs of genes, on pairs of homologous chromosomes. Most genes come in slightly different molecular forms called alleles. Different alleles specify different versions of the same trait. An allele at any given location on a chromosome may or may not be identical to its partner on the homologous chromosome.

Shortly after his university training, Mendel started to study *Pisum sativum*, the garden pea plant (Figure 11.3). This plant is self-fertilizing. Its flowers produce both male and female gametes—call them sperm and eggs—that can come together and give rise to a new plant. One lineage of pea plants can "breed true" for certain traits. This means that successive generations will be like parents in one or more traits, as when all offspring grown from seeds of self-fertilized, whiteflowered parent plants also have white flowers.

Pea plants also cross-fertilize when plant breeders transfer pollen from one plant to the flower of another plant. As Mendel knew, breeders open a floral bud of a plant that bred true for white flowers or some other trait and snip out its stamens. (Pollen grains, in which sperm develop, start forming in stamens.) The buds can be brushed with pollen from a plant that bred true for a *different* version of the trait—say, purple flowers.

As Mendel hypothesized, such clearly observable differences might help him track a given trait through many generations. If there were patterns to the trait's inheritance, *then those patterns might tell him something about heredity itself*.

TERMS USED IN MODERN GENETICS

In Mendel's time, no one knew about genes, meiosis, or chromosomes. As we follow his thinking, we will clarify the picture by substituting some modern terms used in inheritance studies, as stated here and in Figure 11.4:

1. **Genes** are units of information on heritable traits, which parents transmit to offspring. Each gene has a specific location (locus) in chromosomal DNA.

2. Cells with a **diploid** chromosome number (2*n*) have pairs of genes, on pairs of homologous chromosomes.

3. **Mutation** alters a gene's molecular structure and its message about a trait. It may cause a trait to change, as when a gene for flower color specifies yellow and a mutant form of the gene specifies white. All molecular forms of the same gene are known as **alleles**.

4. When offspring inherit a pair of *identical* alleles for a trait generation after generation, they typically are a true-breeding lineage. Offspring of a cross between two individuals that breed true for different forms of a trait are **hybrids**; each one has inherited *nonidentical* alleles for the trait.

5. A pair of identical alleles on a pair of homologous chromosomes is a *homozygous* condition. A pairing of nonidentical alleles is a *heterozygous* condition.

6. An allele is *dominant* when its effect on a trait masks the effect of any *recessive* allele paired with it. Capital letters signify dominant alleles, and lowercase letters signify recessive ones. *A* and *a* are examples.

7. Pulling this all together, a **homozygous dominant** individual has a pair of dominant alleles (*AA*) for the trait under study. A **homozygous recessive** individual has a pair of recessive alleles (*aa*), and a **heterozygous** individual has a pair of nonidentical alleles (*Aa*).

8. Two terms help keep the distinction clear between genes and the traits they specify. *Genotype* refers to the particular alleles that an individual carries. *Phenotype* refers to an individual's observable traits.

9. P stands for true-breeding parents, F_1 for the firstgeneration offspring, and F_2 for the second-generation offspring of self-fertilized or intercrossed F_1 individuals.

Mendel hypothesized that tracking clearly observable differences in forms of a given trait might reveal patterns of inheritance. He recognized patterns of dominance and recessiveness in certain traits, which later were connected with pairs of alleles on pairs of homologous chromosomes.



11.2 Mendel's Theory of Segregation

Mendel used monohybrid experiments to test a hypothesis: Pea plants inherit two "units" of information (genes) for a trait, one from each parent.

In **monohybrid experiments**, two homozygous parents differ in a trait that is governed by alleles of one gene. They are crossed to produce F_1 offspring that are all heterozygous ($AA \times aa - Aa$). Next, depending on the species, F_1 individuals are allowed to self-fertilize or mate in order to produce an F_2 generation.

MONOHYBRID EXPERIMENT PREDICTIONS

Mendel tracked seven traits for two generations. In one set of experiments, he crossed plants that bred true for purple *or* white flowers. All F_1 offspring had purple flowers, but in the next generation, some F_2 offspring had white flowers! So what was going on? Pea plants have pairs of homologous chromosomes. Assume one

plant is homozygous dominant (*AA*) and another is homozygous recessive (*aa*) at the locus that governs flower color. Following meiosis, each sperm or egg that forms has only one of these alleles (Figure 11.5). Therefore, when a sperm fertilizes an egg, only one outcome is possible: A + a - Aa.

With his background in mathematics, Mendel knew about sampling error (Figure 1.12). He crossed seventy plants. He also counted and recorded the number of dominant and recessive forms of traits in thousands of offspring. On average, three of every four F_2 plants were dominant, and one was recessive (Figure 11.6).

The ratio hinted that fertilization is a chance event having a number of possible outcomes. Mendel knew about probability—which applies to chance events and thus could help him predict possible outcomes of genetic crosses. **Probability** means this: The chance that each outcome of an event will occur is proportional to the number of ways in which the outcome can be reached.





Figure 11.6 *Right,* from some of Mendel's monohybrid experiments with pea plants, counts of F_2 offspring having dominant or recessive hereditary "units" (alleles). On average, the 3:1 phenotypic ratio held for traits.



A **Punnett-square method**, explained and applied in Figure 11.7, shows the possibilities. If half of a plant's sperm or eggs are *a* and half are *A*, then we can expect four outcomes with each fertilization:

POSSIBLE EVENT	PROBABLE OUTCOME		
sperm A meets egg A	1/4 AA offspring		
sperm A meets egg a	1/4 Aa		
sperm a meets egg A	1/4 Aa		
sperm a meets egg a	1/4 <i>aa</i>		

Each F_2 plant has 3 chances in 4 of inheriting at least one dominant *A* allele (purple flowers). It has 1 chance in 4 of inheriting two recessive *a* alleles (white flowers). That is a probable phenotypic ratio of 3:1.

Mendel's observed ratios were not *exactly* 3:1. Yet he put aside the deviations. To understand why, flip a coin several times. As we all know, a coin is as likely to end up heads as tails. But often it ends up heads, or tails, several times in a row. If you flip the coin only a few times, the observed ratio might differ greatly from the predicted ratio of 1:1. Flip it many times, and you are more likely to approach the predicted ratio.

That is why Mendel used rules of probability and counted so many offspring. He minimized sampling error deviations in the observed results.

TESTCROSSES

Testcrosses supported Mendel's prediction. In such experimental tests, an organism shows dominance for a specified trait but its genotype may be unknown, so it is crossed with a homozygous recessive individual. The test results may reveal whether it is homozygous dominant or heterozygous.

For example, Mendel crossed F_1 purple-flowered plants with true-breeding white-flowered plants. If all were homozygous dominant, then F_2 offspring would all be purple flowered. If heterozygous, only about half would be. As it happened, about half of the testcross offspring had purple flowers (*Aa*) and half had white (*aa*). To predict outcomes of this testcross, construct a Punnett square.

The results from Mendel's monohybrid experiments became the basis of a theory of **segregation**, which we state here in modern terms:

MENDEL'S THEORY OF SEGREGATION Diploid cells have pairs of genes, on pairs of homologous chromosomes. The two genes of each pair are separated from each other during meiosis, so they end up in different gametes.



a Step-by-step construction of a Punnett square. Circles signify gametes. *A* and *a* signify a dominant and recessive allele, respectively. Possible genotypes among offspring are written in the squares.



b Cross between two plants that breed true for different forms of a trait, followed by a monohybrid cross between their F₁ offspring.

Figure 11.7 *Animated!* (a) Punnett-square method of predicting probable outcomes of genetic crosses. (b) Results from one of Mendel's monohybrid experiments. On average, the ratio of dominant-to-recessive that showed up among second-generation (F₂) plants was 3:1.

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11.3 Mendel's Theory of Independent Assortment

Mendel used dihybrid experiments to explain how two pairs of genes are sorted into gametes.

Dihybrid experiments start with a cross between truebreeding homozygous parents that differ in two traits governed by alleles of two genes. The F_1 offspring are all heterozygous for the alleles of both genes.

Let's duplicate one of Mendel's dihybrid crosses for flower color (alleles *A* or *a*) and for height (*B* or *b*):

True-breeding parents:	AABB X aabb
	A A
Gametes:	AB AB ab ab
	\mathbf{X}
F ₁ hybrid offspring:	AaBb

As Mendel would have predicted, F_1 offspring from this cross are all purple-flowered and tall (*AaBb*).

How will genes that control these traits assort in the F_1 plants? It depends in part on their chromosome locations. Suppose that the *Aa* alleles are on one pair of homologous chromosomes and the *Bb* alleles are on a different pair. Remember, chromosome pairs align midway between the spindle poles at metaphase I of meiosis (Figures 10.5 and 11.8). The pair bearing the *A* and *a* alleles will be tethered to opposite poles. The same will happen to the other chromosome pair that bears the *B* and *b* alleles. After meiosis, there can be four possible combinations of alleles in the sperm or eggs that form: 1/4 AB, 1/4 Ab, 1/4 aB, and 1/4 ab.

Given the alternative metaphase I alignments, many allelic combinations can result at fertilization. Simple



Figure 11.9 *Animated!* Results from one of Mendel's dihybrid experiments with the garden pea plant. The parent plants were true-breeding for different versions of two traits: flower color and plant height. *A* and *a* signify the dominant and recessive alleles for flower color. *B* and *b* signify dominant and recessive alleles for height. The Punnett square on the facing page shows all of the allelic combinations possible in the F₂ generation.

Adding up the corresponding F_2 phenotypes, we get:

9/16 or 9 purple-flowered, tall
3/16 or 3 purple-flowered, dwarf
3/16 or 3 white-flowered, tall
1/16 or 1 white-flowered, dwarf





multiplication (four sperm types \times four egg types) tells us that sixteen combinations of gametes are possible among F₂ offspring of a dihybrid cross (Figure 11.9).

Adding all possible phenotypes gives us a ratio of 9:3:3:1. We can expect to see 9/16 tall purple-flowered, 3/16 dwarf purple-flowered, 3/16 tall white-flowered, and 1/16 dwarf white-flowered F_2 plants. The results from the dihybrid experiment that Mendel reported were close to this ratio.

Mendel analyzed the numerical results from such experiments, but he did not know that seven pairs of homologous chromosomes carry a pea plant's "units" of inheritance. He could only hypothesize that two units for flower color were sorted out into gametes independently of the two units for height.

In time, his hypothesis became known as the theory of **independent assortment**. In modern terms, after meiosis ends, the genes on each pair of homologous chromosomes are sorted into gametes independently of how genes on other pairs of homologues are sorted out. Independent assortment and segregation give rise to genetic variation. In a monohybrid cross for one gene pair, three genotypes are possible: *AA*, *Aa*, and *aa*. We represent this as 3^n , where *n* is the number of gene pairs. The more pairs, the more combinations are possible. If, say, the parents differ in twenty gene pairs, the number approaches 3.5 billion!

In 1866 Mendel published his work. Apparently his article was read by few and understood by no one. In 1871 he became monastery abbot, and his pioneering experiments ended. He died in 1884, never to know that his experiments would be the starting point for modern genetics. Mendel's theory of segregation still stands for most genes in most organisms: the units of hereditary material (genes) do retain their identity all through meiosis. However, his theory of independent assortment requires qualification, because the alleles of gene pairs do not *always* assort independently into gametes, as Section 11.5 explains.

MENDEL'S THEORY OF INDEPENDENT ASSORTMENT As meiosis ends, genes on pairs of homologous chromosomes have been sorted out for distribution into one gamete or another, independently of gene pairs on other chromosomes.



Δ More Patterns Than Mendel Thought

LINKS TO SECTIONS 4.6, 6.6

Mendel happened to focus on traits that have clearly dominant and recessive forms. However, expression of genes for some traits is not as straightforward.



Figure 11.10 Animated! Possible allelic combinations that are the basis for ABO blood typing



homozygous parent Х

All F1 offspring heterozygous for flower color



Cross two of the F1 plants, and the F2 offspring will show three phenotypes in a 1:2:1 ratio:

Figure 11.11 Incomplete dominance in heterozygous (pink) snapdragons, in which an allele that affects red pigment is paired with a "white" allele.

CODOMINANCE IN ABO BLOOD TYPES

In codominance, a pair of nonidentical alleles affecting two phenotypes are both expressed at the same time in heterozygotes. For example, red blood cells have a type of glycolipid at the plasma membrane that helps give them their unique identity. The glycolipid comes in slightly different forms. An analytical method, ABO blood typing, reveals which form a person has.

An enzyme dictates the glycolipid's final structure. Three alleles for this enzyme are present in all human populations. Two, I^A and I^B , are codominant when paired. (These superscripts represent two dominant alleles for the gene.) The third allele, *i*, is recessive when paired with I^A or I^B . The occurrence of three or more alleles for a single gene locus among individuals of a population is called a **multiple allele system**.

Each of these glycolipid molecules was assembled in the endomembrane system (Section 4.6). First, an oligosaccharide chain was attached to a lipid, then a series of sugars was attached to the chain. But alleles I^A and I^B specify different forms of the enzyme that attaches the last sugar. The two attach different sugars, which gives the glycolipid a different identity: A or B.

If you have *IAIA* or *IAi*, your blood is type A. With $I^{B}I^{B}$ or $I^{B}i$, it is type B. With codominant alleles $I^{A}I^{B}$, it is AB; you have both versions of the sugar-attaching enzyme. If you are (ii), the glycolipid molecules never did get a final sugar on the side chain, so your blood type is not A or B. It is O. Figure 11.10 is a simple way to think about these combinations.

INCOMPLETE DOMINANCE

In *incomplete* dominance, one allele of a pair is not fully dominant over its partner, so the heterozygote's phenotype is somewhere between the two homozygotes. Cross true-breeding red and white snapdragons and their F₁ offspring will be pink-flowered. Cross two F₁ plants and you can expect to see red, white, and *pink* flowers in a particular ratio (Figure 11.11). Why? Red snapdragons have two alleles that let them make a lot of molecules of a red pigment. White snapdragons have two mutant alleles and are pigment-free. Pink snapdragons have a "red" allele and a "white" allele; these genotypes have not "blended." Heterozygotes make enough pigment to color flowers pink, not red.

Two interacting gene pairs also can give rise to a phenotype that neither produces by itself. In chickens, interactions among alleles at the R and P gene loci specify walnut, rose, pea, and single combs, as shown in Figure 11.12.

EPISTASIS

Traits also arise through **epistasis**: interactions among products of two or more gene pairs. Two alleles might mask expression of another gene's alleles, and some expected phenotypes might not appear at all.

As an example, several gene pairs govern whether a Labrador retriever has black, yellow, or brown fur (Figure 11.13). Its coat color depends on how enzymes and other products of alleles at more than one gene locus make a dark pigment, melanin, and deposit it in tissues. Allele *B* (black) is dominant to *b* (brown). At a different locus, allele *E* promotes melanin deposition but two recessive alleles (*ee*) reduce it. In this case, fur appears yellow regardless of alleles at the *B* locus.

SINGLE GENES WITH A WIDE REACH

Alleles at one locus on a chromosome may affect two or more traits in good or bad ways, an outcome called **pleiotropy**. Many genetic disorders, including cystic fibrosis, sickle-cell anemia, and Marfan syndrome, are examples. *Marfan syndrome* arises from an autosomal dominant mutation of the gene for fibrillin, a protein in the most abundant, widespread vertebrate tissues —connective tissues. Thin, loose or crosslinked strands of fibrillin passively recoil after being stretched, as by the beating heart.

Altered fibrillin weakens the connective tissues in 1 of 10,000 men and women and puts the heart, blood vessels, skin, lungs, and eyes at risk. One mutation disrupts the synthesis of fibrillin 1, its secretion from cells, and its tissue deposition. It alters the structure and function of smooth muscle cells inside the wall of the aorta, a big vessel carrying blood out of the heart. Immune cells infiltrate and multiply inside the wall's lining. Calcium deposits accumulate and inflame the wall. Elastic fibers split into fragments. The aorta wall, thinned and weakened, can rupture abruptly during strenuous exercise. Until recent advances in medicine, Marfan syndrome killed most affected people before their fifties. Flo Hyman was one of them (Figure 11.14).

An allele at a given gene locus may be fully dominant, incompletely dominant, or codominant with its partner on a homologous chromosome.

Some gene products may interact with each other and influence the same trait through epistasis.

A single gene's product may have pleiotropic effects, or positive or negative impact on two or more traits.







a black labrador b yellow labrador

c CHOCOLATE LABRADOR

Figure 11.13 Coat color among Labrador retrievers. The trait arises through epistatic interactions among alleles of two genes.



Figure 11.14 Flo Hyman, left, captain of the United States volleyball team that won an Olympic silver medal in 1984. Two years later, at a game in Japan, she slid to the floor and died. A dime-sized weak spot in the wall of her aorta had burst. We know at least two affected college basketball stars also died abruptly as a result of Marfan syndrome.



Impact of Crossing Over on Inheritance

LINKS TO SECTIONS 3.2, 10.3, 10.4 Crossing over between homologous chromosomes is one of the main pattern-busting events in inheritance.

We now know there are many genes on each type of autosome and sex chromosome. All the genes on one chromosome are called a linkage group. For instance, the fruit fly (Drosophila melanogaster) has four linkage groups, corresponding to its four pairs of homologous chromosomes. Indian corn (Zea mays) has ten linkage groups, corresponding to its ten pairs, and so on.

If genes on the same chromosome stayed together through meiosis, then there would be no surprising mixes of parental traits. You could expect parental phenotypes among, say, the F2 offspring of dihybrid experiments to show up in a predictable ratio. As early experiments with fruit flies showed, however, that ratio was often predictably different for linked genes. In one dihybrid experiment, 17 percent of the F₂ offspring inherited a new combination of alleles that did not occur in either of their parents.

Many genes on the same chromosome do not stay linked through meiosis, but some stay together more often than others. Why? They are closer together on the chromosome, and so they are separated less often by crossing over. The probability that crossing over will disrupt the linkage between any two genes is proportional to the distance between the two genes.

If genes A and B are twice as far apart as genes C and D on a chromosome, then we can expect crossing over to disrupt the linkage between genes A and B more frequently than between the other two genes:



Two genes are very closely linked when the distance between them is small. Their combinations of alleles nearly always end up in the same gamete. Linkage is more vulnerable to crossing over when the distance between two gene loci is greater (Figure 11.15). When two loci are far apart, crossing over is so frequent that the genes assort independently into gametes.

Human gene linkages were identified by tracking DNA inheritance in families over the generations. One thing is clear from such studies: Crossovers are not rare. For most eukaryotes, meiosis cannot even be completed properly until at least one crossover occurs between each pair of homologous chromosomes.

All of the genes at different locations along the length of a chromosome belong to the same linkage group. Crossing over between homologous chromosomes disrupts gene linkages and results in nonparental combinations

The farther apart two genes are on a chromosome, the greater will be the frequency of crossing over and genetic recombination between them.

of alleles in chromosomes.

AC



genotype, half have the other



ac

a Full linkage between two genes; no crossing over. Genes very close together along the length of the same chromosome typically stay together during gamete formation.

b Incomplete linkage; crossing over affected the outcome. Any two genes that are far apart along the length of a chromosome are more vulnerable to crossing over.

Figure 11.15 Animated! Examples of outcomes of crossing over between two gene loci: (a) full linkage and (b) incomplete linkage.

11.6 Genes and the Environment

The environment often contributes to variable gene expression among a population's individuals.

Possibly you have noticed a Himalayan rabbit's coat color. Like a Siamese cat, this mammal has dark hair in some parts of its body and lighter hair in others. The Himalayan rabbit is homozygous for the c^h allele of the gene specifying tyrosinase. Tyrosinase is one of the enzymes involved in melanin production. The c^h allele specifies a heat-sensitive form of this enzyme. This form is active only when the temperature around body cells is below 33°C, or 91°F.

When cells that give rise to this rabbit's hair grow under warmer conditions, they cannot make melanin, so hairs appear light. This happens in body regions that are massive enough to conserve a fair amount of metabolic heat. The ears and other slender extremities tend to lose metabolic heat faster, so they are cooler. Figure 11.16 shows one experiment that demonstrated how the environmental temperature can influence the production of melanin.

One classic experiment identified environmental effects on yarrow plants. These plants can grow from cuttings, so they are a useful experimental organism. Why? Cuttings from the same plant all have the same genotype, so experimenters can discount genes as a basis for differences that show up among them.

In this study, cuttings (clones) from each of several yarrow plants were grown at three elevations. The researchers periodically observed the growth of the plants in their habitats. They found that cuttings from the same parent plants grew differently at different altitudes. For example, cuttings from one plant grew tall at the lowest and the highest elevation, but a third cutting remained short at mid-elevation (Figure 11.17). Even though these plants were genetically identical, their phenotypes differed in different environments.

Similarly, plant a hydrangea in a garden and it may have pink flowers instead of the expected blue ones. Soil acidity affects the function of gene products that color hydrangea flowers.

What about humans? One of our genes codes for a transporter protein that moves serotonin across the plasma membrane of brain cells. This gene product has several effects, one of which is to counter anxiety and depression when traumatic events challenge us. For a long time, researchers have known that some people handle stress without getting too upset, while others spiral into a deep and lasting depression.

Mutation of the gene for the serotonin transporter compromises responses to stress. It is as if some of us are bicycling through life without an emotional helmet.



Figure 11.16 *Animated!* Observable effect of an environmental factor that alters gene expression. A Himalayan rabbit normally has black hair only on its long ears, nose, tail, and leg regions farthest from the body mass. In one experiment, a patch of a rabbit's white coat was removed and an icepack was placed over the hairless patch. Where the colder temperature had been maintained, the hairs that grew back were black.

Himalayan rabbits are homozygous for an allele that encodes a mutant version of tyrosinase, an enzyme required to make melanin. As described in the text, this allele encodes a heat-sensitive form of the enzyme, which functions only when air temperature is below about 33°C.



Figure 11.17 Experiment demonstrating the impact of environmental conditions of three different habitats on phenotype in yarrow (*Achillea millefolium*). Cuttings from the same parent plant were grown in the same kind of soil at three different elevations.

Only when we take a fall does the phenotypic effect depression—appear. Other genes also affect emotional states, but mutation of this particular gene reduces our capacity to snap out of it when bad things happen.

Variation in traits arises not only from gene mutations and interactions, but also in response to variations in environmental conditions that each individual faces.



11.7 Complex Variations in Traits

For most populations or species, individuals show rich variation for many of the same traits. Sometimes the phenotypes cannot be predicted, and most of the time they are part of a continuous range of variation.

REGARDING THE UNEXPECTED PHENOTYPE

Think back on Mendel's dihybrid crosses. Nearly all of the traits that he tracked occurred in predictable ratios because the two genes happened to be on different chromosomes or far apart on the same chromosome. They tended to segregate cleanly. Track two or more different pairs of genes—as Mendel did—and you might observe phenotypes that you would not have predicted at all. And not all of the variation is a result of tight linkage or crossing over.

As one example, *camptodactyly*, a rare abnormality, affects the shape and movement of fingers. Some of the people who carry a mutant allele for this heritable trait have immobile, bent fingers on both hands. Others have immobile, bent fingers on the left or right hand only. Fingers of still other people who have the mutant allele are not affected in any obvious way at all.

What causes such odd variation? Remember, most organic compounds are synthesized by a sequence of metabolic steps. *Different enzymes, each a gene product, control different steps*. One gene may have mutated in a number of ways. A gene product might be blocking some pathway or making it run nonstop or not long enough. Perhaps poor nutrition or some other variable factor in the individual's environment is influencing the activity of one of the pathway's enzymes. Such variable factors can introduce big or small variations even in otherwise expected phenotypes.





Figure 11.18 Sampling of the range of continuous variation in human eye color. Products of different gene pairs interact in making and distributing the pigment melanin, which helps color the iris. Small color differences arise from different combinations of alleles. The frequency distribution for the eye-color trait is continuous over a far larger range than this, from black to light blue.

CONTINUOUS VARIATION IN POPULATIONS

Another point: Individuals of populations generally show a range of small differences in most traits. This feature of natural populations is known as **continuous variation**. It arises through **polygenic inheritance**, or the inheritance of multiple genes that affect the same trait. The distribution of all forms of a trait becomes more and more continuous when greater numbers of genes and environmental factors are involved.

Look in a mirror at your eye color. The colored part is the iris, a doughnut-shaped, pigmented structure just under the cornea (Figure 11.18). The color results from several gene products. Some products help make and distribute different kinds and amounts of melanins, which are similar to the light-absorbing pigment that affects coat color in mammals. Almost black irises have



Figure 11.19 *Animated!* Continuous variation. (**a**) A bar graph can reveal continuous variation in a population. The proportion of individuals in each category is plotted against the range of measured phenotypes. (**b**) The curved line above this particular set of bars is a real-life example of a bell-shaped curve that emerged for the population in Figure 11.20. It reflects continuous variation in body height, one of the traits that help characterize human populations.

dense melanin deposits, which can absorb most of the incoming light. Deposits are not as extensive in brown eyes, so some unabsorbed light is reflected out. Light brown or hazel eyes have even less melanin.

Green, gray, or blue eyes have lesser amounts of the pigments. Many or most of the blue wavelengths of light that enter the eyeball are simply reflected out.

How can you describe the continuous variation of some trait in a group? Divide the range of phenotypes for a trait—say, height—into measurable categories, such as numbers of inches. Next, do a count of how many individuals fall into each category; this will give you the relative frequencies of phenotypes across the range of measurable values. Finally, plot out the data as a bar chart, such as the one in Figure 11.19*a*.

In this figure, the shortest bars represent categories having the fewest individuals. The tallest bar signifies the category that has the most individuals. In this case, a graph line skirting the top of all of the bars will be a bell-shaped curve. Such **bell curves** are typical of any trait showing continuous variation. Figure 11.19*b* is a bell curve based on real-life measurements at the University of Florida (Figure 11.20).

And so we conclude this chapter, which introduces heritable and environmental factors that give rise to great variation in traits. What is the take-home lesson? Simply this: An individual's phenotype is an outcome of complex interactions among its genes, enzymes and other gene products, and the environment. Chapter 18 will consider some of the evolutionary consequences.

Enzymes and other gene products control each step of most metabolic pathways. Mutations, interactions among genes, and environmental conditions typically affect one or more steps in ways that contribute to variation in phenotypes.

Individuals of populations or species show continuous variation—a range of small differences. Usually, the more genes and environmental factors that influence a trait, the more continuous the distribution of phenotypes.



http://biology.brookscole.com/starr11

Summary

Section 11.1 Genes are heritable units of information about traits. Each gene has its own locus, or location, along the length of a particular chromosome. Different molecular forms of the same gene are known as alleles.

By experimenting with garden pea plants, Mendel was the first to gather evidence of patterns by which genes are transmitted from parents to offspring.

Offspring of a cross between two individuals that breed true for different forms of a trait are hybrids; each inherited nonidentical alleles for a trait being studied.

An individual with two dominant alleles for a trait (AA) is homozygous dominant. A homozygous recessive has two recessive alleles (aa). A heterozygote has two nonidentical alleles (Aa) for a trait. A dominant allele may mask the effect of a recessive allele partnered with it on the homologous chromosome.

Genotype refers to the particular alleles at any or all gene locations on an individual's chromosomes. *Phenotype* refers to an individual's observable traits.

Biology **S**Now

Learn how Mendel crossed garden pea plants and the definitions of important genetic terms on BiologyNow.

Section 11.2 A cross between parents of different genotypes yields hybrid offspring. For monohybrid experiments, two parents that bred true for different forms of a trait produce F_1 heterozygotes that are identical for one pair of genes. Mendel's monohybrid experiments gave indirect evidence that some forms of a gene may be dominant over recessive forms.

All F_1 offspring of a parental cross $AA \times aa$ were Aa. Crosses between F_1 monohybrids resulted in these allelic combinations among the F_2 offspring:



Mendel's monohybrid experiment results led to a theory of segregation: Diploid organisms have pairs of genes, on pairs of homologous chromosomes. Genes of each pair segregate from each other at meiosis, so each gamete formed gets one or the other gene.

Biology **S**Now

Carry out monohybrid experiments with the interaction on BiologyNow.

Section 11.3 Dihybrid experiments start with a cross between true-breeding heterozygous parents that differ for alleles of two genes (*AABB* × *aabb*). All F_1 offspring are heterozygous for both genes (*AaBb*). In Mendel's dihybrid experiments, phenotypes of the F_2 offspring of F_1 hybrids were close to a 9:3:3:1 ratio:

- 9 dominant for both traits
- 3 dominant for *A*, recessive for *b*
- 3 dominant for *B*, recessive for *a*
- 1 recessive for both traits

His results support a theory of independent assortment: Before gamete formation, meiosis assorts gene pairs of homologous chromosomes independently of how gene pairs of all the other chromosomes are sorted. Random alignment of all pairs of homologous chromosomes at metaphase I is the basis of this outcome.

Biology 🖇 Now

Observe the results of a dihybrid cross with the interaction on BiologyNow.

Section 11.4 Inheritance patterns are not always straightforward.

Some alleles are not fully dominant over their partner allele on the homologous chromosomes, and both are expressed at the same time. The phenotype that results from this allelic combination is somewhere between the two homozygous conditions.

Some alleles are codominant and are expressed at the same time in heterozygotes. An example occurs in the multiple allele system underlying ABO blood typing.

Also, products of one or more genes commonly interact in ways that influence the same trait, and a single gene may have effects on two or more traits.

Biology 🔊 Now

Explore patterns of non-Mendelian inheritance with the interactions on BiologyNow.

Section 11.5 A linkage group consists of all genes along the length of one chromosome. Crossing over between pairs of homologous chromosomes disrupts expected inheritance patterns by breaking linkages. Its outcome is nonparental combinations of alleles in gametes. The farther apart two genes are on a chromosome, the greater will be the frequency of crossing over and genetic recombination between them.

Section 11.6 Environmental factors also can alter how genes are expressed in individuals of a population. An example is a difference in temperature that affects the activity of a heat-sensitive form of an enzyme—a gene product—that helps produce a coat color pigment.

Biology 🔊 Now

See how the environment can affect phenotype with animation on BiologyNow.

Section 11.7 Gene interactions and environmental factors influence many enzymes differently among individuals, and many phenotypes result. They also contribute to small, incremental differences—a range of continuous variation—in a population.

Biology 🔊 Now

Plot the continuous distribution of height for a class with the interaction on BiologyNow.

Self-Quiz

Answers in Appendix II

1. Alleles are _

a. different molecular forms of a gene

- b. different phenotypes
- c. self-fertilizing, true-breeding homozygotes

- 2. A heterozygote has a ______ for a trait being studied.
 a. pair of identical alleles
 b. pair of nonidentical alleles
 c. haploid condition, in genetic terms
- The observable traits of an organism are its _ a. phenotype c. genotype b. sociobiology d. pedigree
- 4. Second-generation offspring of a cross between parents
- who are homozygous for different alleles are the ______
 a. F₁ generation c. hybrid generation
 b. F₂ generation d. none of the above
- 5. F_1 offspring of the cross $AA \times aa$ are ______ . a. all AA c. all Aab. all aa d. 1/2 AA and 1/2 aa
- 6. Refer to Question 5. Assuming complete dominance, the F₂ generation will show a phenotypic ratio of ______
 - a. 3:1 b. 9:1 c. 1:2:1 d. 9:3:3:1

7. Crosses between two dihybrid F_1 pea plants, which are offspring from a parental cross $AABB \times aabb$, result in F_2 phenotypic ratios close to ______.

a. 1:2:1 b. 3:1 c. 1:1:1:1 d. 9:3:3:1

8. The probability of a crossover occurring between two genes on the same chromosome is ______.

- a. unrelated to the distance between them b. increased if they are close together
- c. increased if they are far apart

9. Two genes that are close together on the same chromosome are ______.

a. linkedc. homologouse. all of theb. identical allelesd. autosomesabove

10. Match each example with the most suitable description.

- _____ dihybrid experiment a. *bb*
- _____ monohybrid experiment b. AABB × aabb
- _____ homozygous condition c. Aa
- _____ heterozygous condition $d.Aa \times Aa$

Additional questions are available on Biology € Now™

Genetics Problems Answers in Appendix III

1. A gene encodes the second enzyme in a melaninsynthesizing pathway. An individual who is homozygous for a recessive mutant allele of this gene cannot produce or deposit melanin in body tissues. *Albinism*, the absence of melanin, is the result.

Humans and a number of other organisms can have this phenotype. Figure 11.21 shows two examples. In the following situations, what are the possible genotypes of the father, the mother, and their children?

a. Both parents have normal phenotypes; some of their children are albino and others are unaffected.

b. Both parents are albino and have albino children.

c. The woman is unaffected, the man is albino, and they have one albino child and three unaffected children.

2. As rose breeders know, several alleles influence specific traits, such as long, symmetrical, urn-shaped buds, double flowers, glossy leaves, and resistance to mildew (Figure 11.22). Alleles of a single gene govern whether a plant will



Figure 11.21 Two albino organisms. By not posing his subjects as objects of ridicule, the photographer of human albinos is attempting to counter the notion that there is something inherently unbeautiful about them.





recessive

Figure 11.22 (a) Climbing rose and (b) shrub rose. (c) Globe-shaped buds versus (d) urn-shaped buds.

recessive

be a climber (dominant) or shrubby (recessive). When a true-breeding climber is crossed with a shrubby plant, all F_1 offspring are climbers. If an F_1 plant is crossed with a shrubby plant, about 50 percent of the offspring will be shrubby and 50 percent will be climbers. Using symbols *A* and *a* to represent the dominant and recessive alleles, make a Punnett-square diagram of the expected genotypic and phenotypic outcomes in the F_1 offspring and the offspring of the cross between an F_1 plant and a shrubby plant.



Figure 11.23 The Manx, a breed of cat that has no tail.

3. One gene has alleles *A* and *a*. Another has alleles *B* and *b*. For each of the following genotypes, what type(s) of gametes will form, assuming independent assortment during meiosis occurs?

a. AABB	c. Aabb
b. AaBB	d. AaBb

4. Refer to Problem 3. What will be the genotypes of offspring from the following matings? Indicate the frequencies of each genotype among them.

a. $AABB \times aaBB$	c. $AaBb \times aabb$
b. $AaBB \times AABb$	d. $AaBb \times AaBb$

5. Return to Problem 3. Assume you now study a third gene having alleles *C* and *c*. For each genotype listed, what type(s) of gametes will be produced, assuming that independent assortment occurs?

a. AABBCC	c. AaBBCc
b. AaBBcc	d.AaBbCc

6. Certain alleles are so essential for normal development that an individual who is homozygous recessive for a mutant form cannot survive. Such recessive, *lethal alleles* can be perpetuated in the population by heterozygotes.

Consider the allele *Manx* (M^L) in cats. Homozygous cats (M^LM^L) die when they are still embryos inside the mother cat. In heterozygotes (M^LM), the spine develops abnormally. The cats end up with no tail (Figure 11.23).

Two $M^{L}M$ cats mate. What is the probability that any one of their *surviving* kittens will be heterozygous?

7. In one experiment, Mendel crossed a pea plant that bred true for green pods with one that bred true for yellow pods. All the F_1 plants had green pods. Which form of the trait (green or yellow pods) is recessive? Explain how you arrived at your conclusion.

8. Mendel crossed a pea plant that produced plump and rounded seeds with a pea plant that produced wrinkled seeds. In the F_1 generation, all seeds were round. Mendel planted the F_1 seeds, which grew into plants that, when self-fertilized, produced 5,474 round seeds and 1,850 wrinkled seeds in the F_2 generation. The alleles that govern seed shape are designated *R* and *r*.

a. What are the genotypes of the parents?

b. What are the possible outcomes of a cross between a homozygous round-seeded plant and a wrinkle-seeded plant?

9. Mendel crossed a true-breeding tall, purple-flowered pea plant with a true-breeding dwarf, white-flowered plant. All F_1 plants were tall and had purple flowers. If an F_1 plant self-fertilizes, then what is the probability that a randomly selected F_2 offspring will be heterozygous for the genes specifying height and flower color?

10. Suppose you identify a new gene in mice. One of its alleles specifies white fur. A second allele specifies brown fur. You want to determine whether the relationship between the two alleles is one of simple dominance or incomplete dominance. What sorts of genetic crosses would give you the answer? What types of observations would you require to form conclusions?

11. In sweet pea plants, an allele for purple flowers (*P*) is dominant to an allele for red flowers (*p*). An allele for long pollen grains (*L*) is dominant to an allele for round pollen grains (*l*). Bateson and Punnett crossed a plant having purple flowers/long pollen grains with one having white flowers/round pollen grains. All F_1 offspring had purple flowers and long pollen grains. In the F_2 generation, the researchers observed the following phenotypes:

296 purple flowers/long pollen grains19 purple flowers/round pollen grains27 red flowers/long pollen grains85 red flowers/round pollen grains

What is the best explanation for these results?

12. A dominant allele *W* confers black fur on guinea pigs. A guinea pig that is homozygous recessive (*ww*) has white fur. Fred would like to know whether his pet black-furred guinea pig is homozygous (*WW*) or heterozygous (*Ww*). How might he determine his pet's genotype?

13. Red-flowering snapdragons are homozygous for allele R^1 . White-flowering snapdragons are homozygous for a different allele (R^2). Heterozygous plants (R^1R^2) bear pink flowers. What phenotypes should appear among first-generation offspring of the crosses listed? What are the expected proportions for each phenotype?

a. $R^1R^1 \times R^1R^2$	c. $R^1 R^2 \times R^1 R^2$
b. $R^1 R^1 \times R^2 R^2$	d. $R^1 R^2 \times R^2 R^2$

(In cases of incomplete dominance, alleles are usually designated by superscript numerals, as shown here, not by the uppercase letters for dominance and lowercase letters for recessiveness.)

For each cross, list which of these F ₁ phenotypes show up as well as the proportion of each:	S	
ared	pink	white
bred	pink	white
cred	pink	white
d red	pink	white

14. Two pairs of genes affect comb type in chickens (Figure 11.12), and they assort independently. When both are homozygous for recessive alleles, a chicken has a single comb. But a dominant allele of one gene, *P*, gives rise to a pea comb, and a dominant allele of the other gene (*R*) gives rise to a rose comb. An *epistatic* interaction occurs when a chicken has at least one of both dominant alleles, *P*_ *R*_ , which gives rise to a walnut comb.

Predict the ratios resulting from a cross between two walnut-combed chickens that are heterozygous for both genes (PpRr) and list them below:



15. As Section 3.6 explains, a single mutant allele gives rise to an abnormal form of hemoglobin (Hb^{S} instead of Hb^{A}). Homozygotes ($Hb^{S}Hb^{S}$) develop the genetic disease sickle-cell anemia. Heterozygotes ($Hb^{A}Hb^{S}$) show few obvious symptoms.

A couple who are both heterozygous for the *HbA* allele plan to have children. For *each* of the pregnancies, state the probability that this couple will have a child who is:

- a. homozygous for the Hb^S allele
- b. homozygous for the *HbA* allele
- c. heterozygous *Hb^AHb^S*

16. Watermelons (*Citrullus*) are important crops around the world (Figure 11.24). A single gene determines the density of green pigment that colors the rind, with solid light green (g) recessive to solid dark green (G). When a true-breeding plant having a dark-green rind is crossed with a plant having a light-green rind, what fraction of the dark-green F_2 offspring is expected to be heterozygous for this trait?

17. The rind of a watermelon that is homozygous for recessive allele e bursts, or splits explosively, when cut. Genotype *EE* results in a "nonexplosive" rind that is better for shipping watermelons to market. The rind of a watermelon that is homozygous for the recessive allele f has a furrowed surface. A furrowed rind has less market appeal than a smooth rind, which results from expression of dominant allele F.

For one testcross, a dihybrid plant that produces melons with a smooth, nonexplosive rind is crossed with a plant that produces melons with a furrowed, explosive rind. Make a Punnett square of the following results:

- 118 smooth, nonexplosive
- 112 smooth, explosive
- 109 furrowed, nonexplosive
- 121 furrowed, explosive

What is the smooth rind/furrowed rind ratio among the testcross offspring? What is the ratio of nonexplosive



Figure 11.24 A sampling of the variation in the rind characteristics of watermelon (*Citrullus*).

rind/explosive rind? Are the two gene loci assorting independently of each other?

18. Two pairs of genes determine kernel color in wheat plants. Alleles of one pair show incomplete dominance over the other pair. The product of allele A^1 at one locus produces enough pigment to add a dose of red color to the kernels, but that of allele A^2 does not. The product of allele B^1 at the second locus also adds a dose of red color to the kernels, but that of allele B^2 does not.

The chart shown below lists the numbers of different wheat kernel colors observed during a recent harvest, together with their corresponding genotypes. Using the information in this table, draw a graph showing the percentage of kernels in the wheat population that inherited each of the five kernel colors.

Explain why the kernel color in wheat plants shows a varied phenotypic distribution.

Genotype	Phenotype	Number Displaying the Trait	Percentage of Population
A ¹ A ¹ B ¹ B ¹	Dark red	181	
A ¹ A ¹ B ¹ B ² or A ¹ A ² B ¹ B ¹	Red	360	
$A^{1}A^{2}B^{1}B^{2}$ or $A^{1}A^{1}B^{2}B^{2}$ or $A^{2}A^{2}B^{1}B^{1}$	Salmon	922	
$A^{1}A^{2}B^{2}B^{2}$ or $A^{2}A^{2}B^{1}B^{2}$	Pink	358	
A ² A ² B ² B ²	White	179	
Totals		2,000	