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Humans have known for centuries that traits are inherited by offspring from their parents. Through trial and error we have manipulated breeding to achieve desired characteristics in our animals. We now understand more about the molecules controlling inheritance and the positive and negative effects of humans interacting with animal reproduction (see pages 55 and 56).

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 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 from individuals of one generation to the next generation. The classical approach to genetics involves experimental manipulation of reproduction and observing patterns of inheritance between generations. This work began with Gregor Mendel (1822–1884), and it 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 understand 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.
3.1 Eukaryotic Chromosomes

Learning Outcomes

1. Compare structural levels of eukaryotic chromosomes.
2. Differentiate between sex chromosomes and autosomes in a diploid animal.

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 (chromosome condensation) and regulating DNA activity.

There are five different histone proteins. The amino acid composition of these proteins creates positive charges that attract the negative charges of DNA's phosphate groups. 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 solenoid. Higher-order folding forms chromatin loops, rosettes, and the final chromosome. The details of this higher-order folding are still under investigation.

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. Alterations of chromatin structure including the addition of chemical groups to histone proteins and DNA, removal or repositioning nucleosomes, and hypercondensation of chromatin can control chromatin activity.

FIGURE 3.1
Organization of Eukaryotic Chromosomes. Chromosomes consist of long DNA molecules that wrap histone proteins. The DNA and histone complex is called a nucleosome, and the chain of nucleosomes is coiled into a solenoid. The solenoid is then looped into rosettes around a scaffold protein. Further compaction results in the eukaryotic chromosome.
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, whereas 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. autos, 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 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.) Even though the X and Y chromosomes are called “sex chromosomes,” they also help determine non-sex-related traits. This is especially true for the X chromosome of most animals. It is very large and has genes that code for many traits. Similarly, autosomal chromosomes frequently carry genes that influence sexual characteristics. This mode of sex determination also results in approximately equal numbers of male and female offspring:

$$\begin{align*}
\text{Sperm} & : X \quad Y \\
\text{Egg} & : XX \quad XY \\
\text{1 female : 1 male}
\end{align*}$$

Number of Chromosomes

Even though the number of chromosomes is constant within a species, chromosome number varies greatly among species. The chromosome number of animals usually varies between 10 and 50.

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

Section Review 3.1

In eukaryotic cells, DNA and protein associate in nucleosomes. Further condensation produces chromatin and eventually chromosomes. In this condensed state, one can distinguish chromosomes from each other. Sex chromosomes are represented differently in opposite sexes and autosomes are similar in members of both sexes.

Prokaryotic organisms (e.g., bacteria) have chromatin that remains in a dispersed state throughout their
life cycles. Prokaryotes lack histone proteins and have much less DNA than do eukaryotes. Why do you think that the chromatin of all eukaryotic organisms undergoes condensation?

3.2 The Cell Cycle and Mitotic Cell Division

Learning Outcomes
1. Contrast an embryonic cell and a mature bone cell as regards cell-cycle activities.
2. Explain why the events of mitotic cell division result in daughter cells being identical to parental cells.

The life of a cell begins when a parent cell divides to produce the new cell. The new cell then goes through maintenance and growth processes until it matures and ultimately divides to produce another generation of two cells. The life of a cell, from its beginning until it divides to produce the new generation of cells, is called the cell cycle (figure 3.3).

Mitosis (Gr. mitos, thread) is the distribution of chromosomes between two daughter cells, and cytokinesis (Gr. kytos, hollow vessel + kinesis, motion) is the partitioning of the cytoplasm between the two daughter cells. Interphase (L. inter, between) is the time between the end of cytokinesis and the beginning of the next mitotic division. It is a time of cell growth, DNA synthesis, and preparation for the next mitotic division.

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.

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

Interphase: Replicating the Hereditary Material

Interphase typically occupies about 90% of the total cell cycle. The first portion of interphase is gap phase 1 (G1). It is usually the longest interval of interphase and is a period of cell growth and the metabolic activities characteristic of the particular cell type. G1 ends with the beginning of the S phase.

Before a cell divides, an exact copy of the DNA is made during the S (synthesis) phase. 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 identical genetic material to that present in the parent cell. The result is a pair of identical sister chromatids (figure 3.4). A chromatid is a copy of a chromosome produced by replication. Each chromatid attaches to its other

FIGURE 3.4
Chromosome Replication and Homologous Chromosomes. Chromosome replication occurs during interphase of the cell cycle. Before replication (S phase of the cell cycle), chromosomes consist of a single chromatid. Nonreplicated chromosomes are shown diagrammatically in a condensed state for comparative purposes. They would actually be in the form of uncondensed chromatin during replication. Following replication, chromosomes consist of two identical chromatids held together at the centromere. Homologous chromosomes (described later in this chapter) are represented by red and blue colors. These chromosomes carry genes for the same traits; one homolog was received from the maternal parent and the other from the paternal parent.
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.

The final stage of interphase is gap phase 2 (G_2). 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 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.

The time spent by a cell in interphase varies greatly depending on the cell. Rapidly dividing embryonic cells move very quickly through G_1 to S, and again quickly through G_2 to M. The entire cell cycle may occur within a few minutes time. Rapidly dividing cells produce a many-celled embryo from a single fertilized egg within hours. On the other hand, maturing cells spend relatively more time in G_1 because they are growing and taking on functions of adult cells. Many adult cells are not dividing. Mature bone, muscle, and nerve cells enter G_1 and pause. They may remain in this G_0 phase indefinitely or until cell division is required, for example, to repair an injury.

**M-Phase: Mitosis**

Mitosis is divided into five phases: prophase, prometaphase, 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 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).

Prometaphase follows the break-up of the nuclear envelope. A second group of microtubules attach at one end to the kinetochore of each chromatid and to one of the poles of the cell at the other end of the microtubule. This bipolar attachment of spindle fibers to chromatids is critical to the movement of the chromatids of each chromosome to opposite poles of the cell in subsequent phases of mitosis.
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, and perhaps the activity of motor proteins of the kinetochore, pulls each daughter chromosome apart from its copy and moves it 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 re-forms 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.

M-Phase: Cytokinesis
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.

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 zygote is the first cell of the new animal. The fusion of nuclei within the zygote brings together genetic information from the two parents, and each parent 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. Gametes are produced by cells set aside for that purpose early in development. These cells are called germ-line cells and eventually undergo a type of cell division called meiosis (Gr. meiosis, diminution). Meiosis occurs in germ-line 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 G2 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 (see figure 3.4). 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, one is maternal in origin and one is paternal in origin (figure 3.7). An elaborate network of protein is laid down between the two homologous chromosomes. This network holds the homologous chromosomes in a precise union so that corresponding genetic regions of the homologous chromosomes are exactly aligned.

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. This random distribution of members of each homologous pair to
spermatogenesis in that only one of the four meiotic products.

The result of meiosis in most animals is the formation of sperm.

The Second Meiotic Division

The second meiotic division (meiosis II) resembles an ordinary mitotic division (see figure 3.6b), except that 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).

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 by a sperm cell.

Section Review 3.3

Meiotic cell division is the process that results in the formation of haploid (1N) gametes. Gamete formation involves two meiotic and cytoplasmic divisions during which homologous pairs of chromosomes undergo synapsis, including crossing-over, followed by the separation of members of each pair into gametes that have one-half the number of chromosomes of the parental cells. Fertilization restores the diploid (2N) chromosome number in the zygote.

Why are the events of the first meiotic division so very important in the outcome of the entire meiotic cell division process?

3.4 DNA: The Genetic Material

Learning Outcome

1. Explain the features of DNA that allow it to perform all of the four functions required of the genetic molecule.

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 nuclei of eukaryotic cells. Fourth, it must be able to change over time to 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 in the form of either a double ring (purine) or a single ring (pyrimidine). Nucleotides also contain a pentose (five-carbon) sugar and a phosphate (−PO₄) 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.
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 (−OH) would replace the hydrogen shaded purple.

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. Thus, the two strands of DNA have opposite polarity and the DNA molecule is 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.

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, across + laten, 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.
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.

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 maintains tRNA's configuration. The presence of some unusual bases (i.e., other than adenine, cytosine, guanine, or uracil) disrupts the normal base pairing and forms loops in the molecule. The central loop (the "anticodon loop") has a sequence of three unpaired
1. Original double helix.

2. Strands separate.

3. Complementary bases align opposite templates.

4. Enzymes link sugar-phosphate elements of aligned nucleotides into a continuous new strand.

FIGURE 3.10
DNA Replication. (1) Replication begins simultaneously at many initiation sites along the length of a chromosome, and replication proceeds in both directions from the initiation site. Only one direction is shown here for simplicity. (2) An enzyme causes the double helix to unwind and the two strands to separate. Each original strand serves as a template for the synthesis of a new strand. (3) Other enzymes help align nucleotides with exposed, unpaired bases on the unwound portions of the original DNA and (4) link nucleotides into continuous new strands.

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 into 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.

**FIGURE 3.12**

Transcription. Transcription involves the production of an mRNA 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.
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.
Chapters 4 and 5 describe mutations as the fuel for the evolution of populations because they are the only source for new genetic variations. Point mutations and crossing-over are two sources of genetic variations covered thus far in this chapter. Mutations are the only source of new genetic material. For individuals, mutations can be a source of great suffering because mutations in genes that disturb the structure of proteins are the products of millions of years of evolution are usually negative and cause many of our genetic diseases. The majority of mutations arise in body cells. These often remain hidden and cause no problems for the individual because either they are within a gene that is not being expressed in the cell or they may be altering the structure of DNA that is not coding for a protein. We all harbor hundreds of millions of these somatic mutations. The only mutations that affect future generations are those that arise in germ cells of the testes or ovaries.

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 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 separate during meiosis I or when chromatids fail to separate at meiosis II (figure 3.15). Gametes produced either lack 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.
Section Review 3.4

DNA is the genetic material. It is a double-stranded molecule in which nucleotides are joined to form each strand and the two strands are held together by hydrogen bonds between complementary bases. In DNA replication, each strand serves as a template for the synthesis of a new strand. DNA can code for protein because one strand has a sequence of bases that codes for a sequence of amino acids. Changes in base sequence, or in the number or structure of chromosomes, create new variations that fuel evolutionary change.

One strand of DNA has the base sequence 3'AGTGCAATCT5'. Write the sequence of bases in the second strand. Using the strand provided here as a template, show the mRNA produced in transcription and the sequence of amino acids produced in translation.

3.5 Inheritance Patterns in Animals

Learning Outcomes

1. Solve genetics problems by applying the principles of segregation and independent assortment.
2. Predict the results of crosses involving incompletely dominant and codominant alleles.

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 helps us 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, shrunken 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 (F₁) generation (figure 3.17). If these flies are allowed to mate with each other, their progeny are the second filial (F₂) generation. Approximately a fourth of these F₂ generation of flies have vestigial wings, and three-fourths have wild-type wings (figure 3.17). Note that the vestigial characteristic, although present in the parental generation, disappears in the F₁ generation and reappears in the F₂ generation. Approximately a fourth of these F₂ generation of flies have vestigial wings, and three-fourths have wild-type wings (figure 3.17). Note that the vestigial characteristic, although present in the parental generation, disappears in the F₁ generation and reappears in the F₂ generation. In addition, the ratio of wild-type flies to vestigial-winged flies in the F₂ 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. allelos, each other). In the fruit-fly cross, the vestigial allele is present in the F₁ 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 F₂.
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).

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 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 (alleles of each other). Thus, in the example, all members of the parental generation are homozygous because only truebreeding 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

FIGURE 3.18
Use of a Punnett Square. A Punnett square helps predict the results of a cross. The kinds of gametes that each member of a cross produces are determined and placed along the axes of a square. Combining gametes in the interior of the square shows the results of mating; a phenotypic ratio of three flies with wild-type wings (vg+) to one fly with vestigial wings (vg).
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 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 vg⁻ vg⁻).

**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 gene or the 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.

This independent assortment of maternal and paternal chromosomes is the third source of genetic variation covered in this chapter. Independent assortment as well as crossing-over and point mutations provide the genetic variation upon which evolutionary processes act (see chapters 4 and 5).

**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⁺, I⁻, 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⁺ and to I⁻. I⁺ and I⁻, however, are neither dominant nor recessive to each other. When I⁺ and I⁻ 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⁺I⁻ 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
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.
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 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 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

**TABLE 3.1**

<table>
<thead>
<tr>
<th>GENOTYPE(S)</th>
<th>PHENOTYPE</th>
</tr>
</thead>
<tbody>
<tr>
<td>r^r^r, r^r i</td>
<td>A</td>
</tr>
<tr>
<td>r^b r^b, r^b i</td>
<td>B</td>
</tr>
<tr>
<td>r^r^r, A and B</td>
<td></td>
</tr>
<tr>
<td>ii</td>
<td>O</td>
</tr>
</tbody>
</table>

**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.
California Chrome, Northern Dancer, Seattle Slew, Secretariat, and all the other horses in the Thoroughbred breed have been bred for speed. They all trace their genetic makeup back to three stallions in England in the early 1700s. They are fast, they command stud fees that have soared up to $1 million, and their foals sell for as much as $13 million. Inbreeding for speed may be killing the breed. Recent genetic analysis has revealed that Thoroughbreds are so genetically similar that they are almost clones of one another—a potentially dangerous situation.

Breeding for speed is not breeding for health. Large powerful muscles acting on slim legs and small hooves create legs that are more likely to break when hooves strike the track (Barbaro, 2006 Preakness Stakes and Eight Belles, 2008 Kentucky Derby) and leg bones that chip at the joints. The lungs of Thoroughbreds bleed and wheeze in an effort to get adequate air into the lungs. Inbreeding is also suspected as the cause of a higher rate of infertility and miscarriage in this breed and possibly a greater susceptibility to disease as compared to other breeds of horses. Apparently breeding for speed is not breeding for durability.

There has been an explosion of genetic research searching for the genetic basis of traits that have accumulated over centuries of inbreeding. The horse genome has been sequenced, and gene chips are being developed to screen horses for genetic defects. It is yet to be seen whether this information will be used to breed for health or faster finishes.

Quantities of two enzymes and products, and the phenotype that results would either be intermediate or show the products of both alleles.

**Section Review 3.5**

Classical genetics involves studying the transfer of genes between generations of animals. The principle of segregation describes the separation of two genes coding for the same trait into separate gametes. The principle of independent assortment describes the fact that during gamete formation, the distribution of genes determining one trait does not influence how genes for a second trait are distributed. These principles permit us to predict the results of genetic crosses. The presence of multiple alleles, incomplete dominance, and codominance influences how one interprets the results of genetic crosses, but the cellular events involved with the segregation and independent assortment still govern how these traits are inherited.

**What events of meiotic cell division are reflected in the principles of segregation and independent assortment?**

**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. 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 (see figure 5.2). 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 improves the likelihood 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 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.

One example of a conservation program attempting to preserve an endangered species is focused on the snow leopard (*Panthera uncia*). There are between 4,000 and 6,500 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 and bones and other body parts for use in traditional Asian medicine are serious threats to the cats that remain. Hunting wild prey and habitat destruction for farming and grazing livestock also threaten these cats (box figure 3.1). Unfortunately, when the blue sheep (*Pseudois nayaur*) and ibex (*Capra sibirica*) prey become scarce snow leopards prey on livestock, which often results in retribution killing of snow leopards by farmers. Because of these threats to the snow leopards, many of those living do not have a reasonable chance at successfully reproducing. The effective population size of snow leopards takes into account the likelihood of successful reproduction and is probably closer to 2,500 individuals. The American Zoo and Aquarium Association is coordinating an effort to maintain genetic diversity among the snow leopards in captivity in North America. At the same time, conservation organizations are helping farmers and herders understand how to live with these cats by securing barns and livestock holding areas from these cats and reimbursing farmers for livestock lost to predation by the snow leopard. In 2008, the International Conference on Range-wide Conservation Planning for Snow Leopards formulated a National Action Plan for preserving this majestic cat species.

![Snow leopard (*Panthera uncia*)](image)

**Box Figure 3.1** Snow leopard (*Panthera uncia*).

**Summary**

### 3.1 Eukaryotic Chromosomes

Eukaryotic chromosomes are complexly coiled associations of DNA and histone proteins.

The presence or absence of certain chromosomes that are represented differently in males and females determines the sex of an animal. The X-Y system of sex determination is most common.

### 3.2 The Cell Cycle and Mitotic Cell Division

The replication of DNA and its subsequent allocation to daughter cells during mitotic cell division 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.

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.
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.

Mitosis is divided into five phases. During prophase, the mitotic spindle forms and the nuclear envelope disintegrates. During prometaphase the microtubules attach at one end to the kinetochore of a chromatid and at the opposite end to one pole of the cell. 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 re-forms, and chromosomes unfold.

Cytokinesis, the division of the cytoplasm, begins in late anaphase and is completed in telophase.

3.3 Meiosis: The Basis of Sexual Reproduction
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.

In the life cycle of most animals, germ-line 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).

3.4 DNA: The Genetic Material
Deoxyribonucleic acid (DNA) is the hereditary material of the cell. Ribonucleic acid (RNA) participates in protein synthesis.

Nucleotides are nucleic acid building blocks. Nucleotides consist of a nitrogenous (purine or pyrimidine) base, a phosphate, and a pentose sugar.

DNA replication is semiconservative. During replication, the DNA strands separate, and each strand is a template for a new strand.

Protein synthesis is a result of two processes. Transcription occurs in the nucleus and involves the production of a messenger RNA (mRNA) molecule from a DNA molecule. Translation involves the movement of mRNA to the cytoplasm, where transfer RNA and ribosomes link amino acids in a proper sequence to produce a polypeptide.

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.

3.5 Inheritance Patterns in Animals
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.

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.

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.

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.

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.

**Concept Review Questions**

1. These are represented differently in males and females of the same species.
   a. Autosomes
   b. Nucleosomes
   c. Sex chromosomes
   d. Histones

2. Which of the following would be more nearly identical?
   a. Homologous chromosomes
   b. Nonhomologous chromosomes
   c. Sister chromatids before meiotic prophase I
   d. Sister chromatids after meiotic prophase I
   e. Chromosomes at metaphase II

3. Chromatids move toward opposite poles of the cell during
   a. prophase I of meiosis.
   b. metaphase of mitosis.
   c. anaphase of mitosis.
   d. anaphase I of meiosis.
   e. anaphase II of meiosis.
   f. Both c and d are correct.
   g. Both c and e are correct.

4. A student carried out a cross between two fruit flies. One fly is heterozygous for the vestigial-wing trait and one is homozygous for the vestigial-wing trait. The offspring expected from this cross would
   a. be all vestigial winged.
   b. be all wild winged.
   c. include flies with vestigial wings and wild wings in a ratio of 3:1.
   d. include flies with vestigial wings and wild wings in a ratio of 1:1.

5. A student carried out a cross between two fruit flies. One fly was homozygous for vestigial wings and also homozygous for sepa eyes. The second fly was heterozygous for vestigial wings and homozygous for wild eyes. The offspring expected from this cross would
   a. be all vestigial winged, but one-half of the flies would have sepa eyes and one-half would have wild eyes.
   b. all have wild eyes, but one-half of the flies would have vestigial wings and one-half would have wild wings.
   c. show the following phenotypes in equal numbers: wild wings, wild eyes; wild wings, sepa eyes; vestigial wings, wild eyes; and vestigial wings, sepa eyes.
   d. show the following phenotypes in a 9:3:3:1 ratio: wild wings, wild eyes; wild wings, sepa eyes; vestigial wings, wild eyes; and vestigial wings, sepa eyes.
ANALYSIS AND APPLICATION

QUESTIONS

1. Which do you think evolved first—meiotic cell division or mitotic cell division? Why? What do you think may have been some of the stages in the evolution of one from the other?

2. Assume that a cell containing a 2N chromosome number of 6 has just completed prophase of mitosis. Assume mitosis will be completed. What would result if prometaphase kinetochore microtubules of both chromatids of one chromosome were attached to the same pole of the cell?

3. Why is it important that all regions of chromosomes are not continually active?

4. 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.

Enhance your study of this chapter with study tools and practice tests. Also ask your instructor about the resources available through Connect, including a media-rich eBook, interactive learning tools, and animations.