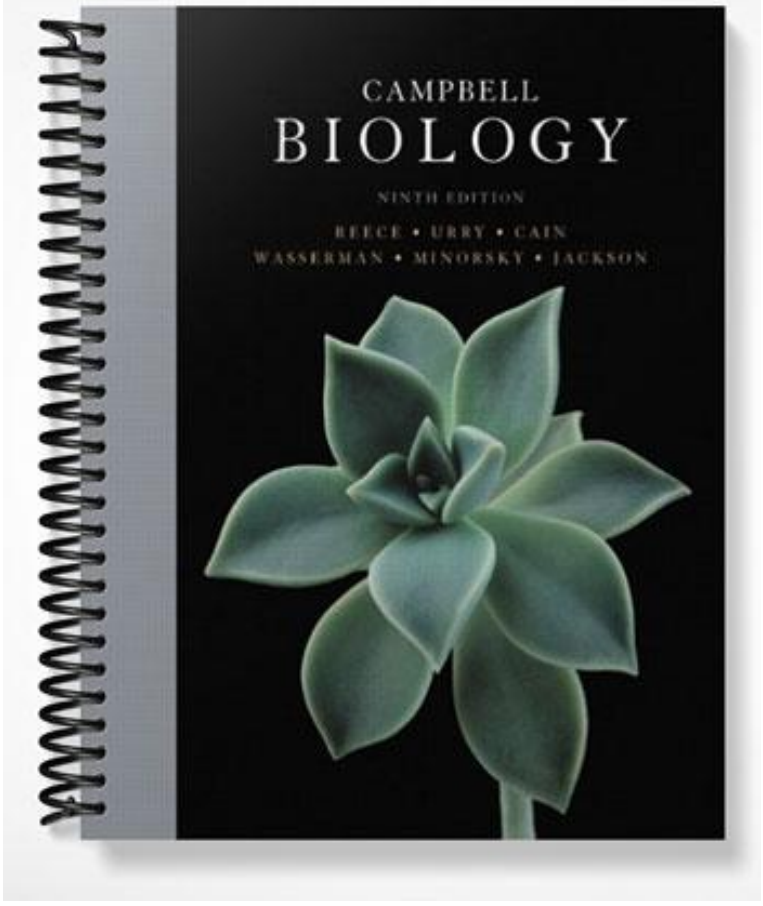
SOLUTIONS MANUAL



4. The cell's supply of ADP, P_i, and NAD^+ is finite (limited). What happens to cellular respiration when all of the cell's NAD^+ has been converted to NADH?

   If NAD is unavailable, the cell is unable to conduct any processes that involve the conversion of NAD^+ to NADH. Because both glycolysis and the Krebs cycle produce NADH, both of these processes shut down when there is no available NAD^+.

5. If the Krebs cycle does not require oxygen, why does cellular respiration stop after glycolysis when no oxygen is present?

   When no oxygen is present, oxidative phosphorylation cannot occur. As a result, the NADH produced in glycolysis and the Krebs cycle cannot be oxidized to NAD^+. When no NAD^+ is available, pyruvate cannot be converted to the acetyl CoA that is required for the Krebs cycle.

6. Many organisms can withstand periods of oxygen debt (anaerobic conditions). Yeast undergoing oxygen debt converts pyruvic acid to ethanol and carbon dioxide. Animals undergoing oxygen debt convert pyruvic acid to lactic acid. Pyruvic acid is fairly nontoxic in even high concentrations. Both ethanol and lactic acid are toxic in even moderate concentrations. Explain why this conversion occurs in organisms.

   As noted in question 4, when no NAD^+ is available, even glycolysis stops. No ATP will be produced and the cell (or organism) will die. The conversion of pyruvic acid (pyruvate) to lactic acid (or ethanol) requires the input of NADH and generates NAD^+. This process, called fermentation, allows the cell to continue getting at least 2 ATP per glucose.

7. How efficient is fermentation? How efficient is cellular respiration? Remember that efficiency is the amount of useful energy (as ATP) gained during the process divided by the total amount of energy available in glucose. Use 686 kcal as the total energy available in 1 mole of glucose and 8 kcal as the energy available in 1 mol of ATP.

   Efficiency of fermentation

   $$\text{kcal/mole of ATP} \times 2 \text{ ATP} = 16 \text{ kcal}$$

   $$\frac{16 \text{ kcal} / 2 \text{ moles of ATP}}{686 \text{ kcal} / \text{mole of glucose}} = 2.3\%$$

   Efficiency of aerobic respiration

   $$8 \text{ kcal/mole of ATP} \times 38 \text{ ATP (maximum)} = 304 \text{ kcal}$$

   $$\frac{304 \text{ kcal} / 38 \text{ moles of ATP}}{686 \text{ kcal} / \text{mole of glucose}} = 44.3\%$$

8. a. Why can't cells store large quantities of ATP? (*Hint:* Consider both the chemical stability of the molecule and the cell's osmotic potential.)

      ATP is highly reactive at normal body temperatures and therefore difficult for cells to store for any period of time. (In the lab, ATP is usually stored at very low temperatures, for example, at -20°C.) In addition, ATP is a relatively small molecule. As a result, if cells could store high concentrations of ATP, their osmotic potential would change. This is also why cells don't store glucose. The cells would become hypertonic to the fluid around them and could pick up enough water to burst.

   b. Given that cells can't store ATP for long periods of time, how do they store energy?

      Instead of storing ATP, cells tend to store energy as fats, oils, or starches

c. What are the advantages of storing energy in these alternative forms?

These are very large molecules and, as a result, do not have as great an effect on osmotic potential. They are also much more stable chemically than ATP.

9. To make a 5 *M* solution of hydrochloric acid, we add 400 mL of 12.5 *M* hydrochloric acid to 600 mL of distilled water. Before we add the acid, however, we place the flask containing the distilled water into the sink because this solution can heat up so rapidly that the flask breaks. How is this reaction similar to what happens in chemiosmosis? How is it different?

a. Similarities	b. Differences
In both processes, as we add the acid to the water, we are generating a difference in concentration between the two, or a H^+ ion gradient. As the H^+ ions flow down this gradient (that is, mix with the water),they release energy in the form of heat.	Both processes set up a H^+ ion concentration gradient. However, in chemiosmos is the energy release is controlled as the H^+ ions pass through the ATP synthase molecules and ATP is generated. Some energy is lost as heat, but much of it is captured in the chemical bonds of ATP.

9.2 Test Your Understanding

1. If it takes 1,000 g of glucose to grow 10 g of an anaerobic bacterium, how many grams of glucose would it take to grow 10 g of that same bacterium if it was respiring aerobically? Estimate your answer. For example, if it takes *X* amount of glucose to grow 10 g of anaerobic bacteria, what factor would you have to multiply or divide *X* by to grow 10 g of the same bacterium aerobically? Explain how you arrived at your answer.

   Aerobic respiration can produce a maximum of 38 ATP per glucose molecule. Anaerobic respiration can produce 2 ATP per glucose molecule. As a result, aerobic respiration is about 19 times more efficient. Therefore, you would need 19 times less glucose if respiring aerobically: 1,000 g of glucose divided by 19 equals approximately 50 g of glucose required if respiration is aerobic.

2. Mitochondria isolated from liver cells can be used to study the rate of electron transport in response to a variety of chemicals. The rate of electron transport is measured as the rate of disappearance of O_2 from the solution using an oxygen-sensitive electrode.

   How can we justify using the disappearance of oxygen from the solution as a measure of electron transport?

   Use the balanced equation for aerobic respiration:

   $$C_6H_{12}O_6 + 6\ O_2\ \&ARROW;\ 6\ CO_2 + 6\ H_2O + \text{Energy}$$

   If the final energy produced is 38 ATP, then for every 6 oxygen molecules consumed (or 6 moles of oxygen consumed), we expect 38 molecules of ATP (or moles of ATP) to be produced.

3. Humans oxidize glucose in the presence of oxygen. For each mole of glucose oxidized, about 686 kcal of energy is released. This is true whether the mole of glucose is oxidized in human cells or burned in the air. A calorie is the amount of energy required to raise the temperature of 1 g of water by 1°C; 686 kcal = 686,000 calories. The average human requires about 2,000 kcal of energy per day, which is equivalent to about 3 mol of glucose per day. Given this, why don't humans spontaneously combust?

   As noted in question 9, during cellular respiration, the energy from the oxidation of glucose is not released all at once (as it is in burning). Instead, each of the reactions in glycolysis, the Krebs cycle, and electron transport releases a small amount of the energy stored in the molecules. Much of this energy is captured as NADH, $FADH_2$, ATP, or GTP. Some is lost as heat; however, the heat loss also occurs at each step and not

all at once.

4. A gene has recently been identified that encodes for a protein that increases longevity in mice. To function in increasing longevity, this gene requires a high ratio of NAD^+/NADH. Researchers have used this as evidence in support of a "caloric restriction" hypothesis for longevity—that a decrease in total calorie intake increases longevity. How does the requirement for a high NAD^+/NADH ratio support the caloric restriction hypothesis?

   A decrease in calorie intake will decrease the rate of glycolysis and the Krebs cycle. Therefore, over a 24-hour period, there will be less NADH produced by glycolysis and the Krebs cycle, and the NAD^+/NADH ratio will increase.

5. An active college-age athlete can burn more than 3,000 kcal/day in exercise).

   a. If conversion of one mole of ATP to ADP + P_i releases about 7.3 kcal, roughly speaking, how many moles of ATP need to be produced per day in order for this energy need to be met?

      3000 kcal/day divided by 7.3 kcal/mole of ATP = 411 moles of ATP

   b. If the molecular weight of ATP is 573, how much would the required ATP weigh in kilograms?

      411 moles of ATP times 573 grams per mole = 235,503 grams or 235 kilogram (about 518 pounds)

   c. Explain these results

      ATP is broken down to ADP = Pi, which is continuously recycled to ATP during cell respiration.

Activity 10.1 Modeling photosynthesis: How can cells use the sun's energy to convert carbon dioxide and water into glucose?

Activity 10.1 is designed to help you understand:

1. The roles photosystems I and II and the Calvin cycle play in photosynthesis, and
2. How and why C_4 and CAM photosynthesis differ from C_3 photosynthesis.

Using your textbook, lecture notes, and the materials available in class (or those you devise at home), model photosynthesis as it occurs in a plant cell.

Your model should be a dynamic (working or active) representation of the events that occur in the various phases of C_3 photosynthesis.

Building the Model

- Use chalk on a tabletop or a marker on a large sheet of paper to draw the cell membrane and the chloroplast membranes.
- Use playdough or cutout pieces of paper to represent the molecules, ions, and membrane transporters or pumps.
- Use the pieces you assembled to model the processes involved in C_3 photosynthesis. Develop a dynamic (claymation-type) model that allows you to manipulate or move carbon dioxide and water and its breakdown products through the various steps of the process.
- When you feel you have developed a good working model, demonstrate and explain it to another student or to your instructor.

Your model of C_3 photosynthesis should include what occurs in photosystems I and II and in the Calvin cycle. For **photosystems I and II**, be sure your model includes and explains the roles of the following:

$NADP^+$ ATP chemiosmosis

NADPH water and oxygen H^+

ADP ATP synthase

P_i e^- e^- carriers in thylakoid membranes

Also indicate where in the plant cell each item is required or produced.

For the **Calvin cycle**, be sure your model includes and explains the roles of the following:

glucose NADPH

C_3 or 3C sugars ATP

carbon dioxide

Also indicate where in the plant cell each item is required or produced.

After you've modeled C_3 photosynthesis, indicate how the system would be altered for C_4 and CAM photosynthesis.

- Indicate where in the cells of the leaf PEP carboxylase exists and how it reacts to capture CO_2. Be sure to indicate the fate of the captured CO_2.
- Do the same for PEP carboxylase in CAM plants.

Use your model and the information in Chapter 10 of Campbell Biology, 9th edition, to answer the questions.

1. The various reactions in photosynthesis are spatially segregated from each other within the chloroplast. Draw a simplified diagram of a chloroplast and include these parts: outer membrane, grana, thylakoid, lumen, stroma/matrix.

a. Where in the chloroplast do the light reactions occur?	In the thylakoid membranes
b. Where in the chloroplast is the chemiosmotic gradient developed?	Across the thylakoid membrane; H^+ ions are pumped into the thylakoid space
c. Where in the chloroplast does the Calvin cycle occur?	In the stroma or liquid portion of the chloroplast

Refer to Figure 10.4, page 186, in *Campbell Biology*, 9th edition.

2. In photosynthesis, the reduction of carbon dioxide to form glucose is carried out in a controlled series of reactions. In general, each step or reaction in the sequence requires the input of energy. The sun is the ultimate source of this energy.

a. What is/are the overall function(s) of photosystem I?	b. What is/are the overall function(s) of photosystem II?	c. What is/are the overall function(s) of the Calvin cycle?

In noncyclic photosphosphorylation, photosystem I produces NADPH. In cyclic photophosphorylation, photosystem I produces ATP.	Photosystem II generates ATP. To fill the electron hole in photosystem II, water is split into 2 H^+, 2e^-, and 1/2 O_2. (The electron from photosystem II fills the electron hole in photosystem I.)	The Calvin cycle uses the ATP and NADPH generated in the light reactions to reduce CO_2 to three-carbon compounds in a cyclic series of reactions that regenerates the original five-carbon sugar required to accept the CO_2. The three-carbon compounds can be used to make glucose or other organic compounds required by the cells.

3. Are the compounds listed here *used* or *produced* in:	Photosystem I?	Photosystem II?	The Calvin cycle?
Glucose			Produced
O_2		Produced from the breakdown of H_2O	
CO_2			Used
H_2O		Used to produce 2 H^+, 2e^-, and 1/2 O_2	
ATP	Produced (in cyclic photophosphorylation)	Produced	Used
ADP + P_i	Used	Used	Produced

4. Which light reaction system (cyclic or noncyclic) would a chloroplast use in each situation?

a. Plenty of light is available, but the cell contains little $NADP^+$.	b. There is plenty of light, and the cell contains a high concentration of $NADP^+$.
If there is little $NADP^+$, there must be much NADPH. This could occur if the Calvin cycle is not using up the NADPH. For example, if CO_2 levels are low, little NADPH will be used to make glucose. Under these circumstances, the system would switch to cyclic photophosphorylation and gain ATP, which can be used both in photo-synthesis and in other types of metabolism.	In this case, it appears that NADPH is being used rapidly (therefore the high levels of $NADP^+$). As a result, the system would switch to noncyclic photophosphorylation, which produces both ATP and NADPH.

5. All living organisms require a constant supply of ATP to maintain life. If no light is available, how can a plant make ATP?

   Keep in mind that it is not always light and that not all cells of a plant are directly exposed to light. For example, cells on the interior of a plant stem and those in the roots have little, if any, exposure to light. Plants, like other eukaryotic organisms on Earth, also contain mitochondria. Plant cells undergo glycolysis in the cytoplasm and transfer acetyl CoA to mitochondria, where it enters the Krebs cycle. The NADH and $FADH_2$ produced during the Krebs cycle then undergo oxidative phosphorylation to produce ATP.

10.1 Test Your Understanding

Chloroplast thylakoids can be isolated and purified for biochemical experiments. Shown below is an experiment in which pH was measured in a suspension of isolated thylakoids before and after light illumination (first arrow). At the time indicated by the second arrow, a chemical compound was added to the thylakoids. Examine these data and address the following questions.

[Unnumbered Figure Comes Here]

a. Based on your understanding of the function of the chloroplasts, why does turning on the light cause the pH in the solution outside the thylakoids to increase?

   Electron transfer (Photosystems II and I) in the thylakoid membrane resulted in pumping of H^+ from stroma (outside) to thylakoid (inside). As a consequence, the H^+ concentration outside the thylakoids became lower and the pH increased.

b. Given the response, the chemical added was probably an inhibitor of:

   i. oxidative phosphorylation

   ii. ATP synthase

   iii. NADPH breakdown

   iv. Electron transport chain between photosystems II and I

   v. Rubisco

   The answer is iv. Disrupting or inhibiting the electron transport chain between photosystems II and I would prevent transport of H^+ ions into the thylakoid space. As a result, the concentration of H^+ ions would be reduced and the pH would increase.

Activity 10.2 How do C_3, C_4, and CAM photosynthesis compare?

1. Carbon dioxide enters plant leaves through the stomata, while oxygen (the photosynthetic waste product) and water from the leaves exit through the stomata. Plants must constantly balance both water loss and energy gain (as photosynthesis). This has led to the evolution of various modifications of C_3 photosynthesis.

Draw simplified diagrams of the cross sections of a leaf from a C_3, a C_4 and a CAM plant.	See Figure 10.4.	See Figure 10.30.	CAM leaf anatomy is similar to C_3 leaf anatomy.
a. How are the leaves	All have stomata, epidermal cells that lack		

similar?	chloroplasts, mesophyll cells with chloroplasts, and veins that conduct water and the products of photosynthesis.		
b. How are the leaves different?	C_4 plants have large bundle sheath cells not found in the others. In C_4 plants, the Calvin cycle occurs only in the bundle sheath cells.		
c. How and when does carbon dioxide get into each leaf?	During daylight hours, when stomata are open	During cooler parts of the day, when stomata are open	At night, when it is cool and stomata are open
d. Which enzyme(s) (1) capture carbon dioxide and (2) carry it to the Calvin cycle?	The CO_2 is picked up by the enzyme, rubisco, which catalyzes the first step in the Calvin cycle.	PEP carboxylase in the mesophyll cells converts CO_2 to a four-carbon organic acid, which is transported to the bundle sheath cells, where it is converted to CO_2 and PEP, and rubisco catalyzes the first step in the Calvin cycle.	PEP carboxylase in the mesophyll cells converts CO_2 to a four-carbon organic acid, which is transported to the cells' central vacuoles and can later be converted back to CO_2 and PEP. The CO_2 can then be picked up by rubisco and used in the Calvin cycle in mesophyll cells.

e. What makes C_4 photosynthesis more efficient than C_3 photosynthesis in tropical climates?

PEP carboxylase is much more efficient than rubisco at picking up CO_2. As a result, C_4 plants can capture large quantities of CO_2 and store it as a four-carbon organic compound in a relatively short period of time. This means that during the hottest parts of the day, the stomata can close to reduce water loss. Even with the stomata closed, however, the Calvin cycle can continue by using the stored CO_2. This system also maintains a relatively high ratio of CO_2 to O_2 in the cells that rely on rubisco, the bundle sheath cells. This greatly reduces the amount of photorespiration in these plants.

f. How is CAM photosynthesis advantageous in desert climates?

Stomata can be open at night when there is less evaporative loss of water and closed during the day. At night, PEP carboxylase allows desert plants to store CO_2 as a four-carbon organic acid. However, the amount that can be stored in the central vacuole of its photosynthetic cells is finite. This stored CO_2 can then be used during the day to support the Calvin cycle.

2 Photosynthesis evolved very early in Earth's history. Central to the evolution of photosynthesis was the evolution of the enzyme rubisco (an abbreviation for ribulose bisphosphate carboxylase oxidase). To the best of our knowledge, all photosynthetic plants use rubisco. Rubisco's function is to supply carbon dioxide to the Calvin cycle; however, it does this only if the ratio of carbon dioxide to oxygen is relatively high. (For comparison, a relatively high ratio of carbon dioxide to oxygen is 0.03% carbon dioxide to 20% oxygen.) When the carbon-dioxide-to-oxygen ratio becomes low, the role of rubisco switches and it catalyzes photorespiration, the breakdown of glucose to carbon dioxide and water.

a. Why could we call photorespiration a "mistake" in the functioning of the cell?

Photorespiration could be called a "mistake" because under high O_2/CO_2 conditions, rubisco breaks down glucose into carbon dioxide and water but no useful energy is gained.

b. Rubisco is thought to have evolved when Earth had a reducing atmosphere. How does this help explain the photorespiration "mistake?"

When the first photosynthetic organisms arose, the early Earth's atmosphere contained little, if any, oxygen. Rubisco would have functioned very well under these conditions. It was only later, when the concentration of oxygen in the atmosphere increased considerably, that rubisco's ability to oxidize glucose became evident.

10.2 Test Your Understanding

The metabolic pathways of organisms living today evolved over a long period of time—undoubtedly in a stepwise fashion because of their complexity. Put the following processes in the order in which they might have evolved, and give a short explanation for your arrangement.

_4_ Krebs cycle

_3_ Electron transport

_1_ Glycolysis

_2_ Photosynthesis

First, glycolysis is found in all eukaryotes and many prokaryotes. It takes place in the cytoplasm and can occur in the absence of oxygen.

Second, photosynthesis produces oxygen as a by-product. Neither the Krebs cycle nor electron transport can occur in the absence of oxygen.

Third, electron transport is required to convert NADH to NAD^+. Because glycolysis produces 2 ATP (net) and 2 NADH, the addition of electron transport represents an advantage. Organisms can then gain 8 ATP (net) from glycolysis plus electron transport.

Fourth, the Krebs cycle cannot occur without a mechanism to convert NADH to NAD^+. Electron transport must have evolved before the Krebs cycle.

Notes to Instructors

Chapter 11 Cell Communication

What is the focus of this activity?

Most students understand that external signals interact with receptors in cells and that the interaction leads to a response by the cell. However, fewer have a good understanding of these processes:

- how a protein signal that cannot cross the cell membrane can cause a response,
- how very low concentrations of signal molecules can produce high levels of response, and
- exactly what a cell does to respond to a signal.

What is the particular activity designed to do?

Activity 11.1 How are chemical signals translated into cellular responses?

In this activity, students model and compare the functions of a G-protein receptor system and a tyrosine-kinase receptor system. In addition, they are asked to use their knowledge of enzyme function from Chapter 8 to understand how a signal-transduction pathway can amplify the response to a single signal molecule.

What misconceptions or difficulties can this activity reveal?

Activity 11.1

Modeling the G-protein receptor system and the tyrosine-kinase receptor system does not reveal misconceptions; rather, it tends to fill in missing information. Most students at the introductory level have little understanding of these systems.

Questions 1 and 2: These questions ask students to look back at their two models and consider how they are similar and how they differ. Although engaging in this type of comparative process seems standard to those of us who have been working in the sciences for years, it is not something that introductory students do automatically. Posing these types of questions helps students learn not only to ask themselves the questions but also to organize and clarify their own understanding of the individual processes they model.

Question 3: Because these pathways are called signal-transduction pathways, many students seem to get the idea (or misconception) that once each carrier or enzyme in a given pathway "transduces" or moves the signal on to the next carrier or enzyme, its job is done. This question focuses students' attention on Figure 11.16, page 220, to help them understand the process of signal amplification—in other words, to understand that once a single enzyme in the pathway is activated, it can catalyze more than one reaction and the product of that reaction can catalyze more than one, and so on.

Answers

Activity 11.1 How are chemical signals translated into cellular responses?

Chapter 11 in *Campbell Biology*, 9th edition, describes at least four kinds of signal receptors. Three of these—G-protein-linked receptors, tyrosine-kinase receptors, and ion-channel receptors—are plasma membrane proteins. Protein receptors found in the cytoplasm, or nucleus, of the cell are the fourth type. Some signals (for example, a protein hormone) interact with signal receptors in the cell membrane to initiate the process of signal transduction. This often involves changes in a series of different relay molecules in a signal-transduction pathway. Ultimately, the transduced signal initiates an intracellular response. Other types of signals (for example, steroid hormones) can diffuse through the cell membrane and interact with intracellular receptors. For example, testosterone interacts with its receptor in the cell's cytoplasm, enters the nucleus, and causes the transcription of specific genes.

To help you understand how signal transduction occurs in cells, develop dynamic (claymation-type) models of both a G-protein receptor system and a tyrosine-kinase receptor system. Use playdough or cutout pieces of paper to represent all the structural components and molecules listed here under each system.

G-Protein Receptor System	**Tyrosine-Kinase Receptor System**
signal protein	signal protein
G-protein-linked receptor	tyrosine-kinase receptor
plasma membrane	plasma membrane
inactive and active G protein	inactive and active relay proteins
GTP and GDP	ATP and ADP
inactive and active enzyme	signal-transduction pathway
signal-transduction pathway	

Use your models to show how signal reception by each of the systems can lead to the release of Ca^{+} from the

endoplasmic reticulum. Demonstrate and explain your models to another student group or to your instructor.

Then use your models to answer the questions on the next page.

1. How are these two systems similar? Consider both structural similarities and similarities in how the systems function.

   In both systems, the receptor proteins are bound in the cell's membrane. Binding of signal molecules to the receptors activates them. Activated receptor(s) interact with inactive relay protein(s) and activate them. The role of the activated relay protein(s) is to activate other protein(s) to produce the cellular response.

2. How are the two systems different? Consider both structural differences and differences in how the systems function.

   The G-protein-linked receptor protein is a single unit that becomes functional when activated by its signal molecule. Two tyrosine-kinase receptor proteins must be activated by signal molecules and aggregate to become activated.

   The activated G-protein-linked receptor protein activates the G protein, which is also membrane bound, by converting an associated GDP to GTP. The activated G protein then moves along the membrane and activates a specific membrane-bound enzyme, which produces the cellular response.

   The activated tyrosine-kinase receptor aggregate can activate up to ten different specific relay proteins inside the cell and therefore produce multiple responses. The activated relay proteins are not membrane bound. Each type of activated relay molecule can activate a different transduction pathway and produce a different cellular response.

3. Both systems can generate elaborate multistep signal-transduction pathways. These pathways can greatly amplify the cell's response to a signal; the more steps in the pathway, the greater the amplification of the signal. Explain how this amplification can occur. (Review Figure 11.16, page 220, in *Campbell Biology*, 9th edition.)

   In a signal-transduction pathway, each activated enzyme or second messenger has the potential to catalyze more than one reaction. Each of its reaction products similarly has the potential to trigger more than one reaction. As a result, the effects produced by a single signal molecule can be greatly amplified.

11.1 Test Your Understanding

Humans have the ability to detect and recognize many different aromatic chemicals by smell. Many of these chemicals are present in concentrations less than 1 ppm (part per million) in the air. For example, the majority of humans can detect and recognize chlorine at a concentration of about 0.3 ppm.

a. What characteristics of olfactory (smell) receptors would you look for or propose to explain this ability?

   Proposing that olfactory receptors are G-coupled protein receptors would be reasonable here. In fact, this is borne out by the literature. The G-coupled receptor multi-step cascade allows amplification of and therefore detection of stimuli available in extremely low concentration, in this case the chemical, chlorine.

b. Dogs are known to have a much better sense of smell than humans. Given this, what differences may exist in their olfactory system (as compared to humans)?

   Here students could propose either greater expression of receptors in the olfactory tissue of dogs or a greater surface area of olfactory tissue.

Notes to Instructors

Chapter 12 The Cell Cycle

Chapter 13 Meiosis and Sexual Life Cycles

What is the focus of these activities?

Most students can recite what happens in each phase of mitosis and meiosis. However, many have difficulty translating those descriptions into visual pictures of a cell with a particular number of chromosomes.

What are the particular activities designed to do?

Activity 12.1 What is mitosis?

Activity 13.1 What is meiosis?

Activity 13.2 How do mitosis and meiosis differ?

These activities are designed to give students practice in translating their knowledge of what goes on in the various phases of mitosis and meiosis into visual representations.

Activity 13.2 asks students to compare events in each of the various phases of mitosis and meiosis and determine similarities and differences.

What misconceptions or difficulties can these activities reveal?

Most students don't have difficulty reciting what events occur in each stage of mitosis or meiosis. If you ask them to draw what is occurring in each of these stages and give a specific chromosome complement (as in question 3 in both Activities 12.1 and 13.1), however, many have a difficult time. Two common reasons for this are:

- The students do not understand how many chromosomes the cell contains. For example, if a question indicates that a eukaryotic cell has a full complement of eight chromosomes, many students may not understand this means that the cell has eight total chromosomes, or four pairs of chromosomes.
- The students have memorized the list of events that occur in each stage, but they have not translated this into a real understanding of the events.

In either case, asking students to draw cells in different stages of cell division will give them a better understanding of the overall process.

Activity 12.1

Question 2: Some students don't understand that mitosis and meiosis occur only in eukaryotes. This question is meant to point out that mitosis does not occur in prokaryotes, for example, bacteria.

Question 7: Students are often confused about how to count the number of chromosomes in a cell. A general rule or convention is that chromosomes should be counted by the number of centromere regions present. Using this convention, we count two chromatids attached to a common centromere region as one chromosome. When sister chromatids separate to opposite poles, each daughter chromosome has its own centromere region and is now counted separately. To help avoid confusion, this question asks students to indicate both the number of centromeres visible and the number of chromatids attached to centromeres.

Activity 13.2

Most students learn mitosis and meiosis by memorizing the stages of each in order. Few realize that the stages were named because of similarities early microscopists saw. This activity is designed to demonstrate that many

of the events in a given phase—for example, metaphase of mitosis, meiosis I, and meiosis II—are the same. Once students understand that, they can focus on the general processes that occur in each phase. To distinguish between similar phases in mitosis and meiosis, students need only to remember what makes one different from the other.

Answers

Activity 12.1 What is mitosis?

What is mitosis?

1. What is the overall purpose of mitosis?

   The purpose of mitosis is to produce daughter cells that are identical to the parent cell. To do this, the cells must first duplicate all of their chromosomes. Then the chromosomes must be equally divided among the daughter cells such that each has the same complement (number and kinds) of chromosomes as the parent cell.

2. In what types of organism(s) and cells does mitosis occur?

   Mitosis occurs in all eukaryotic organisms.

3. What type of cell division occurs in bacteria?

   Bacteria undergo a type of cell division called fission. Fission involves duplication of the DNA, or genophore, and subdivision of the cell into two daughters, each of which contains a copy of the DNA from the parent.

What are the stages of mitosis?

4. The fruit fly, *Drosophila melanogaster*, has a total of eight chromosomes (four pairs) in each of its somatic cells. Somatic cells are all cells of the body except those that will divide to form the gametes (ova or sperm). Review the events that occur in the various stages of mitosis.

   Keep in mind that the stages of cell division were first recognized from an examination of fixed slides of tissues undergoing division. On fixed slides, cells are captured or frozen at particular points in the division cycle. Using these static slides, early microscopists identified specific arrangements or patterns of chromosomes that occurred at various stages of the cycle and gave these stages names (interphase, prophase, and so on). Later work using time-lapse photography made it clear that mitosis is a continuous process. Once division begins, the chromosomes move fluidly from one phase to the next.

Assume you are a microscopist viewing fruit fly cells that are undergoing mitosis. Within each of the circles (which represent cell membranes) on the following page, draw what you would expect to see if you were looking at a cell in the stage of mitosis indicated. If no circle is present, draw what you would expect to see at the given stage.

[Unnumbered Figure Comes Here]

What are the products of mitosis?

5. How many cells are produced at the end of a single mitotic division?

   Two cells are produced at the end of a single mitotic division.

6. How many different kinds of cells are produced at the end of a single mitotic division?

   Only one kind of cell is produced. Two daughter cells are produced, but they are identical to each other

and to the parent cell that gave rise to them.

7. Six centromeres are observed in a prophase cell from another species of insect.

a. How many pairs of chromosomes does this organism contain? Three pairs		
b.For each stage of mitosis, indicate the number of centromeres you would expect to find and the number of copies of chromosomes attached to each centromere.		
Stage of mitosis:	Number of centromeres visible per cell	Number of chromosome copies attached to each centromere
Prophase	6	2
Anaphase	12	1

12.1 Test Your Understanding

Haplopappus is an annual flowering plant that grows in deserts. It is of interest because its 2n number is only four.

a. This means that cells in the vegetative parts of the plant that are not undergoing mitosis have how many DNA molecules in their nuclei?

   There would be 4 DNA molecules or 4 total chromosomes in cells not undergoing division.

b. During metaphase of mitosis, how many DNA molecules would be in the nucleus?

   During metaphase, there would be 8 DNA molecules in the nucleus. DNA would have duplicated in the S phase of interphase prior to division.

Activity 13.1 What is meiosis?

What is meiosis?

1. What is the overall purpose of meiosis?

   The purpose of meiosis is to reduce the diploid chromosome number by half to the haploid number. Note that this is **a very specific half of the chromosomes**. The haploid cell contains one member of every pair of chromosomes found in the diploid parent cell.

2. In what types of organism(s) does meiosis occur?

   Meiosis occurs in eukaryotes in cells that will produce gametes (ova or sperm).

What are the stages of meiosis?

3. The fruit fly, *Drosophila melanogaster*, has a total of eight chromosomes (four pairs) in each of its somatic cells. Somatic cells are all cells of the body except those that will divide to form the gametes (ova or sperm). Review the events that occur in the various stages of meiosis.

Keep in mind that the stages of cell division were first recognized from an examination of fixed slides of tissues undergoing division. On fixed slides, cells are captured or frozen at particular points in the division cycle. Using these static slides, early microscopists identified specific arrangements or patterns of chromosomes that occurred at various stages of the cycle and gave these stages names (interphase, prophase I, and so on). Later

work using time-lapse photography made it clear that meiosis is a continuous process. Once division begins, the chromosomes move fluidly from one phase to the next.

Assume you are a microscopist viewing fruit fly cells that are undergoing meiosis. Within each of the circles (which represent cell membranes) on the next pages, draw what you would expect to see if you were looking at a cell in the stage of meiosis indicated. If no circle is present, draw what you would expect to see at the given stage.

[Unnumbered Figure Comes Here]

Note: Whether or not the chromosomes uncoil or decondense at this stage will vary by species.

Follow one daughter cell through meiosis II.

What are the products of meiosis?

4. Consider a single cell going through meiosis.

   a. How many cells are produced at the end of meiosis?

      A single cell going through meiosis produces four daughter cells by the end of meiosis.

   b. How many chromosomes, and which chromosomes, does each of the daughter cells contain?

      Each daughter cell has half the number of chromosomes in the parental cell. Each daughter cell contains one member of each pair of chromosomes found in the parent cell.

5. Six centromeres are observed in a prophase I cell from another species of insect.

a. How many pairs of chromosomes does this organism contain? Three pairs		
b. For each stage of meiosis indicate the number of centromeres you would expect to find and the number of copies of chromosomes attached to each centromere.		
Stage of meiosis:	Number of centromeres visible per cell	Number of chromosome copies attached to each centromere
Anaphase I	6	2
Prophase II	3	2

13.1 Test Your Understanding

Nondisjunction of sex chromosomes during human gamete formation may lead to individuals with sex chromosome trisomy. An individual with the sex chromosome trisomy of XXY may have resulted from nondisjunction occurring in (Circle T if true, F if false):

T/F 1. meiosis I in the father's sperm production

True—Meiosis I in sperm production would result in some gametes with both an X and a Y and some with neither an X nor aY. If an XY sperm fertilized an egg carrying an X chromosome, an XXY individual would be produced.

T/F 2. meiosis II in the father's sperm production

False—Nondisjunction during meiosis II of sperm production would produce sperm with either 2 Xs, 2 Ys, or no X or Y. Any of these sperm fertilizing an egg with an X chromosome would not produce an XXY individual.

T/F 3. meiosis I in the mother's egg production

True—Nondisjunction in meiosis I of egg production could produce eggs with 2 Xs or no X. If fertilized by a sperm carrying a Y chromosome an XXY individual would be produced.

T/F 4. meiosis II in the mother's egg production

True—Nondisjuction in meiosis II of egg production could produce eggs with 2 Xs or no X. If fertilized by a sperm carrying a Y chromosome, an XXY individual would be produced.

Activity 13.2 How do mitosis and meiosis differ?

Review the processes of mitosis and meiosis in Chapters 12 and 13 of *Campbell Biology*, 9th edition, then fill in the chart. Keep in mind that the stages of cell division were first recognized from an examination of fixed slides of tissues undergoing division. On fixed slides, cells are captured or frozen at particular points in the division cycle. Using these static slides, early microscopists identified specific arrangements or patterns of chromosomes that occurred at various stages of the cycle and gave these stages names (interphase, prophase, and so on). Later work using time-lapse photography made it clear that mitosis and meiosis are continuous processes. Once division begins, the chromosomes move fluidly from one phase to the next.

1. What events occur during each phase of mitosis and meiosis?

	Interphase	Prophase	Metaphase	Anaphase	Telophase and cytokinesis
Mitosis	For example: *G_1—cell growth S—DNA duplication G_2—cell growth*	Chromosomes coil and condense. Nuclear membrane breaks down. Spindle forms.	For example: *Duplicated chromosomes, each with two sister chromatids, line up independently on the metaphase plate*.	Sister chromatids move to opposite poles of the spindle.	The events of telophase are the opposite of those in prophase. Cytokinesis is division of the two daughter nuclei into separate cells.
Meiosis I	*G_1—cell growth S—DNA* duplication *G_2—cell growth*	Chromosomes coil and condense. Homologous chromosomes synapse. Nuclear membrane breaks down. Spindle forms.	Synapsed pairs of chromosomes, each with two sister chromatids, line up on the metaphase plate	Members of each homologous pair separate to opposite poles of the spindle.	Chromosomes do not generally uncoil. Nuclear membrane reforms and spindle breaks down. Cytokinesis is division of the two daughter nuclei into separate cells.
Meiosis II	There may be a short G phase to prepare the cell for the next division phase. DNA does NOT	Chromosomes coil and condense. Nuclear membrane breaks down.	Duplicated chromosomes each with two sister chromatids, line up independently	Sister chromatids move to opposite poles of the	The events of telophase are the opposite of these in prophase. Cytokinesis is

	duplicate.	Spindle forms.	on the metaphase plate.	spindle.	division of the two daughter nuclei into separate cells.

2. Fill in the chart to summarize the major similarities and differences in the two types of cell division (mitosis vs. meiosis). For similarities, include the event(s) that always happen(s) at that stage, no matter which of the cell division cycles you're describing.

a. What similarities do you see?	This phase is identical for mitosis and meiosis I.	Chromosomes always coil and condense. Spindle always forms. Nuclear membrane always breaks down.	Something always lines up on the equator or metaphase plate of the spindle.	Something always moves to opposite poles of the spindle.	Nuclear membrane reforms Spindle breaks down.
b. What differences do you see?	No DNA duplication in inter phase of meiosis II. G phase may be shortened.	In prophase I, homologous chromosomes synapse.	In mitosis and metaphase II, individual chromosomes line up. In metaphase I, synapsed pairs line up.	In mitosis and anaphase II, sister chromatids separate and move to opposite poles. In anaphase I, members of each homologous pair separate to opposite poles.	Chromosomes usually don't uncoil during telophase I of meiosis.
c. If the amount of DNA in a somatic cell equals *C* during G_1 of interphase, then how much DNA is present in the cell during each phase of mitosis and meiosis?					
Amount of DNA in:	Interphase	Prophase	Metaphase	Anaphase	Telophase
Mitosis	*C* in G_1 2 *C* in G_2	2 *C*	2 *C*	2 *C*	2 *C* (cytokinesis reduces the amount to *C*)
Meiosis I	*C* in G_1 2 *C* in G_2	2 *C*	2 *C*	2 *C*	2 *C* (cytokinesis reduces the amount to *C*)
Meiosis II	*C* in G_1 *C* in G_2	*C*	*C*	*C*	*C* (cytokinesis reduces the amount to 1/2 *C*)

3. How do the similarities in prophase of mitosis and meiosis compare with the similarities in telophase of mitosis and meiosis?

As noted, telophase can be thought of as the opposite of prophase. In other words, what is done in prophase is undone in telophase.

4. At what stage(s) does/do most of the differences among mitosis, meiosis I, and meiosis II occur? Why do these differences exist?

   The primary differences between mitosis and meiosis occur as a result of synapsis in prophase I. It is synapsis that allows the members of homologous pairs to separate to opposite poles and that reduces the chromosome number at the end of meiosis I to half that of the original cell.

Notes to Instructors

Chapter 14 Mendel and the Gene Idea

What is the focus of these activities?

Meiosis is the basis for Mendel's laws of segregation and independent assortment. If students have a good understanding of meiosis and Mendel's laws, they should be able to demonstrate or model them. They should be able to determine the types of gametes an individual can produce and the probability of each type.

What are the particular activities designed to do?

Activity 14.1 A Genetics Vocabulary Review

Activity 14.2 Modeling meiosis: How can diploid organisms produce haploid gametes?

Activity 14.3 A Quick Guide to Solving Genetics Problems

Activity 14.4 How can you determine all the possible types of gametes?

The activities for Chapter 14 are designed to help students integrate their understanding of meiosis and Mendelian genetics using modern terminology. Activity 14.1 provides a quick review of some modern terminology. Activity 14.2 requires students to integrate their understanding of meiosis (Chapter 13) and of basic Mendelian principles (Chapter 14) to develop a dynamic model of meiosis. Activity 14.3 provides a quick review of some of the basic rules for solving genetics problems. Activity 14.4 provides students with a mechanism for determining the type(s) of gametes that can be produced when the genotype of an organism is known.

What misconceptions or difficulties can these activities reveal?

Activity 14.2 Modeling Meiosis

Almost all students will quickly discover that this activity is not as easy as it first seems. They will also discover that they have difficulty translating the information provided in the activity into a total number of chromosomes, placement of genes and alleles on chromosomes, and so on. If you give students time, however, they will work these problems out for themselves.

A misconception that crops up in a large percentage of the students' models concerns what an X-shaped chromosome represents. Because students (and researchers) generally see only duplicated chromosomes under the microscope (the X-shaped ones), many students have the misconception that this X shape represents a single unduplicated chromosome.

Some students will join a maternal and a paternal chromosome to form the X-shaped (duplicated) chromosome prior to cell division. When they do this, half of the X is usually made from one color of playdough and the other half is a different color. Ask them what the two colors represent. Most will say it's a duplicated

chromosome, and one color represents the maternal chromosome (of the pair) and the other represents the paternal chromosome. Then ask why they are connected to each other and point out that they were separate in the gametes that produced this cell. If left to think about this for a few minutes, most of the student groups will correct themselves.

Most students think the Y chromosome is not shaped like an X when duplicated.

In general, students are unaware they have any of these problems until they are asked to develop a dynamic model of the process.

The questions in this modeling activity ask students how many different kinds of gametes a cell from this individual (genotype *CcBb*) produces at the end of meiosis. Students are to assume no crossing over occurs. The correct answer is two. However, most students have learned that an individual heterozygous for two genes can produce four different kinds of gametes. When asked why they have only two different kinds, most can't answer immediately. Again, give students a few minutes and then return and ask the question again. Most will self-correct. If not, ask them to demonstrate Mendel's law of independent assortment using their cell.

Activities 14.3 and 14.4

Many introductory students have not developed good strategies for solving genetics problems involving more than one gene. These activities are designed to help students understand that if the genes involved are not linked, solving genetics problems one gene at a time is generally the easiest and most accurate method.

Answers

Activity 14.1 A Genetics Vocabulary Review

Mendel did not know anything about chromosomes, genes, or DNA. Because modern genetics uses vocabulary that assumes students today understand these ideas, it's helpful to review some key terms.

Match each commonly used genetics term with its appropriate definition or example.

Terms	Definitions and Examples
e heterozygous	a. Blue-eyed blonde mates with brown-eyed brunette
b homozygous	b. *BB* or *bb*
g monohybrid cross	c. not on sex chromosomes
c autosomal	d. blue or brown eyes
h genotype	e. *Bb*
d phenotype	f. locus on a chromosome that codes for a given polypeptide*
f gene	g. Blonde mates with brunette
d allele	h. *BB*, *Bb*, or *bb*
a dihybrid cross	i. Males have only one for each gene on the X chromosome

* *Note:* Though it is true that a gene can code for a polypeptide, it is important to remember that not all genes code for polypeptides. Some code for mRNAs that produce polypeptides, but others code for other forms of RNA—for example, rRNA and tRNA.

Activity 14.2 Modeling meiosis: How can diploid organisms produce haploid gametes?

Integrate your understanding of meiosis (Chapter 13) and of basic Mendelian principles (Chapter 14) to develop a dynamic model of meiosis. When you've completed the model, use it to explain what aspects of meiosis account for Mendel's laws of segregation and independent assortment.

Building the Model

Working in groups of three or four, construct a dynamic (claymation-type) model of meiosis for the organism described on the next page. You may use the materials provided in class or devise your own.

What genetic and chromosomal traits does your organism have?

1. Your individual is male/female (choose one). Females are XX and males are XY.

   For simplicity, assume that the individual is diploid with $2n = 6$, including the sex chromosomes. On one pair of autosomes (the nonsex chromosomes), the individual is heterozygous for hair color (*B* = brown and dominant, *b* = blonde and recessive). On another pair of autosomes, the organism is heterozygous for hair structure (*C* = curly and dominant, *c* = straight and recessive). Assume further that the individual's mother was homozygous dominant for both traits and the father was homozygous recessive for both.

   a. Is your individual's hair curly or straight? Brown or blonde?

      The individual described is heterozygous for both traits. Therefore, s/he has curly, brown hair.

   b. What did the individual's mother's hair look like? What did the father's hair look like?

      The individual's mother was homozygous dominant and therefore had curly, brown hair. The father was homozygous recessive and had straight, blonde hair.

   c. What chromosomes and alleles were in the egg and the sperm that gave rise to your individual?

      The egg contained an X chromosome, a number 1 chromosome with a brown hair gene, and a number 2 chromosome with a curly gene. The sperm contained an X if your individual is female or a Y if your individual is male. It also contained a number 1 chromosome with the blonde hair gene and a number 2 chromosome with the straight hair gene.

What does the nucleus contain?

To answer this question, develop a model of a cell from your individual.

- Use chalk on a tabletop or a marker on a large sheet of paper to draw a cell's membrane and its nuclear membrane. The nucleus should be at least 9 inches in diameter.
- Use playdough or cutout pieces of paper to represent your individual's chromo-somes. Indicate the placement of genes on the chromosomes. Put all the chromosomes from your individual into the nucleus.
- Make a key for your model that indicates how alleles are designated and which of the chromosomes are maternal versus paternal contributions.

Then develop a model of the meiotically active cell.

- Make an identical copy of the original cell. This will be the "active" cell—that is, the one that undergoes meiosis.
- Using the "active" cell only, develop a dynamic model of meiosis. To do this, actively move the chromosomes of this one cell through a complete round of meiosis in a sex cell. (Sex cells are the cells

of the body that give rise to gametes: ova or sperm.)

- Use your model to demonstrate meiosis to another student group or to your instructor. Then use your model to answer the questions on the next page.

When developing and explaining your model, be sure to include definitions or descriptions of all these terms and structures:

diploid autosome spindle fibers

2*n*/*n* crossing over nuclear membrane

chromosome synapsis nucleolus

chromatid dominant allele heterozygous

chromatin recessive allele phenotype

centromere (kinetochore) genotype homozygous

autosome maternal law of segregation

sex chromosome paternal law of independent assortment

sex cell spindle

What are the products of meiosis?

2. From a single sex cell going through meiosis, how many daughter cells are produced?

   Four cells are produced by the end of meiosis.

3. For your model organism or individual (defined in question 1), how many different kinds of gametes can be produced from a single cell undergoing meiosis? (Assume no crossing over occurs.)

   A single cell from this individual that undergoes meiosis (with no crossing over) produces two different kinds of gametes.

4. Your individual is heterozygous for two genes on separate pairs of homologous chromosomes. His/her genotype is *CcBb*. Given this information alone, how many different kinds of gametes could this individual produce? (Again. assume no crossing over occurs.)

   A heterozygous individual like this could, on average, produce four different kinds of gametes in equal proportions. The kinds of gametes are *CB, Cb, cB*, and *cb*.

5. Compare your answer to question 4 with your answer to question 3. How do the numbers of different kinds of gametes in your answers compare? Explain any difference.

   Any single cell going through meiosis (no crossing over) produces only two types of gametes (maximum). However, that individual has the potential to produce four different kinds of gametes. The particular combination of *C* and *B* alleles in the gametes is a result of how the chromosomes line up at metaphase I. They could line up at metaphase I in either of these ways:

A	B
B//Bb//b	b//b B//B

C//Cc//c	C//Cc//c

If they line up as in box A, the gamete types produced are *BC* and *bc*.

If they line up as in box B, the gamete types produced are *bC* and *Bc*.

Because each way of lining up is equally probable, half the time (statistically) they will line up as in A and half the time as in B. As a result, on average, all four types of gametes are expected to occur in equal proportions.

14.2 Test Your Understanding

What aspect(s) of meiosis account(s) for:

1. Mendel's law of segregation?

   Mendel's law of segregation states that although each organism contains two traits (today known as alleles) for a given character (today known as a gene), only one allele is found in each gamete. Synapsis of homologous chromosomes in prophase I and their separation to opposite poles in anaphase I separate or segregate alleles of a given gene into different gametes.

2. Mendel's law of independent assortment?

   Mendel's law of independent assortment states that the pairs of traits that control each character act independently of each other in gamete formation. (Today we know that the assumption is that these traits or alleles are on separate pairs of homologous chromosomes.) In other words, how one set of traits on one pair of homologous chromosomes segregates in gametes does not affect how another set of traits on a different pair of homologous chromosomes segregates.

The alignment of homologous chromsome pairs relative to each other during metaphase I of meiosis is random. As noted in question 5, how any given pair of chromosomes lines up on the metaphase plate during metaphase I is independent of how any other pair lines up.

Activity 14.3 A Quick Guide to Solving Genetics Problems

Over the years, rules have been developed for setting up genetics problems and denoting genes and their alleles in these problems. This activity provides a quick review of some of these rules. After you have read through all of this material, complete Activities 14.4, 15.1, and 15.2.

Basic Assumptions to Make When Solving Genetics Problems

1. Are the genes linked?

If the problem does not (a) indicate that the genes are linked or (b) ask whether the genes are (or could be) linked, then you should assume that the genes are not linked.

2. Are the genes sex-linked?

Similarly, if the problem does not (a) indicate that the genes are sex-linked (that is, on the X chromosome) or (b) ask whether the genes are (or could be) on the X chromosome (or Y chromosome), then you should assume that the genes are on autosomes and are not sex-linked.

3. Is there a lethal allele?

If a gene is lethal, then you should assume that the offspring that get the lethal allele (if dominant) or alleles (if

homozygous recessive) do not appear; that is, they are not born, do not hatch, and so on. Therefore, they are not counted among the offspring. An obvious exception is lethal genes that have their effect late in life. If this is the case, however, it should be noted in the question.

4. Are the alleles dominant, recessive, or neither?

Unless the problem states otherwise, assume that capital letters (*BB*, for example) designate dominant alleles and lowercase letters (*bb*, for example) indicate recessive alleles. When there is codominance or incomplete dominance, the alleles are usually designated by the same capital letter and each one is given a superscript (for example, $C^R C^W$ in Figure 14.10, page 271, of *Campbell Biology*, 9th edition).

5. How are genotypes written?

Assume a gene for fur color in hamsters is located on the number 1 pair of homologous autosomes. Brown fur (*B*) is dominant over white fur (*b*). The genotype for fur color can be designated in different ways:

a. The alleles can be shown associated with the number 1 chromosome. In this notation, an individual heterozygous for this gene is designated as $|^B|^b$.

b. Most commonly, this notation is simplified to *Bb*.

In problems that involve sex-linked genes, the chromosomes are always indicated—for example, $X^A X^a$ and $X^a Y$.

6. What information do you need to gather before trying to solve a genetics problem?

Before trying to solve any problem, answer these questions:

a. What information is provided? For example:

- What type of cross is it? Is it a monohybrid or dihybrid cross?
- Are the genes sex-linked or autosomal?
- Linked or unlinked?

b. What does the information provided tell you about the gene(s) in question? For example:

- What phenotypes can result?
- How many alleles does the gene have?
- Are the alleles of the gene dominant? Recessive? Codominant?

c. Does the question supply any information about the individuals' genotypes? If so, what information is provided?

- Grandparent information?
- Parental (P) information?
- Gamete possibilities?
- Offspring possibilities?

Solving Genetics Problems

1. What is a Punnett square?

Punnett squares are frequently used in solving genetics problems. A Punnett square is a device that allows you to determine all the possible paired combinations of two sets of characteristics. For example, if you wanted to determine all the possible combinations of red, blue, and green shirts with red, blue, and green pants, you could set up this Punnett square:

		Shirts		
Pants		Red shirt	Blue shirt	Green shirt
	Red pants	Red shirt and red pants	Blue shirt and red pants	Green shirt and red pants
	Blue pants	Red shirt and blue pants	Blue shirt and blue pants	Green shirt and blue pants
	Green pants	Red shirt and green pants	Blue shirt and green pants	Green shirt and green pants

Similarly, if you wanted to determine the probability of a male (XY) and a female (XX) having a son or a daughter, you would first determine the possible gametes each could produce and then set up a Punnett square to look at all the possible combinations of male and female gametes. Here, meiosis dictates that the female's gametes get one of her X chromosomes or the other. In the male, the gametes get either the X chromosome or the Y. As a result, the Punnett square would look like this:

		Female's gamete possibilities	
Male's gamete possibilities	X	X	X
	Y	XX	XX
	Y	XY	XY

2. **If you know the parents' genotypes, how can you determine what types of offspring they will produce?**

   a. **Autosomal genes:** For an autosomal gene that has the alleles *A* and *a*, there are three possible genotypes: *AA*, *Aa*, and *aa*.

All possible combinations of matings and offspring for two individuals carrying the autosomal gene with alleles *A* and *a* are shown in the figure below.

If you know how to solve these six crosses you can solve any problem involving one or more autosomal genes.

[Unnumbered Figure Comes Here]

* *Note:* If you take sex into account there are actually nine possible combinations of matings:

	Female genotypes		
Male genotypes	***AA***	***Aa***	***aa***

AA	*AA* x *AA*	*AA* x *Aa*	***AA* x *aa***
Aa	*Aa* x *AA*	*Aa* x *Aa*	*Aa* x *aa*
aa	***AA* x *aa***	*aa* x *Aa*	*aa* x *aa*

Because the results of reciprocal autosomal matings—e.g., *AA* male with aa female and *aa* male with *AA* female are the same—only one of each reciprocal type is included in the six combinations above.

b. Sex-linked genes: For sex-linked genes that have two alleles, e.g., *w*+ and *w*, females have three possible genotypes: $X^{w+}X^{w+}$, $X^{w+}X^{w}$, and $X^{w}X^{w}$. Males have only two possible genotypes: $X^{w+}Y$ and $X^{w}Y$. All the possible combinations of matings and offspring for a sex-linked trait are listed in the next figure. If you know how to solve these six single-gene crosses, then you can solve any genetics problem involving sex-linked genes.

All possible combinations of matings for two individuals with a sex-linked gene are shown in the figure below. Fill in the Punnet squares to determine all possible combinations of offspring.

[Unnumbered Figure Comes Here]

c. Multiple genes: Remember, if genes are on separate chromosomes, then they assort independently in meiosis. Therefore, to solve a genetics problem involving multiple genes, where each gene is on a separate pair of homologous chromosomes:

- Solve for each gene separately.
- Determine probabilities for combination (multiple-gene) genotypes by multiplying the probabilities of the individual genotypes.

Example:

What is the probability that two individuals of the genotype *AaBb* and *aaBb* will have any *aabb* offspring?

To answer this, solve for each gene separately.

A cross of *Aa* × *aa* could produce the following offspring:

A a

a Aa aa

a Aa aa ½ Aa and ½ aa offspring

A cross of *Bb* × *bb* could produce the following offspring:

B b

B BB Bb

b Bb bb ½ Aa and ½ aa offspring

The probability of having any *aabb* offspring is then the probability of having any *aa* offspring times the probability of having any *bb* offspring.

The probability is $^{1}/_{2} \times {}^{1}/_{4} = {}^{1}/_{8}$.

Activity 14.4 How can you determine all the possible types of gametes?

To solve genetics problems in which genotypes are given, you must first know what types of gametes each organism can produce.

1. How many different kinds of gametes can individuals with each of the following genotypes produce?

   a. *AA* 1 kind of gamete = *A*

   b. *aa* 1 kind of gamete = *a*

   c. *Aa* 2 kinds of gametes = either *A* or *a* in equal proportions

   d. *AaBB* 2 kinds of gametes = either *AB* or *aB* in equal proportions

   e. *AaBb* 4 kinds of gametes = *AB, Ab, aB*, and *ab* in equal proportions

   f. *AaBbCC* 4 kinds of gametes = *ABC, AbC, aBC*, and *abC* in equal proportions

   g. *AaBbCc* 8 kinds of gametes = *ABC, ABc, AbC, Abc, aBC, abC, aBc*, and *abc* in equal proportions

   h. *AaBbCcDdEeFf* 32 different kinds of gametes in equal proportions

2. Based on your answer in question 1, propose a general rule for determining the number of different gametes organisms like those described in question 1 can produce.

   Number of different kinds of gametes = 2^n, where n = number of heterozygous alleles (genes). Here the assumption is that the different genes are on separate pairs of homologous chromosomes.

3. Two individuals have the genotypes *AaBbCcDd*.

   a. How many different types of gametes can each produce?

      $2^n = 2^4 = 16$ different kinds of gametes

   Alles: *A* *a*

   B *AB* *aB*

   b *Ab* *ab*

   Alles: *C* *c*

   D *CD* *cD*

   d *Cd* *cd*

   b. What are these gametes?

      One way of figuring this out is to take two genes at a time.

	AB	*aB*	*Ab*	*ab*
CD	*ABCD*	*aBCD*	*AbCD*	*abCD*
cD	*ABcD*	*aBcD*	*AbcD*	*abcD*
Cd	*ABCd*	*aBCD*	*AbCd*	*abCd*

cd	*ABcd*	*aBcd*	*Abcd*	*abcd*

Then here are all the possible combinations:

c. You set up a Punnett square using all the possible gametes for both individuals. How many "offspring squares" are in this Punnett square?

If you used 16 gametes across the top of the Punnett square and 16 down the side, you have 256 offspring possibilities in this table.

d. If you completed this Punnett square, how easy would it be to find all the "offspring squares" that contain the genotype *AaBBccDd*?

It wouldn't be very easy. On the other hand, it would be very easy to make a mistake in filling in or counting the offspring squares in the table.

e. Given that the genes are all on separate pairs of homologous chromosomes, what other method(s) could you use to determine the probability of these individuals having any offspring with the genotype *AaBbccDd*?

You could handle each gene pair as a separate cross. For example, the cross *AaBbCcDd* × *AaBbCcDd* becomes

$$Aa \times Aa\ Bb \times Bb\ Cc \times Cc \text{ and } Dd \times Dd$$

Each of these crosses has similar results; that is, each produces 1⁄4 homozygous dominant offspring, 1⁄2 heterozygous offspring, and 1⁄4 homozygous recessive offspring. Therefore, the probability that any of their offspring will be *AaBbccDd* is 1⁄2 × 1⁄2 × 1⁄2 × 1⁄2 = 1⁄32.

Notes to Instructors

Chapter 15 The Chromosomal Basis of Inheritance

What is the focus of these activities?

Many students have difficulty solving genetics problems. This is especially true for problems that include both autosomal and sex-linked genes.

What are the particular activities designed to do?

Activity 15.1 Solving problems when the genetics are known

This activity is designed to give students practice in solving autosomal genetics problems, sex-linked genetics problems, and problems that involve both autosomal and sex-linked genes.

Activity 15.2 Solving problems when the genetics are unknown

The types of questions presented in Activity 15.1 provided students with practice solving problems when the genetics of the parents are known. Activity 15.2 asks students to discover the genetics of individuals by setting up and analyzing the results of controlled crosses.

What misconceptions or difficulties can these activities reveal?

Activity 15.1

Question 2b: The answer is zero. Given that, many students automatically think this question was designed to trick them. You may present the following scenario to point out the value of zero as an answer: Assume various

members of your family have been born with a genetic disorder that is lethal by age 25. You want to know the probability that you have this gene and can pass it on to your offspring. How would you feel if the genetic counselor told you that you had zero probability of having the trait? (*Note:* A zero probability is usually given only when a genetic counselor has a direct test for the presence of the gene. If, on the other hand, pedigree analysis indicates that neither of an individual's parents carry the gene, then the counselor is likely to indicate that the individual has a one in a million chance of carrying the gene. In this example, one in a million is the rate of spontaneous mutation of the normal allele to the mutant allele.)

Questions 3 and 4: Many students have difficulty solving sex-linked genetics problems because they try to solve them using the alleles alone. In other words, they do not indicate X and Y chromosomes in their Punnett squares. Many others who do solve the problem correctly with the Punnett square have difficulty determining what the question is asking. For example, is it asking what proportion of all offspring have a certain genotype? Or is it asking what proportion of the males alone, for example, have a certain genotype?

Activities 15.2 and 15.3

Both of these activities are designed to give students practice in some of the actual types of problems/situations that might be encountered by geneticists.

For Activity 15.3, only one way of solving each problem is presented. A number of other approaches could be used, however.

Answers

Activity 15.1 Solving Problems When the Genetics Are Known

Refer to Activity 14.3 and to Chapters 14 and 15 in *Campbell Biology*, 9th edition, to complete this activity.

1. An organism that has the genotype *AaBbCc* is crossed with an organism that has the genotype *AABbCc*. Assume all genes are on separate sets of chromosomes (that is, they are not linked).

   a. What is the probability that any of the offspring will have the genotype *AABBCC*? (*Hint:* To get the answer, consider the six possible types of autosomal crosses. Determine the individual probabilities of getting *AA* offspring from the monohybrid cross. Then do the same to determine the probabilities of getting *BB* offspring and *CC* offspring. Multiply these probabilities together.)

      The probability of any offspring being *AA* = 1⁄2, *BB* = 1⁄4, and *CC* = 1⁄4.Therefore, *AABBCC* = 1⁄2 × 1⁄4 × 1⁄4 = 1⁄34.

   b. What is the probability that any of the offspring will have the genotype *AaBbcc*?

      The probability of any offspring being *Aa* = 1⁄2, *Bb* = 1⁄2, and *cc* = 1⁄4. Therefore, *AaBbcc* = 1⁄2 × 1⁄2 × 1⁄4 = 1⁄16.

2. Consider the cross *AaBbCcddEe* × *AABBccDDEe*.

   a. What is the probability that any offspring will have the genotype *AaBBCcDdEE*?

      1⁄2 × 1⁄2 × 1⁄2 × 1 × 1⁄4 = 1⁄32

   b. What is the probability that any offspring will have the genotype *AABBCCDDee*?

      1⁄2 × 1⁄2 × 0 × 0 × 1⁄4 = 0

3. In fruit flies (*Drosophila melanogaster*), the most common eye color is red. A mutation (or allele) of the gene for eye color produces white eyes. The gene is located on the X chromosome.

a. What is the probability that a heterozygous red-eyed female fruit fly mated with a white-eyed male will produce any white-eyed offspring?

$X^{w+}X^{w} \times X^{w}Y$ = heterozygous red female crossed with a white male

	X^{w+}	X^{w}
X	$X^{w+}X^{w}$	$X^{w}X^{w}$
Y	$X^{w+}Y$	$X^{w}Y$

Half of the offspring will be white-eyed. Half of the females will be white-eyed, and half of the males will be white-eyed.

b. What is the probability that the mating in part a will produce any white-eyed females?

The probability that the cross will produce any white-eyed females is 1⁄2. (Note: The question is asking the *probability* that any of the offspring will be white-eyed and female. It is not asking how many of the females will have white eyes.)

c. What is the probability that this mating will produce any white-eyed males?

Similarly, the probability of producing any white-eyed males is 1⁄2.

4. A heterozygous brown-eyed human female who is a carrier of color blindness marries a blue-eyed male who is not color-blind. Color blindness is a sex-linked trait. Assume that eye color is an autosomal trait and that brown is dominant over blue. What is the probability that any of the offspring produced have the following traits?

Bb $X^{+}X^{cb}$ (female) × *bb* $X^{+}Y$ (male)

Use the two separate crosses: *Bb* × *bb* and $X^{+}X^{cb} \times X^{+}Y$

a. Brown eyes 1⁄2

b. Blue eyes 1⁄2

c. Color blindness 1⁄4

d. Color-blind males 1⁄4

e. Brown-eyed, color-blind males 1⁄2 × 1⁄4 = 1⁄18

f. Blue-eyed, color-blind females 1⁄2 × 0 = 0

g. What is the probability that any of the males will be color-blind?

1⁄2 (Note: This question asks only about the males, not about all of the offspring. If we look at all of the offspring we find 1/4 will be color-blind males.)

h. Why do males show sex-linked traits more often than females?

Males have only one X chromosome. The X chromosome carries many more genes than does the Y chromosome. For example, in humans, the X carries a few thousand genes and the Y carries only a few dozen genes. Females have two alleles for every gene on the X chromosome. Females have the recessive phenotype only when both Xs carry the recessive allele. In contrast, for most genes on the X chromosome, males need to have only the recessive allele to show or display the recessive phenotype.

Activity 15.2 Solving Problems When the Genetics Are Unknown

An understanding of Mendelian genetics allows us to determine the theoretical probabilities associated with normal transmission of autosomal and sex-linked alleles during reproduction. This understanding provides us with strategies for solving genetics problems. In real-life situations, geneticists use these strategies to determine the genetics behind specific phenotypic traits in organisms. They do this by conducting controlled crosses of experimental organisms (e.g. *Drosophila*) or by analyzing family pedigrees (as for humans).

Controlled Crosses

Two problems are presented below. In each, you are given:

a. "Wild population"—the phenotypic characteristics of a wild population of fruit flies that were trapped randomly on a remote island.

b. "Cross 1, 2, etc."—the phenotypic characteristics of offspring from a controlled cross. The phenotypes of the parents are indicated after each cross—e.g., "Cross 1: Male Ambler × Female Wild Type."

For each of the problems, analyze the results in each cross and answer the questions that follow.

1. Problem One

Wild population	Wild type	Ambler	Total
Male	33	17	50
Female		31	19
50			
Total	64	36	100

Cross 1: Male Ambler × Female Wild Type

Offspring Vial 1	Wild type	Ambler	Total
Male	29	24	53
Female	29	31	50
Total	58	55	113

a. What does cross 1 tell you about dominance versus recessiveness of the alleles?

Because you get equal numbers of both phenotypes, it is impossible to determine if one is dominant over the other.

b. What does cross 1 tell you about placement of the alleles on autosomes vs. sex chromosomes?

Because the numbers of males and females in each phenotype is approximately the same, it is again impossible to determine if the allele is on an autosome or a sex chromosome.

Cross 2: Female Ambler × Male Wild Type

Offspring Vial 2	Wild type	Ambler	Total

Male	0	32	32
Female	32	0	32
Total	32	32	64

a. What does cross 2 tell you about dominance versus recessiveness of the alleles?

Because all males are ambler and all females are wild type, this indicates that ambler is recessive.

b. What does cross 2 tell you about placement of the alleles on autosomes vs. sex chromosomes? (In your answer show the chromosomal genotypes for the parents in this cross.)

It indicates that the alleles are on the X chromosome. The parents in this cross must have been $X^{am}X^{am}$ female and $X^{+}Y$.

2. Problem Two

Mt = Monocle; Bt = Bifocal; Tr =Trifocal; Sp = Spinner; Sh = Shing

Wild Population	Mt, Sp	Mt, Sh	Bt, Sp	Bt, Sh	Tr, Sp	Tr, Sh	Total	
Male	10	6	6	0	22	3	47	
Female	19	1	9	1	20	4	54	
Total	29	7	15	1	42	7	101	

Cross 1: Bifocal, Spinner Female × Monocle, Shiny Male

Mt = Monocle; Bt = Bifocal; Tr =Trifocal; Sp = Spinner; Sh = Shing

Offspring Vial 1	Mt, Sp	Mt, Sh	Bt, Sp	Bt, Sh	Tr, Sp	Tr, Sh	Total
Male	0	0	0	0	31	34	65
Female	0	0	0	0	34	38	72
Total	0	0	0	0	65	72	137

a. What does cross 1 tell you about dominance versus recessiveness of the alleles?

These results indicate that Mt and Bt are codominant and the heterozygote is Tr.

However, these results don't indicate whether Sp or Sh is dominant since both appear in relatively equal numbers.

b. What does cross 1 tell you about placement of the alleles on autosomes vs. sex chromosomes?

Since all males and females are hybrid, the Mt and Bt alleles must be autosomal.

It is unclear whether the Sp and Sh alleles are autosomal vs sex linked because numbers of males and females with each trait are similar. You could get the same results if the genes were either sex linked or autosomal.

Cross 2: Monocle, Spinner Female × Trifocal, Spinner Male

Mt = Monocle; Bt = Bifocal; Tr =Trifocal; Sp = Spinner; Sh = Shing

Offspring Vial 2	Mt, Sp	Mt, Sh	Bt, Sp	Bt, Sh	Tr, Sp	Tr, Sh	Total
Male	8	8	0	0	8	8	32
Female	23	0	0	0	15	0	38
Total	31	8	0	0	23	8	70

a. What does cross 2 tell you about dominance versus recessiveness of the alleles?

This confirms that the alleles for Mt and Bt are codominant

MtMt × MtBt =>__ MtMt and __ MtBt offspring (Tr).

Because we get some Sh from an Sp × Sp cross, Sh must be recessive.

b. What does cross 2 tell you about placement of the alleles on autosomes vs. sex chromosomes?

This indicates that the Sp and Sh alleles are on the X chromosome.

The female must be $X^{sp}X^{sh}$ and the male must be $X^{sp}Y$.

The offspring are therefore:

	X^{sp}	X^{sp}
X^{sp}	$X^{sp}X^{sp}$ (Sp females)	$X^{sp}X^{sp}$ (Sp females)
Y	X^{sp} Y (Sp males)	X^{sp} Y (Sh males)

We should see no Sh females and the ratios of the others as in this table:

2 Sp females: 1 Sp males: 1 Sh males.

Analysis of Pedigrees

Analyze the pedigree and answer the questions that follow.

The diagram below shows a pedigree of three generations in a family. Black circles/squares indicate persons with a genetic disorder. A square indicates a male and a circle indicates a female. The two males in generation 1 are siblings.

[Unnumbered Figure Comes Here]

3. Looking only at the generation 2 offspring (of the two generation 1 brothers), what can you say about the gene(s) controlling the genetic disorder? Is the disorder caused by a gene that is dominant or recessive, autosomal or sex-linked?

   The gene is most likely dominant. If it is dominant, the gene may be either autosomal or sex-linked based on these data alone. There is a chance that the gene is recessive. However, for this to be true, the two brothers would both have to mate with a heterozygous female in order to produce the offspring in generation 2. This is much less likely but still a possibilty.

4. What additional information do you gain from examining the generation 3 offspring?

The mating between two affected individuals (lineage A – Generation 2) produces one unaffected male offspring. If the disorder were caused by an autosomal recessive gene, all of the offspring in this cross would be homozygous recessive and have the disorder. Because one male does not have it, the disorder must be caused by a dominant allele. Given the information in generations 2 and 3, it is likely that the allele is also sex-linked (since all daughters of affected males have the disorder and males only have the disorder if their mother had it). However, given that this is a relatively small population, there is still a possibility that the disorder is autosomal, dominant.

Activity 15.3 How can the mode of inheritance be determined experimentally?

Outline the experimental crosses you would need to make to solve each problem.

1. Three new traits have been discovered in a population of *Drosophila*:

   - Tapping (a behavioral mutant in which the fly taps one foot constantly)
   - Single stripe (a pigmentation change that leads to a long stripe down the fly's back)
   - Angular (causes angular bends in bristles that are normally straight)

The positions of the three genes on the chromosomes are unknown. Given two pure breeding (homozygous) lines and using an initial cross of normal, normal, normal females with tapping, single stripe, angular males, describe the appropriate genetic experiments needed to establish whether any of these traits are caused by genes that are:

a. Autosomal or sex-linked

First, mate normal, normal, normal homozygous females with tapping, single stripe, angular males. The phenotypes of the F_1 individuals will indicate which alleles are dominant. Next, mate the F_1 males with females that are homozygous recessive for all three traits, and mate the F_1 females with males that are homozygous recessive for all three traits. Examine the ratio of phenotypes for each trait in the offspring as a whole. Compare the ratio for the offspring as a whole with the ratio for each sex. For example, if we assume normal is dominant in all cases, then the crosses would look like this:

$$AABBCC \times aabbcc$$

$$\text{All } F_1 \times AaBbCc$$

F_1 crosses with homozygous recessive mates: $AaBbCc \times aabbcc$

Male	A	a	Female	A	A
a	Aa	aa	a	Aa	aa
A	Aa	aa	a	Aa	aa

OR OR

Male	X^A	Y	Female	X^A	X^A
X^a	X^AX^A	X^AY	X^a	X^AX^A	X^AX^A
X^a	X^AX^A	X^AY	Y	X^AY	X^AY

Note that the ratios of offspring phenotypes are the same for an autosomal cross of a heterozygous male with a homozygous recessive female and for a heterozygous female with a homozygous recessive male.

In both cases, half of the offspring are *Aa* and half are *aa*. If the gene is sex-linked, however, the results differ. When a male F_1 showing the dominant phenotype is mated with a recessive phenotype female, all the females show the dominant phenotype and all the males show the recessive phenotype. When a female F_1 showing the dominant phenotype is mated with a recessive phenotype male, half of the males and half of the females show the recessive phenotype.

b. Linked on the same chromosome or unlinked

If the genes are not linked, we expect the probability of offspring with a given set of phenotypes—for example, normal, one stripe, angular—to be equal to the product of the individual probabilities for each occurring as separate crosses. For example, if the genes are autosomal, then the F_1 mating is *AaBbCc* × *aabbcc*. If the genes are not linked, we expect to see 1⁄2 normal, 1⁄2 one stripe, and 1⁄2 angular among the offspring. The probability of all these characteristics showing in the same offspring is 1⁄2 × 1⁄2 × 1⁄2 = 1⁄18. If *A* and *B* are linked, we get different results. The F_1 cross becomes *AB/ab* × *ab/ab* &ARROW; 1⁄2 *AB/ab* and 1⁄2 *ab/ab* (if no crossing over occurs) and *Cc* × *cc* &ARROW; 1⁄2 *Cc* and 1⁄2 *cc*. The following table lists the combinations of the offspring:

	½ AB/ab	½ ab/ab
½ Cc	¼ AaBbCc	¼ aabbCc
½ Cc	¼ AaBbcc	¼ aabbc

If no crossing over occurs, normal, one stripe, and angular offspring do not appear.

2. A genetics student chose a special project involving a three-gene cross to check the relative positions and map distances separating three genes in *Drosophila* that she thought were all on the third chromosome. To do this, she mated *Drosophila* females that were homozygous for the recessive genes *cu* (curled), *sr* (striped), and *e* (ebony) with males that were homozygous for the wild type, cu^+ (straight), sr^+ (not striped), and e^+ (gray). She then mated (testcrossed) the F_1 females with homozygous recessive curled, striped, ebony males.

Here are the phenotypic results of the testcross:

straight, gray, not striped	820
curled, ebony, striped	810
straight, ebony, striped	100
curled, gray, not striped	97
straight, ebony, not striped	80
curled, gray, striped	90
straight, gray, striped	1
curled, ebony, not striped	2
Total	2,000

a. How are the three genes arranged on the chromosomes?

The three genes appear to be linked on the same chromosome.

b. What evidence allows you to answer the question in part a?

If one of the genes was not linked, we would expect to see results similar to those calculated in part b of question 1, where we looked at the results we would get if *A* and *B* were linked but *C* wasn't. Instead, we see many more of the parental phenotypes (straight, gray, not striped and curled, ebony, striped) than any other type. The other types are therefore most likely the result of crossovers. For example, the F_1 chromosomes might look like this:

–*cu*$^+$_____ *e*$^+$_____ *sr*$^+$_____

–*cu*$^+$_____ *e*$^+$_____ *sr*$^+$_____

–*cu*_____ *e*_____ *sr*_____

–*cu*_____ *e*_____ *sr*_____

A crossover between the *cu*$^+$ and the *e* on one homologous chromosome and the *cu* and the *e* on the other would result in some offspring that have these phenotypes:

Curled, gray, not striped and straight, ebony, striped

–*cu*_____ *e*$^+$_____ *sr*$^+$_____ –*cu*$^+$_____ *e*_____ *sr*_____

–*cu*_____ *e*_____ *sr*_____ –*cu*_____ *e*_____ *sr*_____

c. If any of the genes are linked, how far apart are they on the chromosome? How can you determine this?

First, look at the double crossovers to determine how the genes are arranged on the chromosome. The offspring phenotypes that occur in the smallest numbers are most likely to be the result of double crossovers. They are

straight, gray, striped 1/2000

curled, ebony, not striped 2/2000

For these phenotypes to be the result of double crossovers, the order of genes on the chromosome has to be

–*cu*$^+$_____ *sr*$^+$_____ *e*$^+$

–*cu*_____ *sr*_____ *e*

Given this order, the following phenotypes occurred because of crossovers between *cu*$^+$ and *sr*$^+$:

straight, ebony, striped	100
curled, gray, not striped	97
Subtotal	197

These phenotypes occurred because of crossovers between *sr*$^+$ and *e*$^+$:

straight, ebony, not striped	80
curled, gray, striped	90
Subtotal	170

If we add the double crossovers to each subtotal (because each represents an additional crossover at each of these sites), then the percent crossover between *cu*$^+$ and *sr*$^+$ = 197 + 3 = 200/2000 (× 100) = 10%. The

percent crossover between sr^+ and e^+ = 170 + 3 = 173/2000 (× 100) = 8.7%. Because 1% crossover is said to be equivalent to one centimorgan in distance, the cu^+ and sr^+ genes are 10 centimorgans apart and the Jsr^+ and e^+ genes are 8.7 centimorgans apart.