



CELL DIVISION AND INHERITANCE

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Concepts

1. The genetic material is organized into chromosomes. Chromosomes may be represented differently in males and females. However, the number of chromosomes is constant for a given species.
2. Mitosis is the form of cell division that results in growth and repair processes. It ensures an orderly and accurate distribution of chromosomes during the cell cycle. Cytokinesis results in the division of the cytoplasm.
3. Meiosis is the form of cell division that results in the formation of gametes. It reduces the chromosome number by half and allows for the random distribution of one member of each pair of parental chromosomes to the offspring.
4. Deoxyribonucleic acid (DNA) is the genetic material of the cell. Its double helix structure suggests how it can replicate itself and how it can code for the sequences of amino acids that make proteins.
5. Protein synthesis involves two processes. Transcription is the production of a messenger RNA (mRNA) molecule that is complementary to a gene in DNA. Translation is the assembly of proteins at the ribosomes based on the genetic information in the transcribed mRNA.
6. Changes in DNA and chromosomes increase the variation within a species and account for evolutionary change.
7. Principles of classical genetics explain the inheritance patterns of many animal traits, including dominance, segregation, and independent assortment.
8. Many alternative forms of a gene may exist in a population, and these alternative forms may interact in different ways.
9. Patterns of inheritance observed at an organismal level are explained at a molecular level by the presence or absence of functional enzymes.

Reproduction is essential for life. Each organism exists solely because its ancestors succeeded in producing progeny that could develop, survive, and reach reproductive age. At its most basic level, reproduction involves a single cell reproducing itself. For a unicellular organism, cellular reproduction also reproduces the organism. For multicellular organisms, cellular reproduction is involved in growth, repair, and the formation of sperm and egg cells that enable the organism to reproduce.

At the molecular level, reproduction involves the cell's unique capacity to manipulate large amounts of DNA, DNA's ability to replicate, and DNA's ability to carry information that will determine the characteristics of cells in the next generation. **Genetics** (Gr. *gennan*, to produce) is the study of how biological information is transmitted from one generation to the

This chapter contains evolutionary concepts, which are set off in this font.

next. Modern molecular genetics provides biochemical explanations of how this information is expressed in an organism. It holds the key to understanding the basis for inheritance. Information carried in DNA is manifested in the kinds of proteins that exist in each individual. Proteins contribute to observable traits, such as eye color and hair color, and they function as enzymes that regulate the rates of chemical reactions in organisms. Within certain environmental limits, animals are what they are by the proteins that they synthesize.

At the level of the organism, reproduction involves passing DNA between individuals. The classical approach to genetics involves observing patterns of inheritance between generations. This work began with Gregor Mendel (1822–1884) and continues today.

Gregor Mendel began a genetics revolution that has had a tremendous effect on biology and our society. **Genetic mechanisms explain how traits are passed between generations. They also help explain how species change over time. Genetic and evolutionary themes are interdependent in biology, and biology without either would be unrecognizable from its present form.** Genetic technologies have tremendous potential to improve crop production and health care, but society must deal with issues related to whole-organism cloning, the use of engineered organisms in biological warfare, and the application of genetic technologies to humans. This chapter introduces principles of cell division and genetics that are essential to understanding why animals function as they do, and it provides the background information to help you understand the genetic basis of evolutionary change that will be covered in chapters 4 and 5.

EUKARYOTIC CHROMOSOMES

DNA is the genetic material, and it exists with protein in the form of chromosomes in eukaryotic cells. During most of the life of a cell, chromosomes are in a highly dispersed state called chromatin. During these times, units of inheritance called **genes** (Gr. *genos*, race) may actively participate in the formation of protein. When a cell is dividing, however, chromosomes exist in a highly folded and condensed state that allows them to be distributed between new cells being produced. The structure of these chromosomes will be described in more detail in the discussion of cell division that follows.

Chromatin consists of DNA and histone proteins. This association of DNA and protein helps with the complex jobs of packing DNA into chromosomes and regulating DNA activity.

There are five different histone proteins. Some of these proteins form a core particle. DNA wraps in a coil around the proteins, a combination called a **nucleosome** (figure 3.1). The fifth histone, sometimes called the linker protein, is not needed to form the nucleosome but may help anchor the DNA to the core and promote the winding of the chain of nucleosomes into a cylinder. Further folding and the addition of protective proteins result in the formation of chromosomes during mitosis and meiosis.

Not all chromatin is equally active. Some human genes, for example, are active only after adolescence. In other cases, entire chromosomes may not function in particular cells. Inactive portions of chromosomes produce dark banding patterns with certain staining procedures and thus are called **heterochromatic regions**, whereas active portions of chromosomes are called **euchromatic regions**.

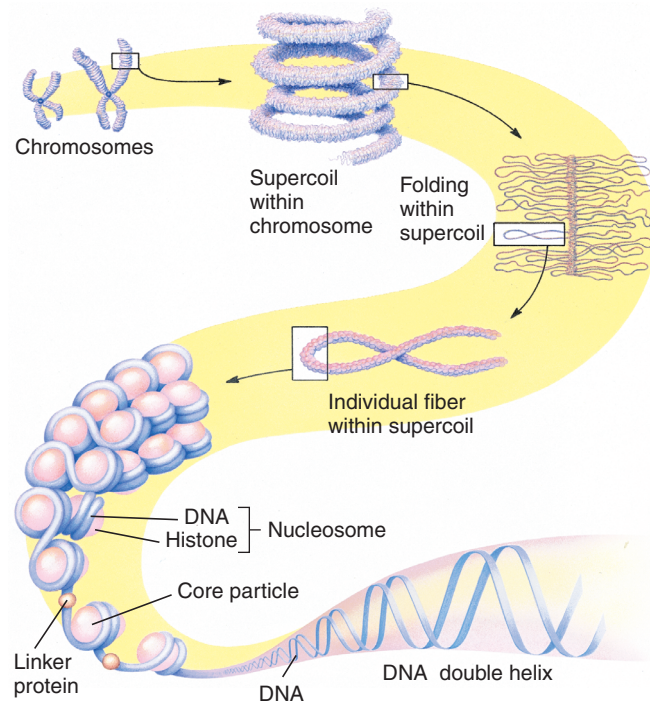


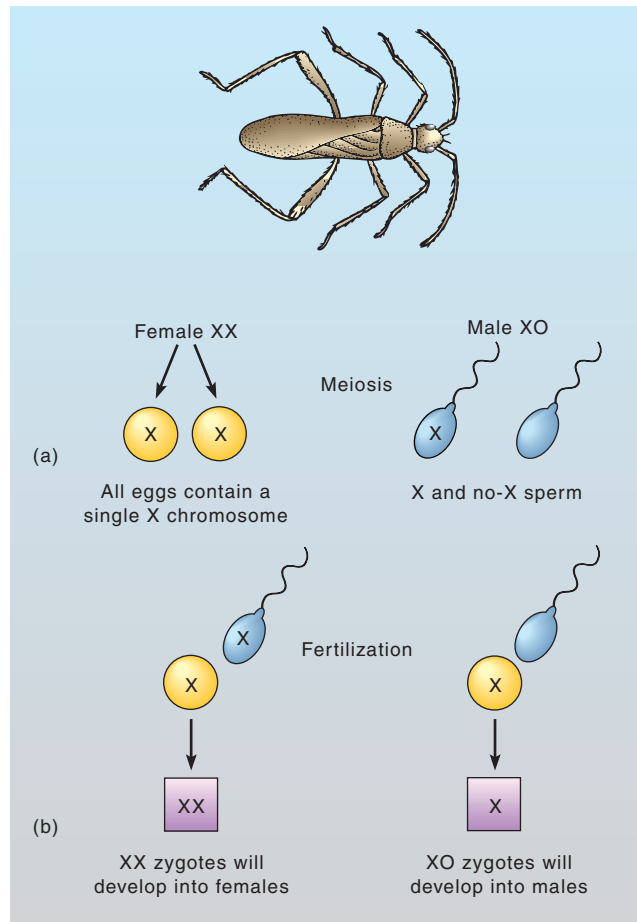
FIGURE 3.1

Organization of Eukaryotic Chromosomes. Chromosomes consist of a supercoil of highly folded chromatin. Chromatin is a chain of nucleosomes. Each nucleosome is comprised of histone proteins wound by a strand of DNA. Linker histone proteins are associated with DNA between adjacent nucleosomes.

SEX CHROMOSOMES AND AUTOSOMES

In the early 1900s, attention turned to the cell to find a chromosomal explanation for the determination of maleness or femaleness. Some of the evidence for a chromosomal basis for sex determination came from work with the insect *Protenor*. One darkly staining chromosome of *Protenor*, called the X chromosome, is represented differently in males and females. All somatic (body) cells of males have one X chromosome (XO), and all somatic cells of females have two X chromosomes (XX). Similarly, half of all sperm contain a single X, and half contain no X, while all female gametes contain a single X. This pattern suggests that fertilization involving an X-bearing sperm will result in a female offspring and that fertilization involving a sperm with no X chromosome will result in a male offspring. As figure 3.2 illustrates, this sex determination system explains the approximately 50:50 ratio of females to males in this insect species. Chromosomes that are represented differently in females than in males and function in sex determination are **sex chromosomes**. Chromosomes that are alike and not involved in determining sex are **autosomes** (Gr. *autus*, self + *soma*, body).

The system of sex determination described for *Protenor* is called the X-O system. It is the simplest system for determining sex because it involves only one kind of chromosome. Many other animals (e.g., humans and fruit flies) have an X-Y system of sex determination. In the X-Y system, males and females have an

**FIGURE 3.2**

XO-System of Sex Determination for the Insect Protenor. (a) In females, all cells except gametes possess two X chromosomes. During meiosis, homologous X chromosomes segregate, and all eggs contain one X chromosome. Males possess one X chromosome per cell. Meiosis results in half of all sperm cells having one X, and half of all sperm cells having no X. (b) Fertilization results in half of all offspring having one X chromosome (males), and half of all offspring having two X chromosomes (females).

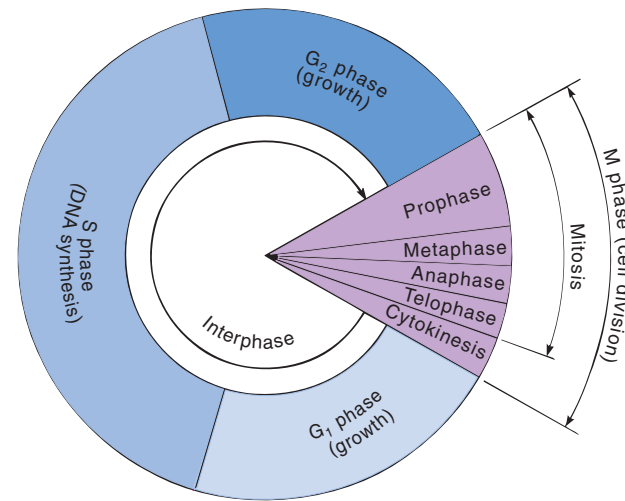
equal number of chromosomes, but the male is usually XY, and the female is XX. (In birds, the sex chromosomes are designated Z and W, and the female is ZW.) This mode of sex determination also results in approximately equal numbers of male and female offspring:

	Sperm	
	X	Y
Egg X	XX	XY
	1 female : 1 male	

NUMBER OF CHROMOSOMES

Even though the number of chromosomes is constant within a species, chromosome number varies greatly among species.

Chromosomes are present in sets, with the number in a set being characteristic of each kind of animal and expressed as “N.”

**FIGURE 3.3**

Life Cycle of a Eukaryotic Cell. During the G₁ phase, cell components are synthesized and metabolism occurs, often resulting in cell growth. During the S (synthesis) phase, the chromosomes replicate, resulting in two identical copies called sister chromatids. During the G₂ phase, metabolism and growth continue until the mitotic phase is reached. This drawing is generalized, and the length of different stages varies greatly from one cell to the next. Source: Stuart Ira Fox, *Human Physiology*, 4th ed., copyright © 1993 Wm. C. Brown Communications, Inc., Dubuque, Iowa.

N identifies the number of different kinds of chromosomes. Most animals have two sets, or 2N chromosomes. This is the **diploid** (Gr. *di*, two + *eoides*, doubled) condition. Some animals have only one set, or N chromosomes (like gametes) and are **haploid** (Gr. *hapl*, single) (e.g., male honeybees and some rotifers).

Very few animals (e.g., brine shrimp, snout beetles, some flatworms, and some sow bugs) have more than the diploid number of chromosomes, a condition called **polyploidy** (Gr. *polys*, more). The upset in numbers of sex chromosomes apparently interferes with reproductive success. Asexual reproduction often accompanies polyploidy.

MITOTIC CELL DIVISION

Cell division occurs in all animals during growth and repair processes. Cells divide in two basic stages: **Mitosis** is division of the nucleus, and **cytokinesis** (Gr. *kytos*, hollow vessel + *kinesis*, motion) is division of the cytoplasm. Between divisions (interphase), the cell must grow and carry out its various metabolic processes. The **cell cycle** is that period from the time a cell is produced until it completes mitosis (figure 3.3).

The G₁ (first growth or gap) phase represents the early growth phase of the cell. During the S (DNA synthesis) phase, growth continues, but this phase also involves DNA replication. The G₂ (second growth or gap) phase prepares the cell for division. It includes replication of the mitochondria and other organelles, synthesis of microtubules and protein that will make up the mitotic spindle fibers, and chromosome condensation. The M (mitotic) phase includes events associated with partitioning

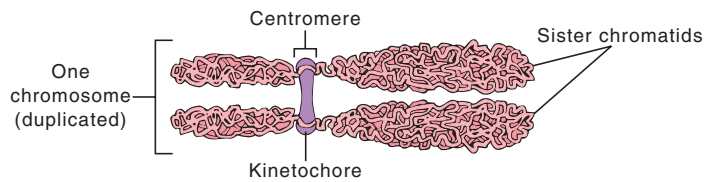


FIGURE 3.4

Duplicated Chromosomes. Each parental chromosome replicates to make two genetically identical sister chromatids attached at a region of DNA called the centromere. The kinetochore is a disk of protein that is bound at the centromere and is an attachment site for microtubules.

chromosomes between two daughter cells and the division of the cytoplasm (cytokinesis).

INTERPHASE: REPLICATING THE HEREDITARY MATERIAL

Interphase (*L. inter*, between) (includes the G_1 , S, and G_2 phases) typically occupies about 90% of the total cell cycle. It is the period during which the normal activities of the cell take place. Interphase also sets the stage for cell division because DNA replication is completed during the S phase of interphase.

Before a cell divides, an exact copy of the DNA is made. This process is called replication, because the double-stranded DNA makes a replica, or duplicate, of itself. Replication is essential to ensure that each daughter cell receives the same genetic material as is present in the parent cell. The result is a pair of **sister chromatids** (figure 3.4). A **chromatid** is a copy of a chromosome produced by replication. Each chromatid attaches to its other copy, or sister, at a point of constriction called a centromere. The **centromere** is a specific DNA sequence of about 220 nucleotides and has a specific location on any given chromosome. Bound to each centromere is a disk of protein called a **kinetochore**, which eventually is an attachment site for the microtubules of the mitotic spindle.

As the cell cycle moves into the G_2 phase the chromosomes begin condensation. During the G_2 phase, the cell also begins to assemble the structures that it will later use to move the chromosomes to opposite poles (ends) of the cell. For example, centrioles replicate, and there is extensive synthesis of the proteins that make up the microtubules.

MITOSIS

Mitosis is divided into four phases: prophase, metaphase, anaphase, and telophase. In a dividing cell, however, the process is actually continuous, with each phase smoothly flowing into the next (figure 3.5).

The first phase of mitosis, **prophase** (Gr. *pro*, before + phase), begins when chromosomes become visible with the light microscope as threadlike structures. The nucleoli and nuclear envelope begin to break up, and the two centriole pairs move apart. By the end of prophase, the centriole pairs are at opposite poles of the cell. The centrioles radiate an array of microtubules called

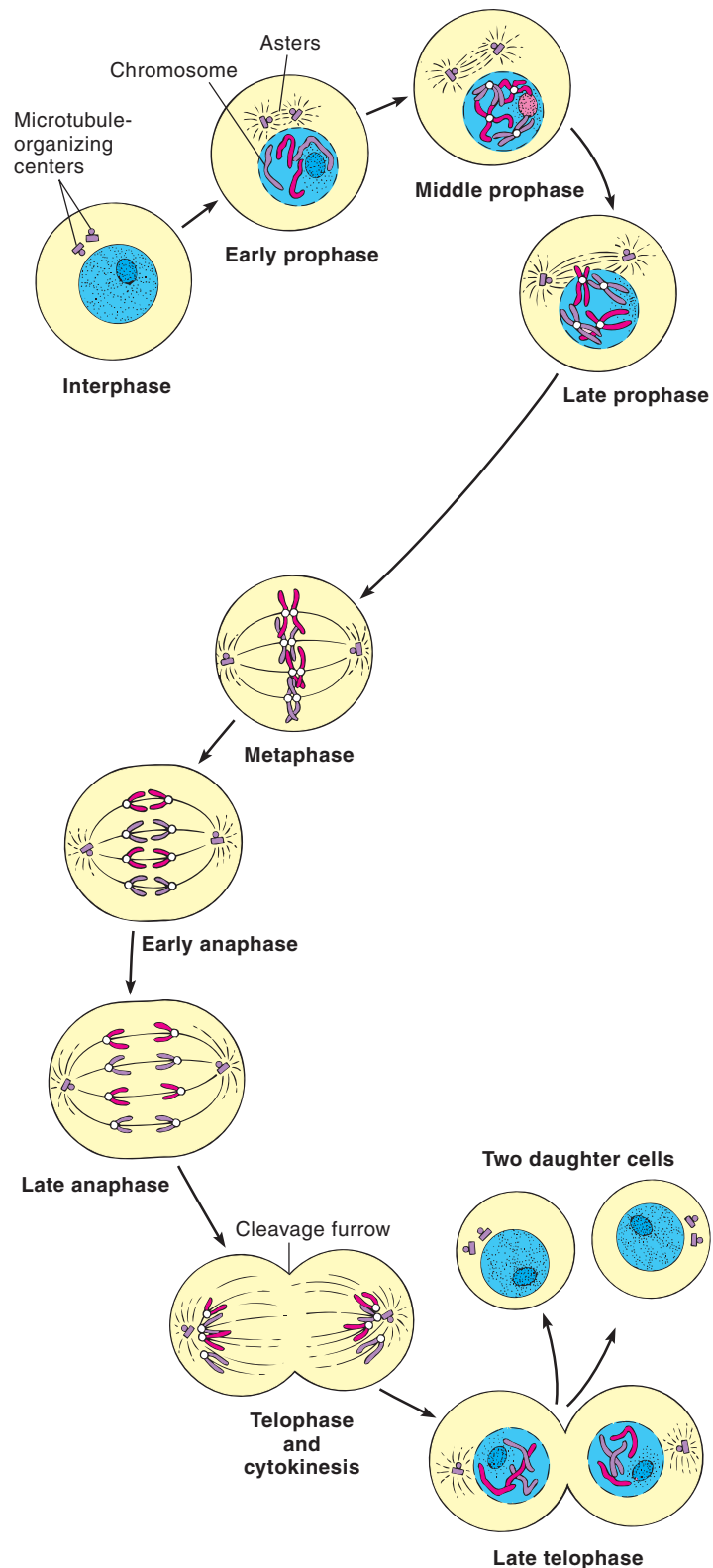


FIGURE 3.5

Continuum of Mitosis and Cytokinesis. Mitosis is a continuous process during which the nuclear parts of a cell divide into two equal portions.

asters (L. *aster*, little star), which brace each centriole against the plasma membrane. Between the centrioles, the microtubules form a spindle of fibers that extends from pole to pole. The asters, spindle, centrioles, and microtubules are collectively called the **mitotic spindle** (or mitotic apparatus). As prophase continues, a second group of microtubules grows out from the kinetochore to the poles of the cell. These kinetochore microtubules connect each sister chromatid to the poles of the spindle.

As the dividing cell moves into **metaphase** (Gr. *meta*, after + phase), the chromatids (replicated chromosomes) begin to align in the center of the cell, along the spindle equator. Toward the end of metaphase, the centromeres divide and detach the two sister chromatids from each other, although the chromatids remain aligned next to each other. After the centromeres divide, the sister chromatids are considered full-fledged chromosomes (called daughter chromosomes).

During **anaphase** (Gr. *ana*, back again + phase), the shortening of the microtubules in the mitotic spindle pulls each daughter chromosome apart from its copy and toward its respective pole. Anaphase ends when all the daughter chromosomes have moved to the poles of the cell. Each pole now has a complete, identical set of chromosomes.

Telophase (Gr. *telos*, end + phase) begins once the daughter chromosomes arrive at the opposite poles of the cell. During telophase, the mitotic spindle disassembles. A nuclear envelope reforms around each set of chromosomes, which begin to uncoil for gene expression, and the nucleolus is resynthesized. The cell also begins to pinch in the middle. Mitosis is over, but cell division is not.

CYTOKINESIS: PARTITIONING THE CYTOPLASM

The final phase of cell division is cytokinesis, in which the cytoplasm divides. Cytokinesis usually starts sometime during late anaphase or early telophase. A contracting belt of microfilaments called the contractile ring pinches the plasma membrane to form the cleavage furrow. The furrow deepens, and two new, genetically identical daughter cells form.

MEIOSIS: THE BASIS OF SEXUAL REPRODUCTION

Sexual reproduction requires a genetic contribution from two different sex cells. Egg and sperm cells are specialized sex cells called **gametes** (Gr. *gamete*, wife; *gametes*, husband). In animals, a male gamete (sperm) unites with a female gamete (egg) during fertilization to form a single cell called a **zygote** (Gr. *zygotos*, yoked together). The fusion of gametes is called **syngamy** (Gr. *gamos*, marriage). The zygote is the first cell of the new animal. Each of the two gametes contributes half of the genetic information to the zygote.

To maintain a constant number of chromosomes in the next generation, animals that reproduce sexually must produce gametes with half the chromosome number of their ordinary body cells (called **somatic cells**). All of the cells in the bodies of most

animals, except for the egg and sperm cells, have the diploid ($2N$) number of chromosomes. A type of cell division called **meiosis** (Gr. *meiosis*, diminution) occurs in specialized cells of the ovaries and testes and reduces the number of chromosomes to the haploid ($1N$) number. The nuclei of the two gametes combine during fertilization and restore the diploid number.

Meiosis begins after the G_2 phase in the cell cycle—after DNA replication. Two successive nuclear divisions, designated meiosis I and meiosis II, take place. The two nuclear divisions of meiosis result in four daughter cells, each with half the number of chromosomes of the parent cell. Moreover, these daughter cells are not genetically identical. Like mitosis, meiosis is a continuous process, and biologists divide it into the phases that follow only for convenience.

THE FIRST MEIOTIC DIVISION

In prophase I; chromatin folds and chromosomes become visible under a light microscope (figure 3.6a). Because a cell has a copy of each type of chromosome from each original parent cell, it contains the diploid number of chromosomes. **Homologous chromosomes** (homologues) carry genes for the same traits, are the same length, and have a similar staining pattern, making them identifiable as matching pairs. During prophase I, homologous chromosomes line up side-by-side in a process called **synapsis** (Gr. *synapsis*, conjunction), forming a **tetrad** of chromatids (also called a bivalent). The tetrad thus contains the two homologous chromosomes, each with its copy, or sister chromatid (figure 3.7). A network of protein and RNA is laid down between the sister chromatids of the two homologous chromosomes. This network holds the sister chromatids in a precise union so that each gene is directly across from its sister gene on the homologous chromosome.

Synapsis also initiates a series of events called **crossing-over**, whereby the nonsister chromatids of the two homologous chromosomes in a tetrad exchange DNA segments (figure 3.7). This process effectively redistributes genetic information among the paired homologous chromosomes and produces new combinations of genes on the various chromatids in homologous pairs. Thus, each chromatid ends up with new combinations of instructions for a variety of traits. **Crossing-over is a form of genetic recombination and is a major source of genetic variation in a population of a given species.**

In metaphase I, the microtubules form a spindle apparatus just as in mitosis (see figures 3.4 and 3.5). However, unlike mitosis, where homologous chromosomes do not pair, each pair of homologues lines up in the center of the cell, with centromeres on each side of the spindle equator.

Anaphase I begins when homologous chromosomes separate and begin to move toward each pole. Because the orientation of each pair of homologous chromosomes in the center of the cell is random, the specific chromosomes that each pole receives from each pair of homologues are also random.

Meiotic telophase I is similar to mitotic telophase. The transition to the second nuclear division is called interkinesis. Cells proceeding through interkinesis do not replicate their DNA. After a varying time period, meiosis II occurs.

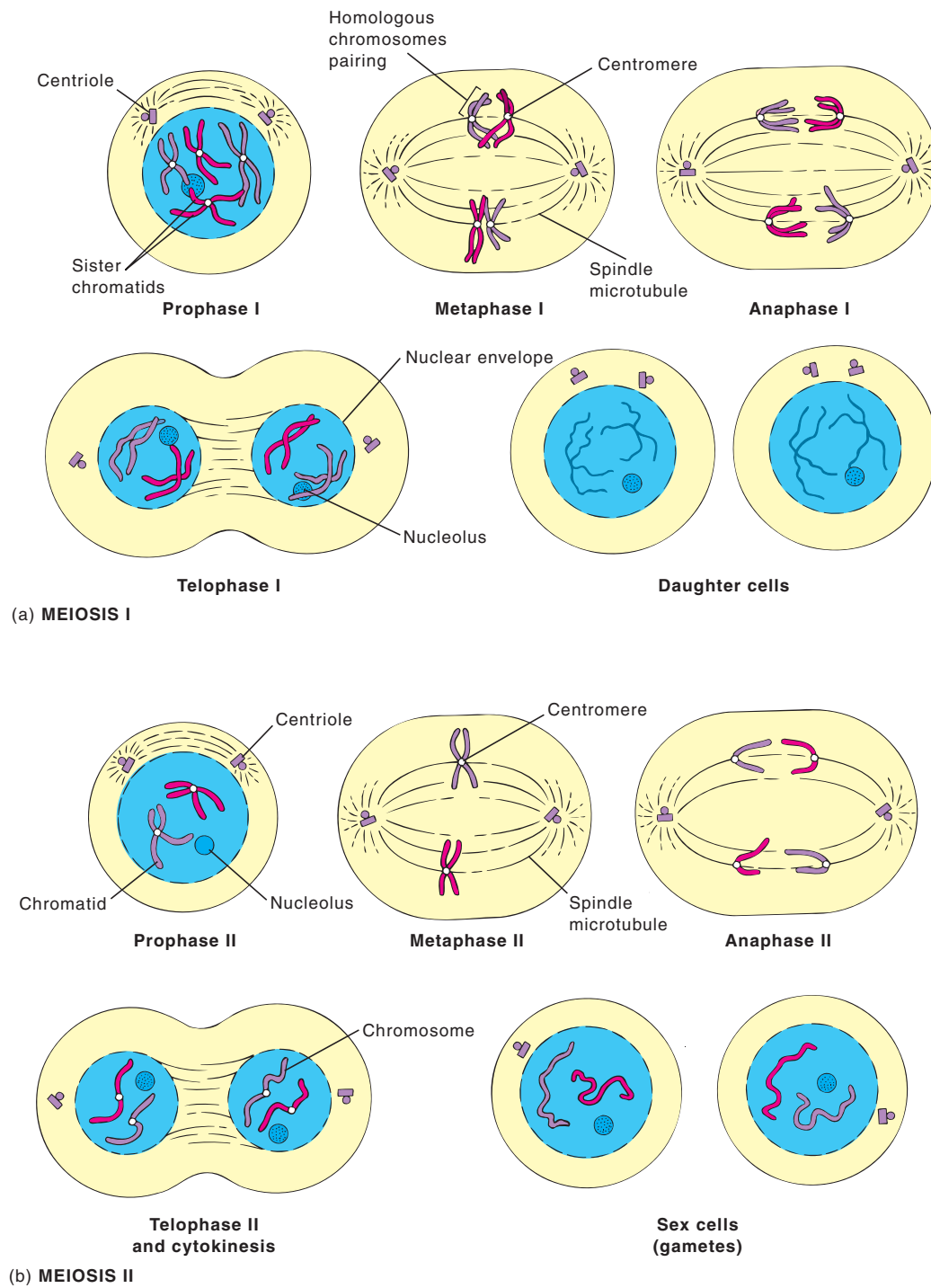


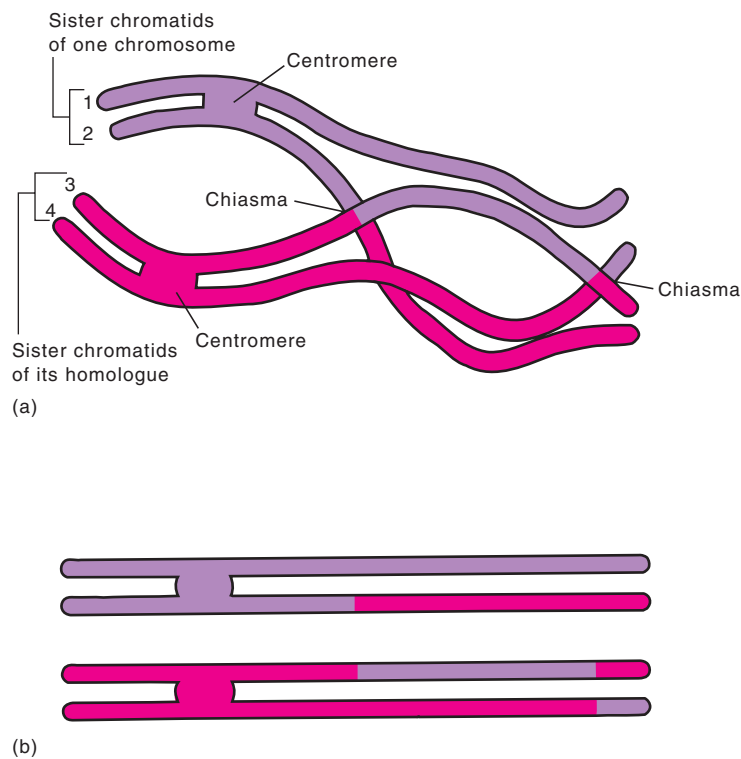
FIGURE 3.6

Meiosis and Cytokinesis. (a) Stages in the first meiotic division. (b) Stages in the second meiotic division.

THE SECOND MEIOTIC DIVISION

The second meiotic division (meiosis II) resembles an ordinary mitotic division (see figure 3.6b), except the number of chromosomes has been reduced by half. The phases are prophase II,

metaphase II, anaphase II, and telophase II. At the end of telophase II and cytokinesis, the final products of these two divisions of meiosis are four new “division products.” In most animals, each of these “division products” is haploid and may function directly as a gamete (sex cell).

**FIGURE 3.7**

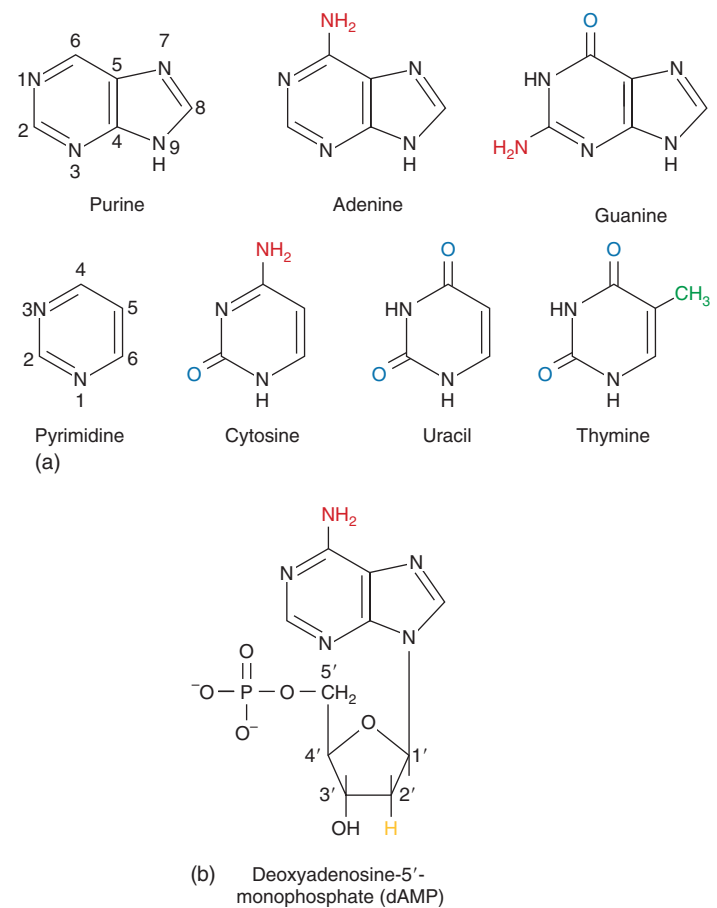
Synapsis and Crossing-Over. (a) Crossing-over and the location of chiasmata, where nonsister chromatids remain temporarily attached. (b) The same chromosomes diagrammatically separated to show the result of crossing-over.

SPERMATOGENESIS AND OOGENESIS

The result of meiosis in most animals is the formation of sperm and egg cells. **Spermatogenesis** produces mature sperm cells and follows the sequence previously described. All four products of meiosis often acquire a flagellum for locomotion and a caplike structure that aids in the penetration of the egg. **Oogenesis** produces a mature ovum or egg. It differs from spermatogenesis in that only one of the four meiotic products develops into the functional gamete. The other products of meiosis are called polar bodies and eventually disintegrate. In some animals the mature egg is the product of the first meiotic division and only completes meiosis if it is fertilized.

DNA: THE GENETIC MATERIAL

Twentieth-century biologists realized that a molecule that serves as the genetic material must have certain characteristics to explain the properties of life: First, the genetic material must be able to code for the sequence of amino acids in proteins and control protein synthesis. Second, it must be able to replicate itself prior to cell division. Third, the genetic material must be in the nucleus of eukaryotic cells. Fourth, it must be able to change over time to

**FIGURE 3.8**

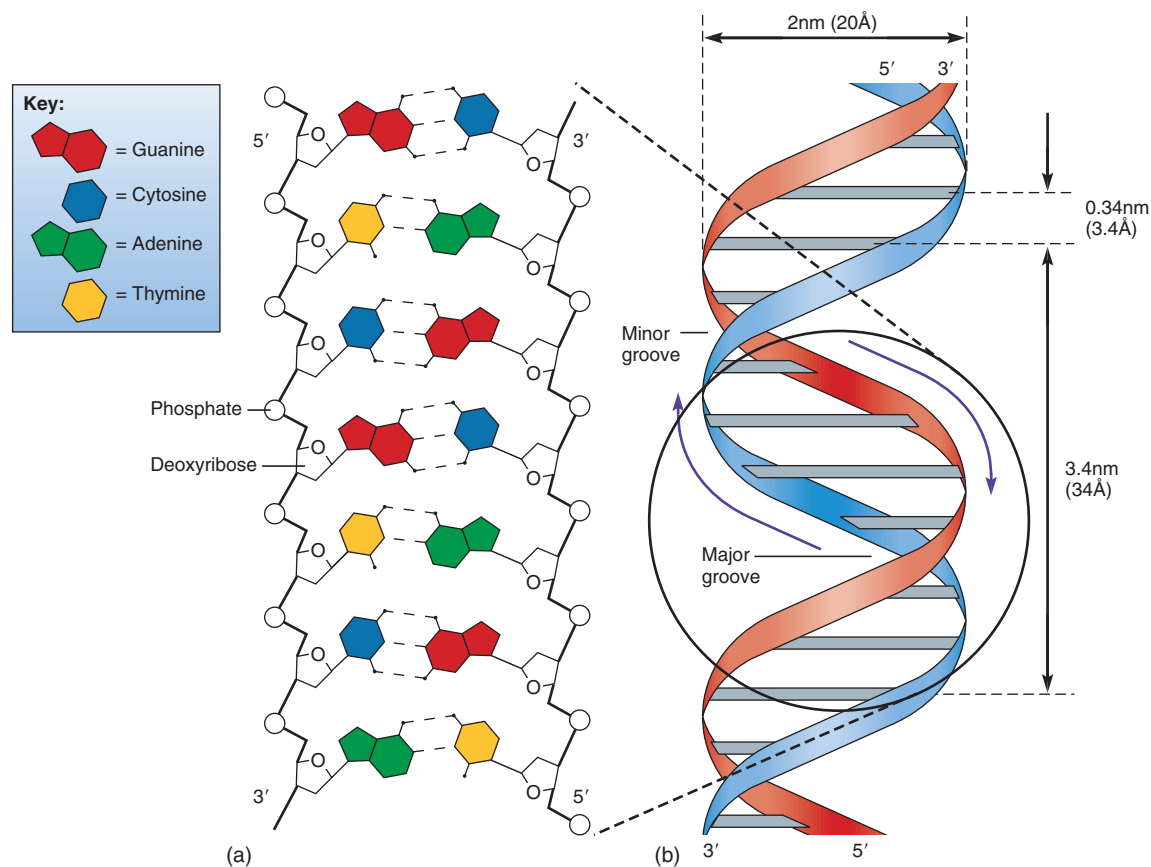
Components of Nucleic Acids. (a) The nitrogenous bases in DNA and RNA. (b) Nucleotides form by attaching a nitrogenous base to the 1' carbon of a pentose sugar and attaching a phosphoric acid to the 5' carbon of the sugar. (Carbons of the sugar are numbered with primes to distinguish them from the carbons of the nitrogenous base.) The sugar in DNA is deoxyribose, and the sugar in RNA is ribose. In ribose, a hydroxyl group ($-\text{OH}$) would replace the hydrogen shaded yellow.

account for evolutionary change. Only one molecule, DNA (deoxyribonucleic acid), fulfills all of these requirements.

THE DOUBLE HELIX MODEL

Two kinds of molecules participate in protein synthesis. Both are based on a similar building block, the nucleotide, giving them their name—nucleic acids. One of these molecules, **deoxyribonucleic acid** or **DNA**, is the genetic material, and the other, **ribonucleic acid** or **RNA**, is produced in the nucleus and moves to the cytoplasm, where it participates in protein synthesis. The study of how the information stored in DNA codes for RNA and protein is **molecular genetics**.

DNA and RNA are large molecules made up of subunits called nucleotides (figure 3.8). A nucleotide consists of a nitrogen-containing organic base, either in the form of a double

**FIGURE 3.9**

Structure of DNA. (a) Nucleotides of one strand of nucleic acid join by linking the phosphate of one nucleotide to the 3' carbon of an adjacent nucleotide. Dashed lines between the nitrogenous bases indicate hydrogen bonds. Three hydrogen bonds are between cytosine and guanine, and two are between thymine and adenine. The antiparallel orientation of the two strands is indicated by using the 3' and 5' carbons at the ends of each strand. (b) Three-dimensional representation of DNA. The antiparallel nature of the strands is indicated by the curved arrows.

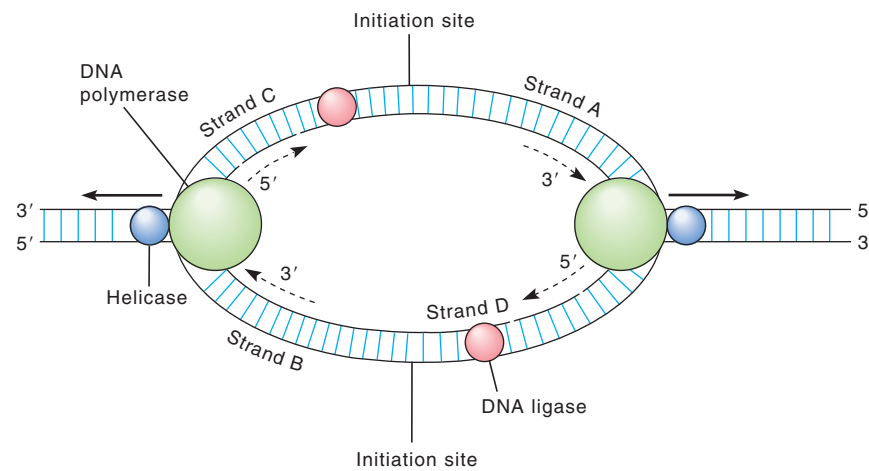
ring (**purine**) or a single ring (**pyrimidine**). Nucleotides also contain a pentose (five-carbon) sugar and a phosphate ($-\text{PO}_4$) group. DNA and RNA molecules, however, differ in several ways. Both DNA and RNA contain the purine bases adenine and guanine, and the pyrimidine base cytosine. The second pyrimidine in DNA, however, is thymine, whereas in RNA it is uracil. A second difference between DNA and RNA involves the sugar present in the nucleotides. The pentose of DNA is deoxyribose, and in RNA it is ribose. A third important difference between DNA and RNA is that DNA is a double-stranded molecule and RNA is single stranded, although it may fold back on itself and coil.

The key to understanding the function of DNA is knowing how nucleotides link into a three-dimensional structure. The DNA molecule is ladderlike, with the rails of the ladder consisting of alternating sugar-phosphate groups (figure 3.9a). The phosphate of a nucleotide attaches at the fifth (5') carbon of deoxyribose. Adjacent nucleotides attach to one another by a covalent bond between the phosphate of one nucleotide and the third (3') carbon of deoxyribose. The pairing of nitrogenous bases between strands holds the two strands together. Adenine (a purine) is

hydrogen bonded to its complement, thymine (a pyrimidine), and guanine (a purine) is hydrogen bonded to its complement, cytosine (a pyrimidine) (figure 3.9a). Each strand of DNA is oriented such that the 3' carbons of deoxyribose in one strand are oriented in the opposite directions from the 3' carbons in the other strand. The strands' terminal phosphates are, therefore, at opposite ends, and the DNA molecule is thus said to be **antiparallel** (Gr. *anti*, against + *para*, beside + *allelon*, of one another). The entire molecule is twisted into a right-handed helix, with one complete spiral every 10 base pairs (figure 3.9b).

DNA REPLICATION IN EUKARYOTES

During DNA replication, each DNA strand is a template for a new strand. The pairing requirements between purine and pyrimidine bases dictate the positioning of nucleotides in a new strand (figure 3.10). Thus, each new DNA molecule contains one strand from the old DNA molecule and one newly synthesized strand. Because half of the old molecule is conserved in the new molecule, DNA replication is said to be semiconservative.

**FIGURE 3.10**

DNA Replication. Replication begins simultaneously at many initiation sites along the length of a chromosome. Notice that synthesis of strands A and B is continuous from the initiation site, and that synthesis of strands C and D is discontinuous from the initiation site. Strands C and D are produced in fragments because DNA polymerase can only produce new DNA strands in the 5' to 3' direction. Helicase enzymes aid in the untwisting of the double helix during replication, and DNA ligase enzymes join DNA fragments produced during replication. Replication is bidirectional from the initiation site. Dashed arrows indicate the direction of DNA elongation. Solid arrows indicate the bidirectional progress of replication.

GENES IN ACTION

A gene can be defined as a sequence of bases in DNA that codes for the synthesis of one polypeptide, and genes must somehow transmit their information from the nucleus to the cytoplasm, where protein synthesis occurs. The synthesis of an RNA molecule from DNA is called **transcription** (*L. trans*, across + *scriba*, to write), and the formation of a protein from RNA at the ribosome is called **translation** (*L. trans*, to transfer + *latere*, to remain hidden).

Three Major Kinds of RNA

Each of the three major kinds of RNA has a specific role in protein synthesis and is produced in the nucleus from DNA. **Messenger RNA (mRNA)** is a linear strand that carries a set of genetic instructions for synthesizing proteins to the cytoplasm. **Transfer RNA (tRNA)** picks up amino acids in the cytoplasm, carries them to ribosomes, and helps position them for incorporation into a polypeptide. **Ribosomal RNA (rRNA)**, along with proteins, makes up ribosomes.

The Genetic Code

DNA must code for the 20 different amino acids found in all organisms. The information-carrying capabilities of DNA reside in the sequence of nitrogenous bases. The genetic code is a sequence of three bases—a triplet code. Figure 3.11 shows the genetic code as reflected in the mRNA that will be produced from DNA. Each three-base combination is a **codon**. More than one codon can specify the same amino acid because there are 64 possible codons, but only 20 amino acids. This characteristic of the code is referred to as **degeneracy**. Note that not all codons code for an amino acid. The base sequences UAA, UAG, and UGA are all stop signals that indicate where polypeptide synthesis should end.

The base sequence AUG codes for the amino acid methionine, which is a start signal.

Transcription

The genetic information in DNA is not translated directly into proteins, but is first transcribed into mRNA. Transcription involves numerous enzymes that unwind a region of a DNA molecule, initiate and end mRNA synthesis, and modify the mRNA after transcription is complete. Unlike DNA replication, only one or a few genes are exposed, and only one of the two DNA strands is transcribed (figure 3.12).

One of the important enzymes of this process is RNA polymerase. After a section of DNA is unwound, RNA polymerase recognizes a specific sequence of DNA nucleotides. RNA polymerase attaches and begins joining ribose nucleotides, which are complementary to the 3' end of the DNA strand. In RNA, the same complementary bases in DNA are paired, except that in RNA, the base uracil replaces the base thymine as a complement to adenine.

Newly transcribed mRNA, called the primary transcript, must be modified before leaving the nucleus to carry out protein synthesis. Some base sequences in newly transcribed mRNA do not code for proteins. RNA splicing involves cutting out noncoding regions so that the mRNA coding region can be read continuously at the ribosome.

Translation

Translation is protein synthesis at the ribosomes in the cytoplasm, based on the genetic information in the transcribed mRNA. Another type of RNA, called transfer RNA (tRNA), is important in the translation process (figure 3.13). It brings the different amino acids coded for by the mRNA into alignment so that a polypeptide can be made. Complementary pairing of bases across the molecule

		Second position				
		U	C	A	G	
U	UUU } Phe	UCU } Ser	UAU } Tyr	UGU } Cys	U	
	UUC } Phe		UAC } Tyr	UGC } Cys	C	
	UUA } Leu		UAA } STOP	UGA } STOP	A	
	UUG } Leu		UAG } STOP	UGG } Trp	G	
C	CUU } Leu	CCU } Pro	CAU } His	CGU } Arg	U	
	CUC } Leu		CAC } His	CGC } Arg	C	
	CUA } Leu		CAA } Gin	CGA } Arg	A	
	CUG } Leu		CAG } Gin	CGG } Arg	G	
A	AUU } Ile	ACU } Thr	AAU } Asn	AGU } Ser	U	
	AUC } Ile		AAC } Asn	AGC } Ser	C	
	AUA } Met		AAA } Lys	AGA } Arg	A	
	AUG } Met		AAG } Lys	AGG } Arg	G	
G	GUU } Val	GCU } Ala	GAU } Asp	GGU } Gly	U	
	GUC } Val		GAC } Asp	GGC } Gly	C	
	GUA } Val		GAA } Glu	GGA } Gly	A	
	GUG } Val		GAG } Glu	GGG } Gly	G	

Ala = Alanine	Leu = Leucine
Arg = Arginine	Lys = Lysine
Asn = Asparagine	Met = Methionine
Asp = Aspartic acid	Phe = Phenylalanine
Cys = Cysteine	Pro = Proline
Gin = Glutamine	Ser = Serine
Glu = Glutamic acid	Thr = Threonine
Gly = Glycine	Trp = Tryptophan
His = Histidine	Tyr = Tyrosine
Ile = Isoleucine	Val = Valine

FIGURE 3.11

Genetic Code. Sixty-four messenger RNA codons are shown here. The first base of the triplet is on the left side of the figure, the second base is at the top, and the third base is on the right side. The abbreviations for amino acids are also shown. In addition to coding for the amino acid methionine, the AUG codon is the initiator codon. Three codons—UAA, UAG, and UGA—do not code for an amino acid but act as a signal to stop protein synthesis.

maintains tRNA's configuration. The presence of some unusual bases (i.e., other than adenine, thymine, cytosine, guanine, or uracil) disrupts the normal base pairing and forms loops in the molecule. The center loop (the "anticodon loop") has a sequence of three unpaired bases called the **anticodon**. During translation, pairing of the mRNA codon with its complementary anticodon of tRNA appropriately positions the amino acid that tRNA carries.

Ribosomes, the sites of protein synthesis, consist of large and small subunits that organize the pairing between the codon and the anticodon. Several sites on the ribosome are binding sites for mRNA and tRNA. At the initiation of translation, mRNA binds to a small, separate ribosomal subunit. Attachment of the mRNA requires that the initiation codon (AUG) of mRNA be

aligned with the P (peptidyl) site of the ribosome. A tRNA with a complementary anticodon for methionine binds to the mRNA, and a large subunit joins, forming a complete ribosome.

Polypeptide formation can now begin. Another site, the A (aminoacyl) site, is next to the P site. A second tRNA, whose anticodon is complementary to the codon in the A site, is positioned. Two tRNA molecules with their attached amino acids are now side-by-side in the P and A sites (figure 3.14). This step requires enzyme aid and energy, in the form of guanine triphosphate (GTP). An enzyme (peptidyl transferase), which is actually a part of the larger ribosomal subunit, breaks the bond between the amino acid and tRNA in the P site, and catalyzes the formation of a peptide bond between that amino acid and the amino acid in the A site.

The mRNA strand then moves along the ribosome a distance of one codon. The tRNA with two amino acids attached to it that was in the A site is now in the P site. A third tRNA can now enter the exposed A site. This process continues until the entire mRNA has been translated, and a polypeptide chain has been synthesized. Translation ends when a termination codon (e.g., UAA) is encountered.

Protein synthesis often occurs on ribosomes on the surface of the rough endoplasmic reticulum. The positioning of ribosomes on the ER allows proteins to move into the ER as the protein is being synthesized. The protein can then be moved to the Golgi apparatus for packaging into a secretory vesicle or a lysosome.

CHANGES IN DNA AND CHROMOSOMES

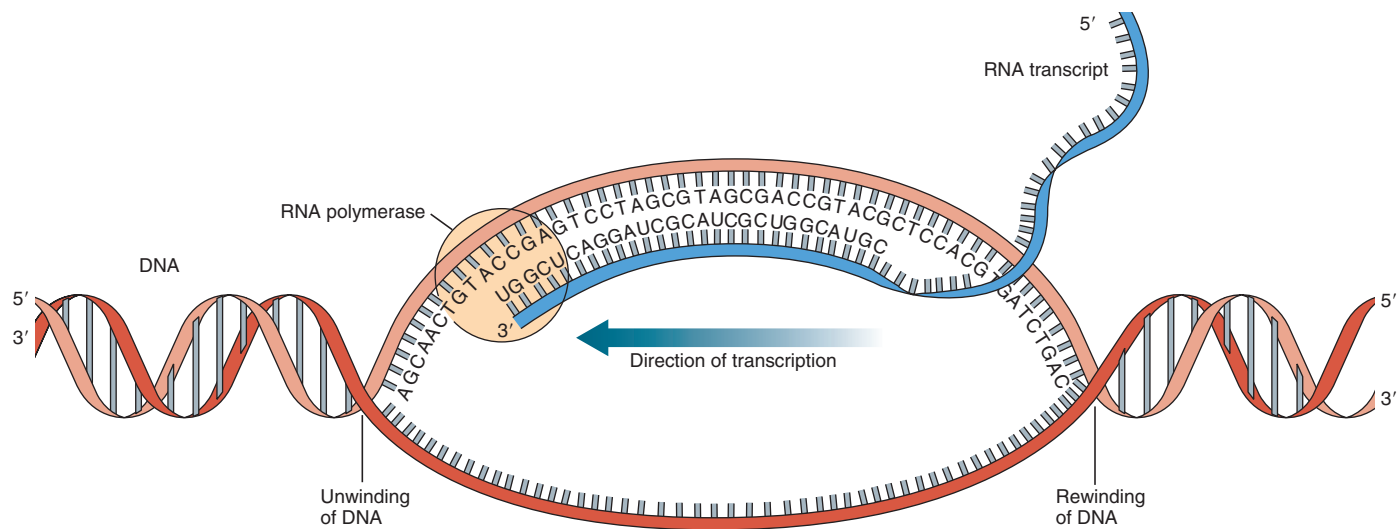
The genetic material of a cell can change, and these changes increase genetic variability and help increase the likelihood of survival in changing environments. These changes include alterations in the base sequence of DNA and changes that alter the structure or number of chromosomes.

Point Mutations

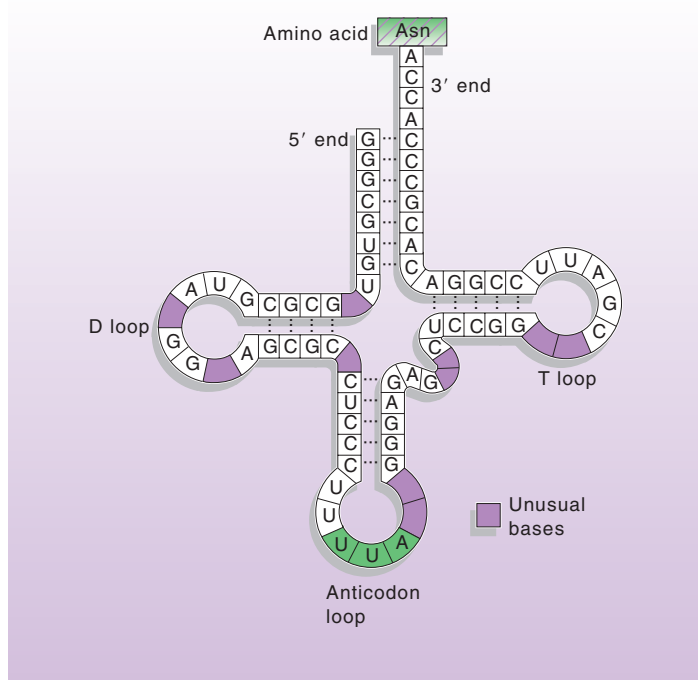
Genetic material must account for evolutionary change. Point mutations are changes in nucleotide sequences and may result from the replacement, addition, or deletion of nucleotides. Mutations are always random events. They may occur spontaneously as a result of base-pairing errors during replication, which result in a substitution of one base pair for another. Although certain environmental factors (e.g., electromagnetic radiation and many chemical mutagens) may change mutation rates, predicting what genes will be affected or what the nature of the change will be is impossible. *Some mutations may be unnoticed or even beneficial. However, the consequences of genetic changes are usually negative, because they disturb the structure of proteins that are the products of millions of years of evolution.*

Variation in Chromosome Number

Changes in chromosome number may involve entire sets of chromosomes, as in polyploidy, which was discussed earlier. **Aneuploidy** (Gr. *a*, without), on the other hand, involves the addition

**FIGURE 3.12**

Transcription. Transcription involves the production of a messenger RNA molecule from the DNA segment. Note that transcription is similar to DNA replication in that the molecule is synthesized in the 5' to 3' direction.

**FIGURE 3.13**

Structure of Transfer RNA. Diagrammatic representation of the secondary structure of transfer RNA (tRNA). An amino acid attaches to the 3' end of the molecule. The anticodon is the sequence of three bases that pairs with the codon in mRNA, thus positioning the amino acid that tRNA carries. Other aspects of tRNA structure position the tRNA at the ribosome and in the enzyme that attaches the correct amino acid to the tRNA.

or deletion of one or more chromosomes, not entire sets. The addition of one chromosome to the normal $2N$ chromosome number ($2N+1$) is a trisomy (Gr. *tri*, three + *ME some*, a group of), and the deletion of a chromosome from the normal $2N$ chromosome number ($2N-1$) is a monosomy (Gr. *monos*, single).

Errors during meiosis usually cause aneuploidy. **Nondisjunction** occurs when a homologous pair fails to segregate during meiosis I or when chromatids fail to separate at meiosis II (figure 3.15). Gametes produced are either deficient in one chromosome or have an extra chromosome. If one of these gametes is involved in fertilization with a normal gamete, the monosomic or trisomic condition results. Aneuploid variations usually result in severe consequences involving mental retardation and sterility.

Variation in Chromosome Structure

Some changes may involve breaks in chromosomes. After breaking, pieces of chromosomes may be lost, or they may reattach, but not necessarily in their original position. The result is a chromosome that may have a different sequence of genes, multiple copies of genes, or missing genes. All of these changes can occur spontaneously. Various environmental agents, such as ionizing radiation and certain chemicals, can also induce these changes. The effects of changes in chromosome structure may be mild or severe, depending on the amount of genetic material duplicated or lost.

INHERITANCE PATTERNS IN ANIMALS

Classical genetics began with the work of Gregor Mendel and remains an important basis for understanding gene transfer between generations of animals. Understanding these genetics principles

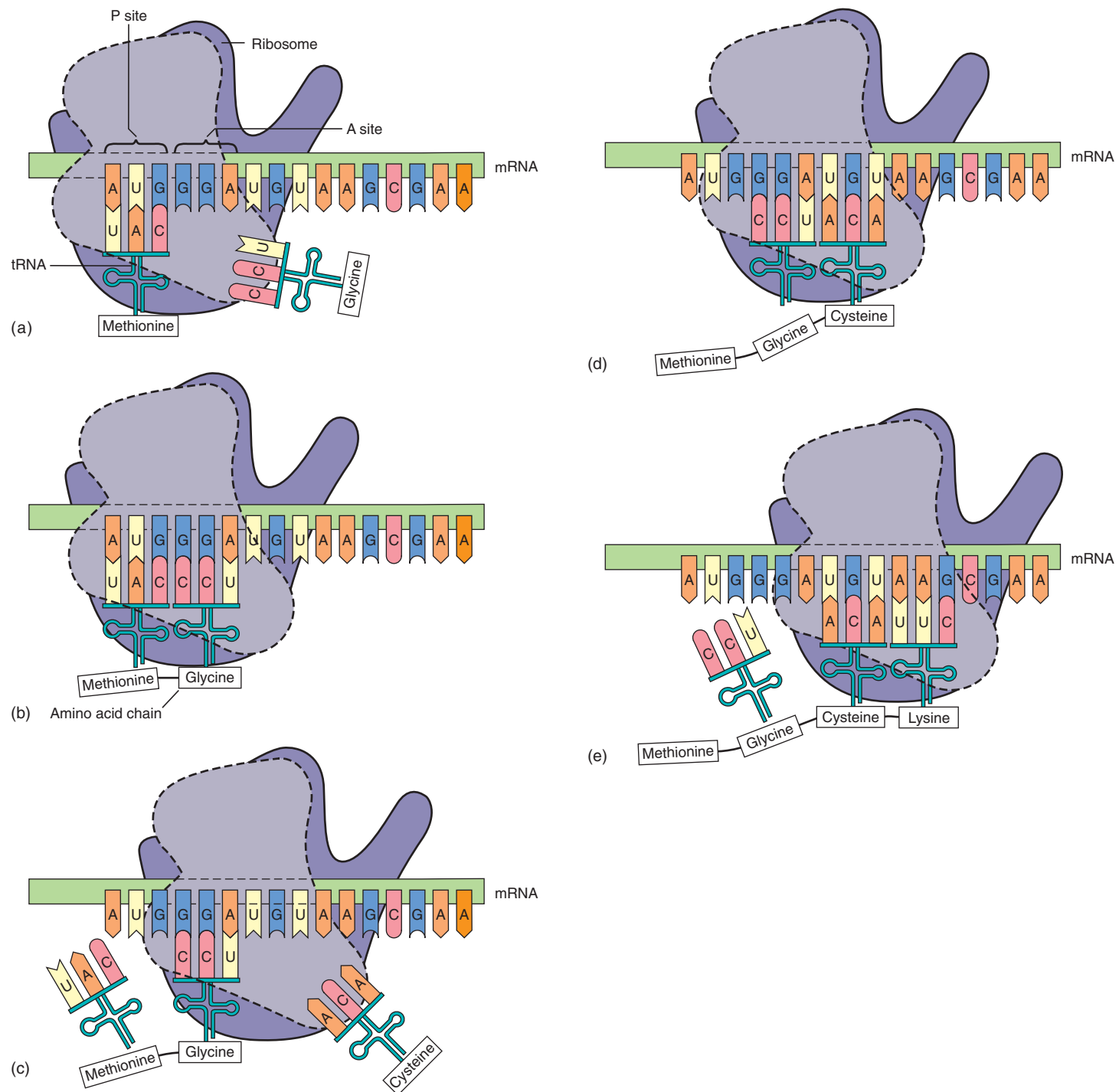
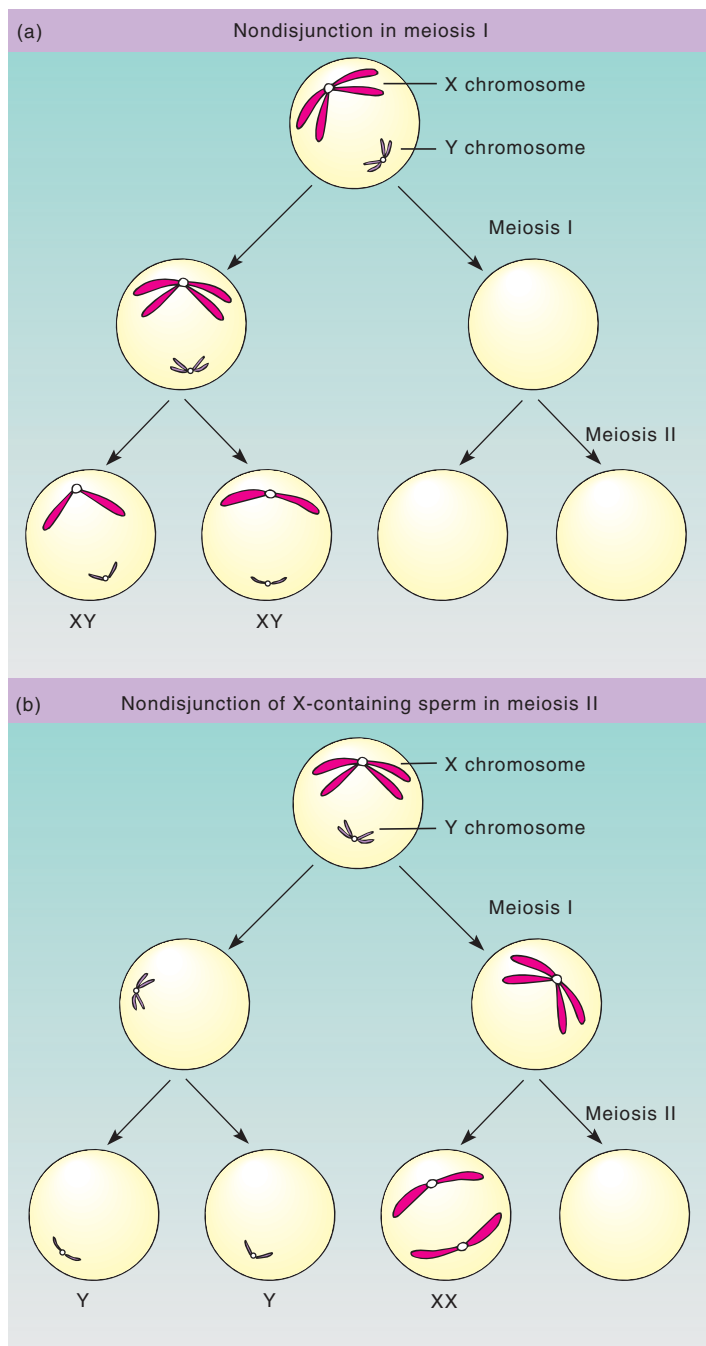


FIGURE 3.14

Events of Translation. (a) Translation begins when a methionine tRNA associates with the P site of the smaller ribosomal subunit and the initiation codon of mRNA associated with that subunit. The larger ribosomal subunit attaches to the small subunit/tRNA complex. (b) A second tRNA carrying the next amino acid enters the A site. A peptide bond forms between the two amino acids, freeing the first tRNA in the P site. (c) The mRNA, along with the second tRNA and its attached dipeptide, moves the distance of one codon. The first tRNA is discharged, leaving its amino acid behind. The second tRNA is now in the P site, and the A site is exposed and ready to receive another tRNA-amino acid. (d) A second peptide bond forms. (e) This process continues until an mRNA stop signal is encountered.

**FIGURE 3.15**

Results of Primary and Secondary Nondisjunction in Sperm Formation. (a) Primary nondisjunction occurs in meiosis I and results in both the X and Y chromosomes ending up in one secondary spermatocyte. A normal second meiotic division results in half of all sperm having both X and Y chromosomes. The other half of all sperm lack any sex chromosomes. (b) Secondary nondisjunction occurs after a normal first meiotic division. Failure of the chromatids of the X chromosomes, for example, to separate in the second division means that a fourth of the sperm will have no sex chromosomes, a fourth will have two X chromosomes, and half will have one Y chromosome (from the normal separation of Y chromatids).

helps us to predict how traits will be expressed in offspring before these offspring are produced, something that has had profound implications in agriculture and medicine. One of the challenges of modern genetics is to understand the molecular basis for these inheritance patterns.

The fruit fly, *Drosophila melanogaster*, is a classic tool for studying inheritance patterns. Its utility stems from its ease of handling, short life cycle, and easily recognized characteristics.

Studies of any fruit fly trait always make comparisons to a wild-type fly. If a fly has a characteristic similar to that found in wild flies, it is said to have the wild-type expression of that trait. (In the examples that follow, wild-type wings lay over the back at rest and extend past the posterior tip of the body, and wild-type eyes are red.) Numerous mutations from the wild-type body form, such as vestigial wings (reduced, shriveled wings) and sepia (dark brown) eyes have been described (figure 3.16).

SEGREGATION

During gamete formation, genes in each parent are incorporated into separate gametes. During anaphase I of meiosis, homologous chromosomes move toward opposite poles of the cell, and the resulting gametes have only one member of each chromosome pair. Genes carried on one member of a pair of homologous chromosomes end up in one gamete, and genes carried on the other member are segregated into a different gamete. The **principle of segregation** states that pairs of genes are distributed between gametes during gamete formation. Fertilization results in the random combination of gametes and brings homologous chromosomes together again.

A cross of wild-type fruit flies with flies having vestigial wings illustrates the principle of segregation. (The flies come from stocks that have been inbred for generations to ensure that they breed true for wild-type wings or vestigial wings.) The offspring (progeny) of this cross have wild-type wings and are the first generation of offspring, or the first filial (F_1) generation (figure 3.17). If these flies are allowed to mate with each other, their progeny are the second filial (F_2) generation. Approximately a fourth of these F_2 generation of flies have vestigial wings, and three-fourths have wild wings (figure 3.17). Note that the vestigial characteristic, although present in the parental generation, disappears in the F_1 generation and reappears in the F_2 generation. In addition, the ratio of wild-type flies to vestigial-winged flies in the F_2 generation is approximately 3:1. Reciprocal crosses, which involve the same characteristics but a reversal of the sexes of the individuals introducing a particular expression of the trait into the cross, yield similar results.

Genes that determine the expression of a particular trait can exist in alternative forms called **alleles** (Gr. *allellos*, each other). In the fruit-fly cross, the vestigial allele is present in the F_1 generation, and even though it is masked by the wild-type allele for wing shape, it retains its uniqueness because it is expressed again in some members of the F_2 generation. **Dominant** alleles hide the expression of another allele; **recessive** alleles are those whose expression can be masked. In the fruit-fly example, the wild-type allele is dominant because it can mask the expression of the vestigial allele, which is therefore recessive.

The visual expression of alleles may not always indicate the

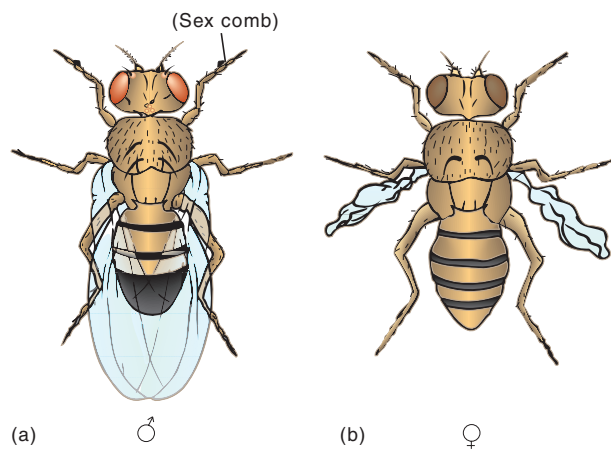


FIGURE 3.16

Distinguishing Sexes and Phenotypes of *Drosophila melanogaster*. (a) Male with wild-type wings and wild-type eyes. (b) Female with vestigial wings and sepia eyes. In contrast to the female, the posterior aspect of the male's abdomen has a wide, dark bank and a rounded tip.

underlying genetic makeup of an organism. This visual expression is the **phenotype**, and the genetic makeup is the **genotype**. In the example, the flies of the F₁ generation have the same phenotype as one of the parents, but they differ genotypically because they carry both a dominant and recessive allele. They are hybrids, and because this cross concerns only one pair of genes and a single trait, it is a **monohybrid cross** (Gr. *monos*, one + L. *hybrida*, offspring of two kinds of parents).

An organism is **homozygous** (L. *homo*, same + Gr. *zygon*, paired) if it carries two identical genes for a given trait and **heterozygous** (Gr. *heteros*, other) if the genes are different. Thus, in the example, all members of the parental generation are homozygous because only true-breeding flies are crossed. All members of the F₁ generation are heterozygous.

Crosses are often diagrammed using a letter or letters descriptive of the trait in question. The first letter of the description of the dominant allele commonly is used. In fruit flies, and other organisms where all mutants are compared with a wild-type, the symbol is taken from the allele that was derived by a mutation from the wild condition. A superscript “+” next to the symbol represents the wild-type allele. A capital letter means that the mutant allele being represented is dominant, and a lowercase letter means that the mutant allele being represented is recessive.

Geneticists use the Punnett square to help predict the results of crosses. Figure 3.18 illustrates the use of a **Punnett square** to predict the results of the cross of two F₁ flies. The first step is to determine the kinds of gametes that each parent produces. One of the two axes of a square is designated for each parent, and the different kinds of gametes each parent produces are listed along the appropriate axis. Combining gametes in the interior of the square shows the results of random fertilization. As figure 3.18 indicates, the F₁ flies are heterozygous, with one wild-type allele and one vestigial allele. The two phenotypes of the F₂ generation are shown inside the Punnett square and are in a 3:1 ratio.

The **phenotypic ratio** expresses the results of a cross according to the relative numbers of progeny in each visually distinct

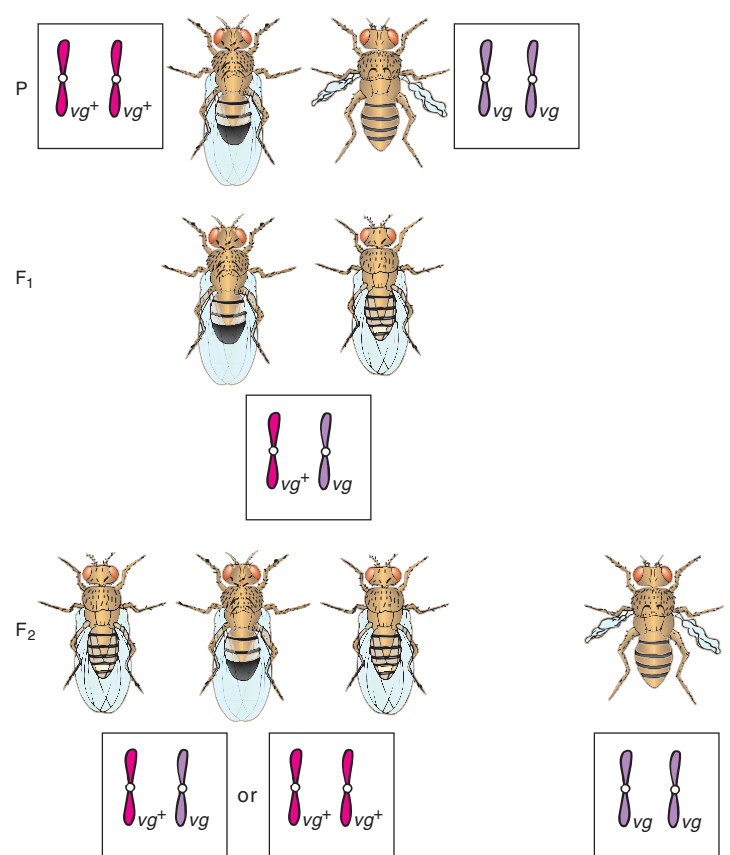


FIGURE 3.17

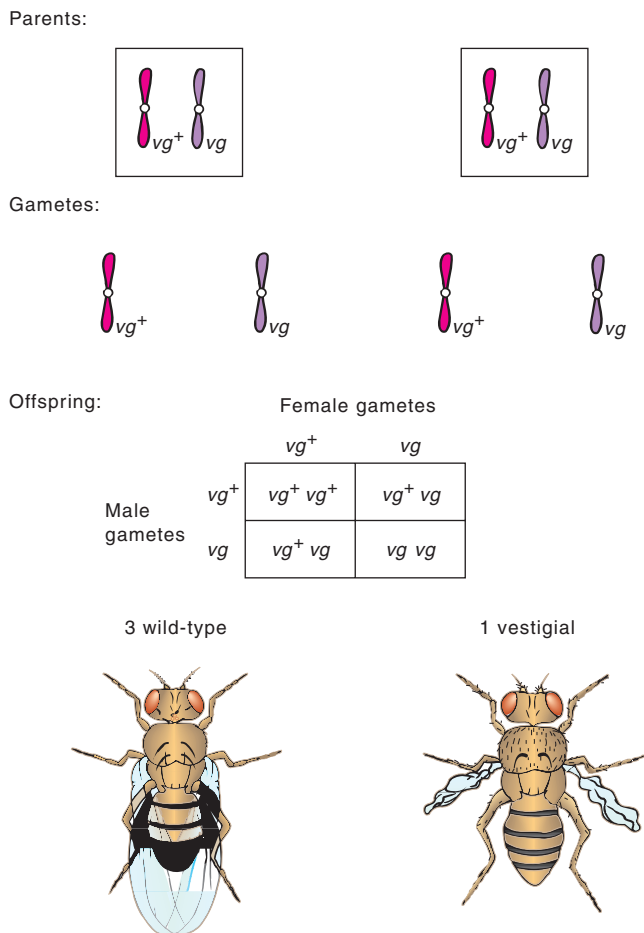
Cross Involving a Single Trait. Cross between parental flies (P) with wild-type (vg^+) wings and vestigial (vg) wings, carried through two generations (F₁ and F₂).

class (e.g., 3 wild-type : 1 vestigial). The Punnett square has thus explained in another way the F₂ results in figure 3.17. It also shows that F₂ individuals may have one of three different genotypes. The **genotypic ratio** expresses the results of a cross according to the relative numbers of progeny in each genotypic category (e.g., 1 vg^+vg^+ : 2 vg^+vg : 1 $vgvg$).

INDEPENDENT ASSORTMENT

It is also possible to make crosses using flies with two pairs of characteristics: flies with vestigial wings and sepia eyes, and flies that are wild for these characteristics. Sepia eyes are dark brown, and wild-type eyes are red. Figure 3.19 shows the results of crosses carried through two generations.

Note that flies in the parental generation are homozygous for the traits in question and that each parent produces only one kind of gamete. Gametes have one allele for each trait. Because each parent produces only one kind of gamete, fertilization results in offspring heterozygous for both traits. The F₁ flies have the wild-type phenotype; thus, wild-type eyes are dominant to sepia eyes. The F₁ flies are hybrids, and because the cross involves two pairs of genes and two traits, it is a **dihybrid cross** (Gr. *di*, two + L. *hybrida*, offspring of two kinds of parents).



The 9:3:3:1 ratio is typical of a dihybrid cross. During gamete formation, the distribution of genes determining one trait does not influence how genes determining the other trait are distributed. In the example, this means that an F₁ gamete with a vg^+ gene for wing condition may also have either the se or se^+ gene for eye color, as the F₁ gametes of figure 3.19 show. Note that all combinations of the eye color and wing condition genes are present, and that all combinations are equally likely. This illustrates the **principle of independent assortment**, which states that, during gamete formation, pairs of factors segregate independently of one another.

The events of meiosis explain the principle of independent

assortment (see figure 3.6). Cells produced during meiosis have one member of each homologous pair of chromosomes. Independent assortment simply means that when homologous chromosomes line up at metaphase I and then segregate, the behavior of one pair of chromosomes does not influence the behavior of any other pair (figure 3.20). After meiosis, maternal and paternal chromosomes are distributed randomly among cells.

OTHER INHERITANCE PATTERNS

The traits considered thus far have been determined by two genes, where one allele is dominant to a second. In this section, you learn that there are often many alleles in a population and that not all traits are determined by an interaction between a single pair of dominant or recessive genes.

Multiple Alleles

Two genes, one carried on each chromosome of a homologous pair, determine traits in one individual. A population, on the other hand, may have many different alleles with the potential to contribute to the phenotype of any member of the population. These are called **multiple alleles**.

Genes for a particular trait are at the same position on a chromosome. The gene's position on the chromosome is called its **locus** (*L. loca*, place). Numerous human loci have multiple alleles. Three alleles, symbolized I^A , I^B , and i , determine the familiar ABO blood types. Table 3.1 shows the combinations of alleles that determine a person's phenotype. Note that i is recessive to I^A and to I^B . I^A and I^B , however, are neither dominant nor recessive to each other. When I^A and I^B are present together, both are expressed.

Incomplete Dominance and Codominance

Incomplete dominance is an interaction between two alleles that are expressed more or less equally, and the heterozygote is different from either homozygote. For example, in cattle, the alleles for red coat color and for white coat color interact to produce an intermediate coat color called roan. Because neither the red nor the white allele is dominant, uppercase letters and a prime or a superscript are used to represent genes. Thus, red cattle are symbolized RR , white cattle are symbolized $R'R'$, and roan cattle are symbolized RR' .

Codominance occurs when the heterozygote expresses the phenotypes of both homozygotes. Thus, in the ABO blood types, the $I^A I^B$ heterozygote expresses both alleles.

THE MOLECULAR BASIS OF INHERITANCE PATTERNS

Just as the principles of segregation and independent assortment can be explained based on our knowledge of the events of meiosis, concepts related to dominance can be explained in molecular terms. When we say that one allele is dominant to another, we do not mean that the recessive allele is somehow "turned off" when the dominant allele is present. Instead, the product of a gene's

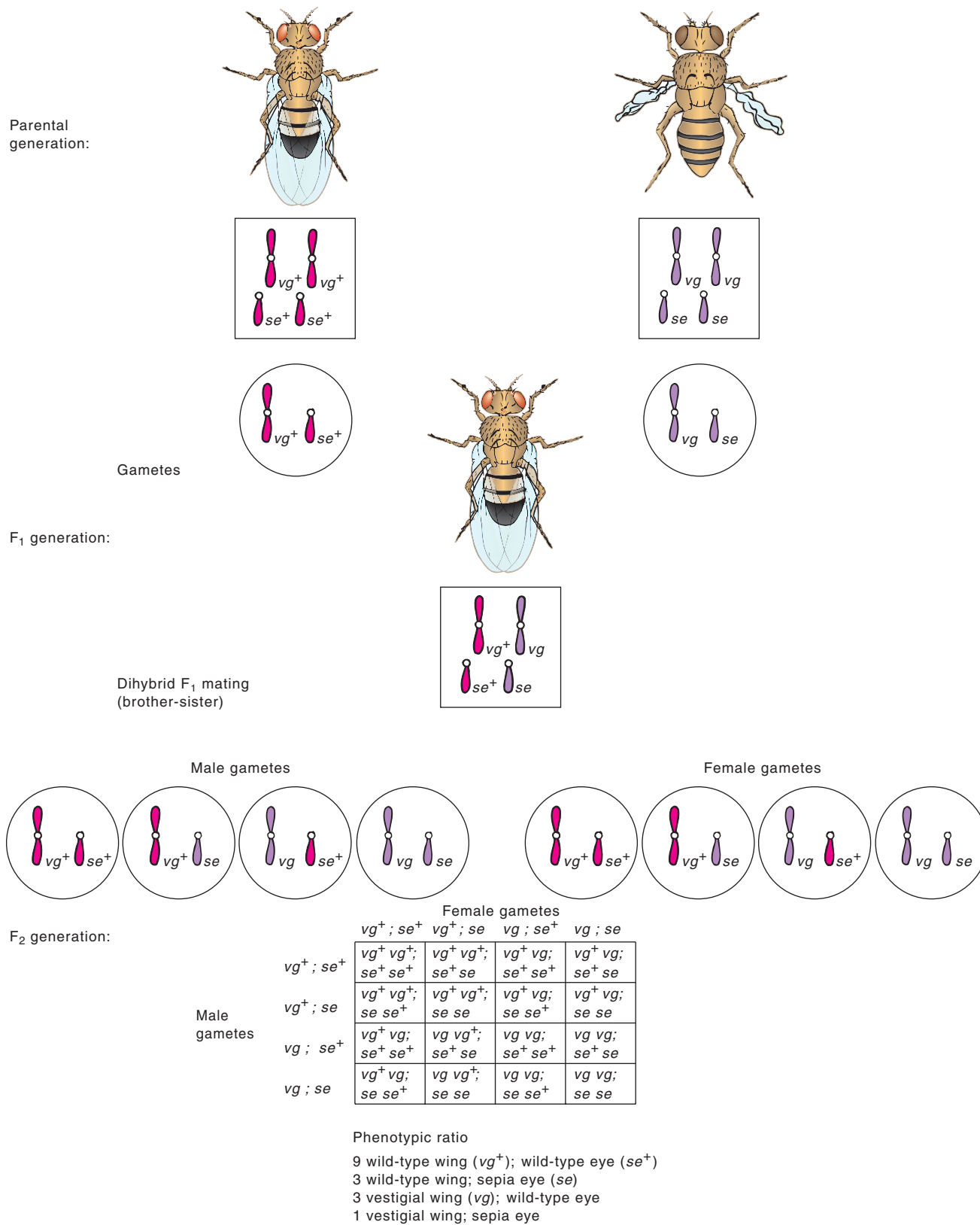


FIGURE 3.19 Constructing a Punnett Square for a Cross Involving Two Characteristics. Note that every gamete has one allele for each trait and that all combinations of alleles for each trait are represented.

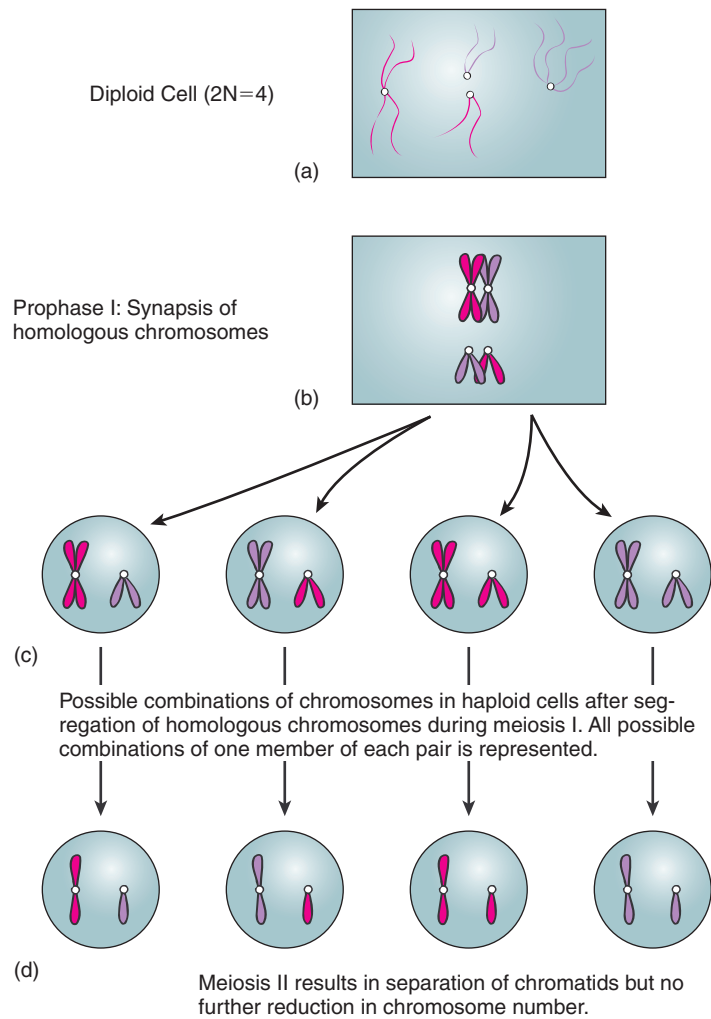


FIGURE 3.20

Independent Assortment of Chromosomes during Meiosis. Color distinguishes maternal and paternal chromosomes. Similar size and shape indicate homologous chromosomes. (a) This cell has a diploid (2N) chromosome number of four. (b) During the first meiotic division, one homologous pair of chromosomes (and hence, the genes this pair carries) is segregated without regard to the movements of any other homologous pair. (c) Thus, all combinations of large and small chromosomes in the cells are possible at the end of meiosis I. (d) Meiosis II simply results in the separation of chromatids without further reduction in chromosome number. Most organisms have more than two pairs of homologous chromosomes in each cell. As the number of homologous pairs increases, the number of different kinds of gametes also increases.

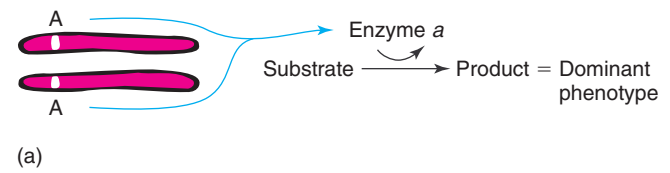
function is the result of a sequence of metabolic steps mediated by enzymes, which are encoded by the gene(s) in question. A functional enzyme is usually encoded by a dominant gene, and when that enzyme is present a particular product is produced. A recessive allele usually arises by a mutation of the dominant gene, and the enzyme necessary for the production of the product is altered and does not function. In the homozygous dominant state, both dominant genes code for the enzyme that produces the product (figure 3.21a). In the heterozygous state, the activity of the single

TABLE 3.1

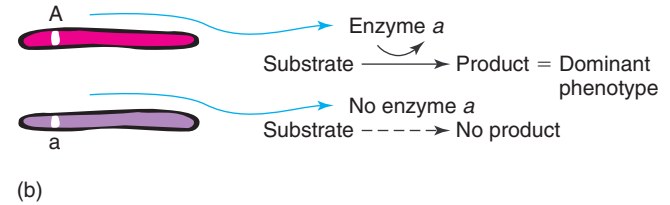
GENOTYPES AND PHENOTYPES IN THE ABO BLOOD GROUPS

GENOTYPE (S)	PHENOTYPE
$I^A I^A, I^A i$	A
$I^B I^B, I^B i$	B
$I^A I^B$	A and B
ii	O

Homozygous Dominant



Heterozygous



Homozygous Recessive

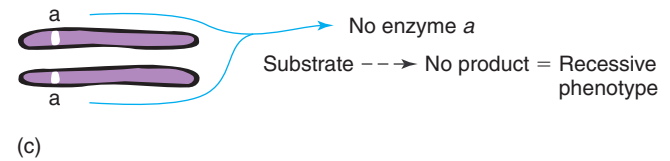


FIGURE 3.21

The Molecular Basis of Dominance. (a) In a homozygous dominant individual, both dominant genes code for enzymes that produce the product and the dominant phenotype. (b) In the heterozygous state, the single dominant allele is sufficient to produce enough enzyme to form the product and the dominant phenotype. (c) In the homozygous recessive state, no product can be formed and the recessive phenotype results.

dominant allele is sufficient to produce enough enzyme to form the product and the dominant phenotype (figure 3.21b). In the homozygous recessive state, no product can be formed and the recessive phenotype results (figure 3.21c).

In the same way, one can explain incomplete dominance and codominance. In these cases both alleles of a heterozygous individual produce approximately equal quantities of two enzymes and products, and the phenotype that results would be either intermediate or show the products of both alleles.

WILDLIFE ALERT

Preserving Genetic Diversity

One of the ways in which scientists evaluate the environmental health of a region is to assess the variety of organisms present in an area. Environments that have a great variety or diversity in species are usually considered healthier than environments with less diversity. Diversity can be reduced through habitat loss, the exploitation of animals or plants through hunting or harvesting, and the introduction of foreign species.

Another criterion used to evaluate environmental health is genetic diversity. Genetic diversity is the variety of alleles within a species.



BOX FIGURE 1 Snow leopard (*Panthera uncia*).

When a species on the brink of extinction is preserved, reduced genetic diversity within the species threatens the health of the species. Near-extinction events, in which many individuals die, eradicate many alleles from populations. Lowered numbers of individuals result in inbreeding, which also reduces genetic diversity. The result is that populations that survive near-extinction events tend to be genetically uniform. The effect of genetic uniformity on populations is nearly always detrimental because, when environmental conditions change, entire populations can be adversely affected. For example, if one individual in a genetically uniform population is susceptible to a particular disease, all individuals will be susceptible, and the disease will spread very quickly. High genetic diversity ensures that some individuals will survive the disease outbreak, and the species will be less likely to face extinction. Since mutation is the ultimate source of new variation within species, lost genetic diversity can only be replaced over evolutionary timescales. For all practical purposes, when genetic diversity is lost it is gone forever.

Conservation geneticists evaluate the genetic health of populations of organisms and try to preserve the genetic variation that exists within species. These efforts involve the use of virtually every genetic tool available to modern science, including the molecular techniques for studying DNA and the proteins of endangered organisms. Conservation geneticists search native populations for related individuals that could be used to enhance the genetic makeup of endangered organisms. They recommend breeding programs to preserve alleles that could easily be lost. Many zoos throughout the world cooperate in breeding programs that exchange threatened animals, or gametes from threatened animals, to preserve alleles. Such a program is underway to help preserve the endangered snow leopard (*Panthera uncia*). There are between 3,000 and 10,000 snow leopards distributed throughout the mountains of central Asia, where they live at altitudes between 2,000 and 5,000 meters. Poaching the snow leopard to supply its coat for black-market trade is a serious threat to the cats that remain (box figure 1). The American Zoo and Aquarium Association is coordinating an effort to maintain genetic diversity among the snow leopards in captivity in North America.

SUMMARY

1. Eukaryotic chromosomes are complexly coiled associations of DNA and histone proteins.
2. The presence or absence of certain chromosomes that are represented differently in males and females determine the sex of an animal. The X-Y system of sex determination is most common.
3. The replication of DNA and its subsequent allocation to daughter cells during mitosis involves a number of phases collectively called the cell cycle. The cell cycle is that period from the time a cell is produced until it completes mitosis.
4. Mitosis maintains the parental number of chromosome sets in each daughter nucleus. It separates the sister chromatids of each (replicated) chromosome for distribution to daughter nuclei.
5. Interphase represents about 90% of the total cell cycle. It includes periods of cell growth and normal cell function. It also includes the time when DNA is replicated.
6. Mitosis is divided into four phases. During prophase, the mitotic spindle forms and the nuclear envelope disintegrates. During metaphase, the replicated chromosomes align along the spindle equator. During anaphase, the centromeres joining sister chromatids divide and microtubules pull sister chromatids to opposite

poles of the cell. During telophase, the mitotic spindle disassembles, the nuclear envelope reforms, and chromosomes unfold.

7. Cytokinesis, the division of the cytoplasm, begins in late anaphase and is completed in telophase.
8. Meiosis is a special form of nuclear division during gamete formation. It consists of a single replication of the chromosomes and two nuclear divisions that result in four daughter cells, each with half the original number of chromosomes.
9. In the life cycle of most animals, certain diploid cells undergo gametogenesis to form haploid gametes (sperm in males and eggs in females). Fusion of a sperm and an egg nucleus at fertilization produces a new diploid cell (zygote).
10. Deoxyribonucleic acid (DNA) is the hereditary material of the cell. Ribonucleic acid (RNA) participates in protein synthesis.
11. Nucleotides are nucleic acid building blocks. Nucleotides consist of a nitrogenous (purine or pyrimidine) base, a phosphate, and a pentose sugar.
12. DNA replication is semiconservative. During replication, the DNA strands separate, and each strand is a template for a new strand.
13. Protein synthesis is a result of two processes. Transcription involves the production of a messenger RNA molecule from a DNA molecule. Translation involves the movement of messenger RNA to the cytoplasm, where transfer RNA and ribosomes link amino acids in a proper sequence to produce a polypeptide.
14. Changes in DNA and chromosomes include point mutations, which alter the bases in DNA, and changes in chromosome number and structure. These changes are usually deleterious for the organism.
15. The principle of segregation states that pairs of genes are distributed between gametes during gamete formation when homologous chromosomes are distributed to different gametes during meiosis.
16. The principle of independent assortment states that, during gamete formation, pairs of genes segregate independently of one another. This is a result of meiotic processes in which members of one homologous pair of chromosomes are not influenced by the movements of any other pair of chromosomes.
17. Populations may have many alternative expressions of a gene at any locus. Human traits, like the ABO blood group, are traits determined by multiple alleles.
18. Incomplete dominance is an interaction between two alleles in which the alleles contribute more or less equally to the phenotype. Codominance is an interaction between two alleles in which both alleles are expressed in the heterozygote.
19. Patterns of inheritance observed at an organismal level are explained at a molecular level by the presence or absence of functional enzymes. A dominant allele usually encodes a functional enzyme, and a recessive allele usually encodes a nonfunctional enzyme.

SELECTED KEY TERMS

alleles (p. 43)	principle of independent assortment (p. 45)
cell cycle (p. 33)	principle of segregation (p. 43)
deoxyribonucleic acid (p. 37)	ribonucleic acid (p. 37)
meiosis (p. 35)	transcription (p. 39)
mitosis (p. 33)	translation (p. 39)

CRITICAL THINKING QUESTIONS

1. Which do you think evolved first—meiosis or mitosis? Why? What do you think may have been some of the stages in the evolution of one from the other?
2. Why is it important that all regions of chromosomes are not continually active?
3. In a laboratory experiment, you analyze the DNA from your own white blood cells. You determine that 15% of the nucleotide bases it contains is thymine. What percentage of the bases is adenine? cytosine? guanine?
4. A wild-type fruit fly, which had one vestigial-winged parent, is crossed with a vestigial-winged fruit fly. Use a Punnett square to predict the phenotypic and genotypic ratios in the offspring of this cross. What is this cross called?
5. A vestigial-winged, wild-eyed fruit fly is crossed with a wild-winged, sepia-eyed fruit fly. At least one parent of both of these flies had vestigial wings and sepia eyes. Use a Punnett square to predict the phenotypic ratio expected in the offspring of this cross.
6. Supply the genotypes, as completely as possible, for the parents and progeny of the following crosses:
 - a. wild-type wing; sepia eye \times wild-type wing; wild-type eye = 3 wild-type wing; sepia eye: 1 vestigial wing; sepia eye: 3 wild-type wing; wild-type eye: 1 vestigial wing; wild-type eye
 - b. wild-type wing; sepia eye \times wild-type wing; wild-type eye = 1 wild-type wing; sepia eye: 1 wild-type wing; wild-type eye
 - c. vestigial wing; wild-type eye \times wild-type wing; sepia eye = all wild-type wing; wild-type eye
 - d. vestigial wing; wild-type eye \times wild-type wing; sepia eye = 1 vestigial wing; wild-type eye: 1 vestigial wing; sepia eye: 1 wild-type wing; sepia eye: 1 wild-type wing; wild-type eye
7. The following progeny are the result of a cross between two fruit flies. Unfortunately, the phenotypes of the parental flies were not recorded. Formulate a hypothesis regarding the genotypes of the parental flies. (Hint: Consider the ratio between wing phenotypes separately from eye phenotypes in formulating your hypothesis.)
Progeny:
 - 293 wild-type wing; wild-type eye
 - 310 wild-type wing; sepia eye
 - 97 vestigial wing; wild-type eye
 - 100 vestigial wing; sepia eye
8. Do you think that Mendel's conclusions regarding the assortment of genes for two traits would have been any different if he had used traits encoded by genes carried on the same chromosome? Explain.
9. To observe the laws of chance, toss a dime and a quarter simultaneously 10 times, and count the number of head-head, head-tail, and tail-tail combinations. How close are your results to a 1:2:1 ratio? Now toss the coins 90 times more for a total of 100 tosses. How close are your new results to a 1:2:1 ratio? Explain the difference.

ONLINE LEARNING CENTER

Visit our Online Learning Center (OLC) at www.mhhe.com/zoology (click on the book's title) to find the following chapter-related materials:

- CHAPTER QUIZZING
- ANIMATIONS
 - DNA Structure

50 PART ONE Biological Principles

DNA Replication
Mitosis
Meiosis
Transcription
Translation
Mutations

• **RELATED WEB LINKS**

Cell Division
Mendelian Genetics
Molecular Basis of Genetics
Protein Synthesis

- **BOXED READINGS ON**
Transgenic Animals
Diabetes
The Participation of the Fetus During Childbirth

• **SUGGESTED READINGS**

• **LAB CORRELATIONS**

Check out the OLC to find specific information on these related lab exercises in the *General Zoology Laboratory Manual*, 5th edition, by Stephen A. Miller:

Exercise 3 *Aspects of Cell Function*

Exercise 4 *Genetics*

