GENETICS

ANALYSIS & PRINCIPLES

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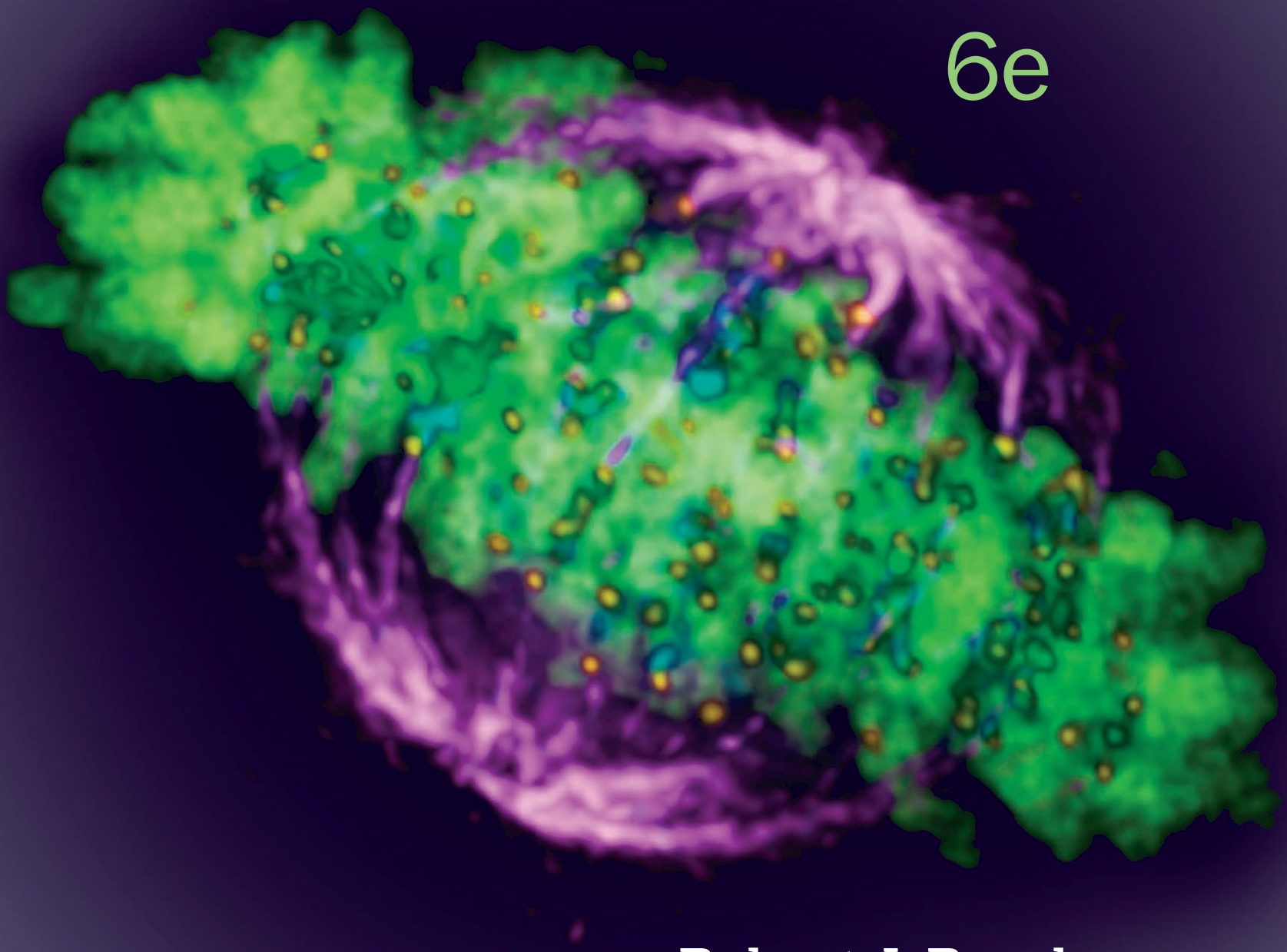

Robert J. Brooker

Mc Graw Hill Education

GENETICS

ANALYSIS & PRINCIPLES

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Sixth Edition

ROBERT J. BROOKER

University of Minnesota

Mc Graw Hill Education

GENETICS: ANALYSIS & PRINCIPLES, SIXTH EDITION

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ABOUT THE AUTHOR

Robert J. Brooker is a professor in the Department of Genetics, Cell Biology, and Development and the Department of Biology Teaching and Learning at the University of Minnesota–Minneapolis. He received his B.A. in biology from Wittenberg University in 1978 and his Ph.D. in genetics from Yale University in 1983. At Harvard, he conducted postdoctoral studies on the lactose permease, which is the product of the *lacY* gene of the *lac* operon. He continued to work on transporters at the University of Minnesota with an emphasis on the structure, function, and regulation of iron transporters found in bacteria and *C. elegans*. At the University of Minnesota, he teaches undergraduate courses in biology and genetics.

DEDICATION

To my wife, Deborah, and our children, Daniel, Nathan, and Sarah

PREFACE

In the sixth edition of *Genetics: Analysis & Principles*, the content has been updated to reflect current trends in the field. In addition, the presentation of the content has been improved in a way that fosters active learning. As an author, researcher, and teacher, I want a textbook that gets students actively involved in learning genetics. To achieve this goal, I have worked with a talented team of editors, illustrators, and media specialists who have helped me to make the sixth edition of *Genetics: Analysis & Principles* a fun learning tool.

Overall, an effective textbook needs to accomplish four goals. First, it needs to provide comprehensive, accurate, and up-to-date content in its field. Second, it needs to expose students to the techniques and skills they will need to become successful in that field. Third, an effective textbook should have pedagogical features, such as formative assessment, that foster student learning. And finally, it should inspire students so they want to pursue that field as a career. The hard work that has gone into the sixth edition of *Genetics: Analysis & Principles* has been aimed at achieving all four of these goals!

FLIPPING THE CLASSROOM

A recent trend in science education is the phenomenon that is sometimes called "flipping the classroom." This phrase refers to the idea that some of the activities that used to be done in class are now done outside of class, and vice versa. For example, instead of spending the entire class time lecturing over textbook and other materials, some of the class time is spent engaging students in various activities, such as problem solving, working through case studies, and designing experiments. This approach is called active learning. For many instructors, the classroom has become more learner centered rather teacher centered. A learner-centered classroom provides a rich environment in which students can interact with each other and with their instructors. Instructors and fellow students often provide formative assessment—immediate feedback that helps each student understand if his or her learning is on the right track.

What are some advantages of active learning? Educational studies reveal that active learning usually promotes greater learning gains. In addition, active learning often focuses on skill development rather than on the memorization of facts that are easily forgotten. Students become trained to "think like scientists" and to develop a skill set that enables them to apply scientific reasoning. A common concern among instructors who are beginning to try out active learning is that they think they will have less time to teach and therefore will cover less material. However, this may not be the case. Although students may be provided with online lectures, "flipping the classroom" typically gives students more responsibility for understanding the textbook material on their own. Along these lines, *Genetics: Analysis & Principles*, Sixth Edition, is intended to provide students with a resource that can be effectively used outside of the classroom. Here are several of the key pedagogical features:

- ***NEW!*** A new feature called **Genetic *TIPS*** provides a consistent approach to help students solve problems in genetics. This approach has three components. First, the student is made aware of the ***T***opic at hand. Second, the question is evaluated with regard to the ***I***nformaiton that is available to the student. Finally, the student is guided through one or more ***P***roblem-Solving ***S***trategies to tackle the question.

GENETIC TIPS **THE QUESTION:** All of the Genetic TIPS begin with a question. As an example, let's consider the following question:

The coding strand of DNA in a segment of a gene is as follows: ATG GGC CTT AGC. This strand carries the information to make a region of a polypeptide with the amino acid sequence, methionine-glycine-leucine-serine. What would be the consequences if a mutation changed the second cytosine (C) in this sequence to an adenine (A)?

TOPIC: ***What topic in genetics does this question address?*** The topic is gene expression. More specifically, the question is about the relationship between a gene sequence and the genetic code.

INFORMATION: ***What information do you know based on the question and your understanding of the topic?*** In the question, you are given the base sequence of a short segment of a gene and told that one of the bases has been changed. From your understanding of the topic, you may remember that a polypeptide sequence is determined by reading the mRNA (transcribed from a gene) in groups of three bases called codons.

PROBLEM-SOLVING STRATEGY: ***Compare and contrast.*** One strategy to solve this problem is to compare the mRNA sequence (transcribed from this gene) before and after the mutation:

Original: AUG GGC **C**UU AGC

Mutant: AUG GGC **A**UU AGC

ANSWER: The mutation has changed the sequence of bases in the mRNA so that the third codon has changed from CUU to AUU. Because codons specify amino acids, this may change the third amino acid to something else. Note: If you look ahead to Chapter 13 (see Table 13.1), you will see that CUU specifies leucine, whereas AUU specifies isoleucine. Therefore, you would predict that the mutation would change the third amino acid from leucine to isoleucine.

- **Genes → Traits:** Because genetics is such a broad discipline, ranging from the molecular level to populations, many instructors have told us that it is a challenge for students to see both "the forest and the trees." It is commonly mentioned that students often have trouble connecting the concepts they have learned in molecular genetics with the traits that occur at the level of a whole organism (i.e., What does transcription have to do with blue eyes?). To try to make this connection more meaningful, certain figure legends in each chapter, designated **Genes → Traits,** remind students that molecular and cellular phenomena ultimately lead to the traits that are observed in each species (see Figure 14.8).
- **Learning Outcomes:** Each section of every chapter begins with a set of learning outcomes. These outcomes help students understand what they should be able to do once they have mastered the material in that section.
- **Formative Assessment:** When students are expected to learn textbook material on their own, it is imperative that they are regularly given formative assessment so they can gauge whether they are mastering the material. Formative assessment is a major feature of this textbook and is bolstered by Connect—a state-of-the art digital assignment and assessment platform. In *Genetics: Analysis & Principles*, Sixth Edition, formative assessment is provided in multiple ways.

  1. As mentioned, a new feature called Genetic TIPS is aimed at helping students refine their problem solving skills.
  2. Each section of every chapter ends with multiple-choice questions. Also, compared with the previous edition, many chapters in the sixth edition are divided into more sections that are shorter in length. Formative assessment at the end of each section allows students to evaluate their mastery of the material before moving on to the next section.
  3. Most figures have Concept Check questions so students can determine if they understand the key points in the figure.
  4. Extensive end-of chapter questions continue to provide students with feedback regarding their mastery of the material.
  5. The textbook material is supported by digital learning tools found in Connect. Questions and activities are assignable in Connect, and students also have access to our valuable adaptive study tool, SmartBook. With this tool, students are repeatedly given questions regarding the textbook material, and depending on their answers, they may advance ahead in their reading, or they are given specific advice on what textbook material to go back and review.

Overall, the pedagogy of *Genetics: Analysis & Principles*, sixth edition, has been designed to foster student learning. Instead of being a collection of facts and figures, *Genetics: Analysis & Principles*, Sixth Edition, by Rob Brooker, is intended to be an engaging and motivating textbook in which formative assessment allows students to move ahead and learn the material in a productive way. We welcome your feedback so we can make future editions even better!

SIGNIFICANT CONTENT CHANGES IN THE SIXTH EDITION

- ***NEW!*** A new problem-solving feature called Genetic TIPS has been added to the sixth edition. The Genetic TIPS are found within each chapter and three or four are found at the end of each chapter.
- ***NEW!*** The topic of Epigenetics has been expanded to a whole chapter, which is now Chapter 16.
- ***NEW!*** A new chapter on non-coding RNA has been added, which is Chapter 17. This long-overdue chapter is in response to a remarkable explosion in our appreciation for the roles of non-coding RNAs in many aspects of molecular biology. Note: Although two new chapters have been added to this edition, the overall page length of the sixth edition is not longer than the fifth edition.
- ***NEW!*** CRISPR-Cas systems: The role of the CRISPR-Cas system in providing prokaryotes with a genome defense mechanism is described in Chapter 17, and its use by researchers to mutate genes is described in Chapter 21.

Examples of Specific Content Changes to Individual Chapters

- Chapter 2. Mendelian Inheritance: Several Genetic TIPS have been added to help students work through problem-solving strategies involving Mendelian inheritance.
- Chapter 3. Chromosome Transmission During Cell Division and Sexual Reproduction: The discussion of the random alignment of homologs during metaphase of meiosis I was expanded.
- Chapter 4. Extensions of Mendelian Inheritance: The topic of gene interaction was streamlined to focus primarily on examples in which the underlying molecular mechanisms are known.
- Chapter 5. Non-Mendelian Inheritance:A common misconception among students is that you can use a Punnett square to deduce nonMendelian inheritance patterns. Throughout the chapter, this misconception has been laid to rest, and students are given effective strategies to predict offspring genotypes and phenotypes.
- Chapter 6. Genetic and Linkage Mapping in Eukaryotes: When looking at experiments involving linkage, student often find it very difficult to identify the recombinant offspring. In various parts of the chapter, a strong effort has been made to make it clear that recombinant offspring have inherited a chromosome that is the product of a crossover. Along these same lines, a new figure (see Figure 6.6) has been added involving the experiments of Curt Stern showing that recombinant offspring carry chromosomes that are the product of a crossover. Also, Figure 6.8 has been revised to emphasis this point.
- Chapter 7. Genetic Transfer and Mapping in Bacteria: Figure 7.13 is a new figure showing the increase in methicillin resistance in certain *Staphylococcus aureus* strains.

- Chapter 8. Variation in Chromosome Structure and Number: Several Genetic TIPS have been added to help students solve problems that involve changes in chromosome structure and chromosome number.
- Chapter 9. Molecular Structure of DNA and RNA: The section on the discovery of the DNA double helix has been streamlined to focus on the key experiments.
- Chapter 10. Chromosome Organization and Molecular Structure: The topic of bacterial chromosome structure has been updated, which includes a new figure (see Figure 10.3) and a discussion of microdomains.
- Chapter 11. DNA Replication: A new figure has been added on the initiation of DNA replication in eukaryotes (see Figure 11.20).
- Chapter 12. Gene Transcription and RNA Modification: The information on alternative splicing has been moved to this chapter.
- Chapter 13. Translation of mRNA: Several Genetic TIPS have been added to help students understand the relationship between the genetic code and the synthesis of polypeptides.
- Chapter 14. Gene Regulation in Bacteria: The information on catabolite activator protein has been updated.
- Chapter 15. Gene Regulation in Eukaryotes I: Transcriptional and Translation Regulation: The material on eukaryotic gene regulation is now divided into two chapters. Chapter 15 focuses on transcriptional and translational regulation.
- Chapter 16. Gene Regulation in Eukaryotes II: Epigenetics: This topic has now been expanded to an entire chapter. A new subsection has been added on the role of epigenetics in vernalization, which is the process in which some plant species require an exposure to cold in order to flower the following spring. Also, a new section has been added on the intriguing topic of paramutation.
- Chapter 17. Non-coding RNA: This new chapter begins with an overview of the general functions of non-coding RNAs, and then the subsequent sections explore certain topics in greater detail, such as their role in chromatin modification, transcription, translation, protein targeting, and genome defense (e.g., the CRISPR-Cas system).
- Chapter 18. Genetics of Viruses: The material on the integration of phage λ has been added to this chapter, along with a brief discussion of Zika virus. Also, information on the origin of HIV and the occurrence of HIV infection worldwide and in the US has been updated.
- Chapter 19. Gene Mutation and DNA Repair: The information on the mismatch repair system has been updated.
- Chapter 20. Recombination, Immunogenetics, and Transposition: Section 20.2 has been revised to focus on immunogenetics.
- Chapter 21. DNA Technologies: A new subsection has been added on gene mutagenesis, which includes a description of the Crispr-Cas system for inactivating and mutating genes.
- Chapter 22. Biotechnology: Several Genetic TIPS have been added to help students appreciate the uses of molecular techniques in biotechnology.
- Chapter 23. Genomics I: Analysis of DNA: The information has been updated regarding completed genome sequences and other aspects of genomics.
- Chapter 24. Genomics II: Functional Genomics, Proteomics, and Bioinformatics: A new subsection has been added on the method called RNA-Seq (see Figure 24.3). The Bioinformatics section has been reorganized with an emphasis on gene prediction and homology.
- Chapter 25. Medical Genetics and Cancer: Several Genetic TIPS have been added to help students understand how mutations play a role in certain diseases, including cancer.
- Chapter 26. Developmental Genetics: The information on *Hox* genes in development, and the role of the *SRY* gene is human sex determination, have been updated.
- Chapter 27. Population Genetics: The topic of inbreeding has been expanded.
- Chapter 28. Complex and Quantitative Traits: The topic of the identification of QTLs is now found in its own subsection.
- Chapter 29. Evolutionary Genetics: The cladistics method for constructing a phylogenetic tree is compared with the UPGMA method.

Suggestions Welcome!

It seems very appropriate to use the word *evolution* to describe the continued development of this textbook. I welcome any and all comments. The refinement of any science textbook requires input from instructors and their students. These include comments regarding writing, illustrations, supplements, factual content, and topics that may need greater or less emphasis. You are invited to contact me at:

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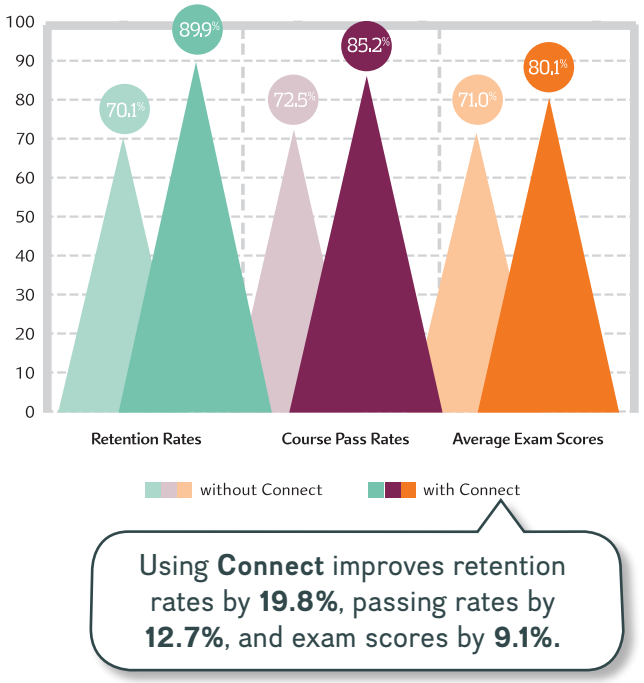

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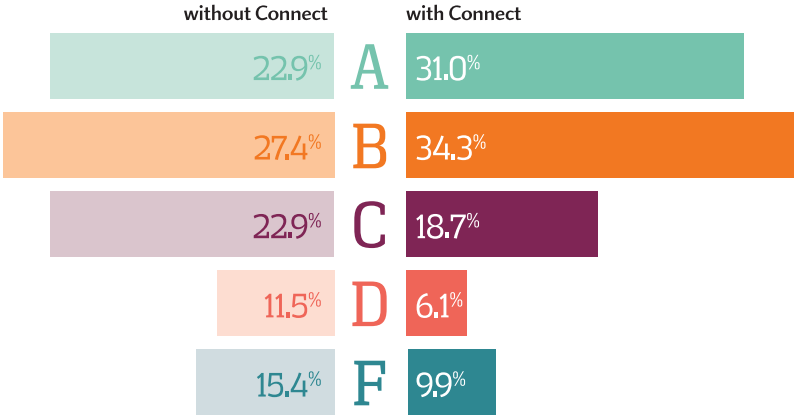

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ACKNOWLEDGMENTS

The production of a textbook is truly a collaborative effort, and I am deeply indebted to many people. All six editions of this textbook went through multiple rounds of rigorous revision that involved the input of faculty, students, editors, and educational and media specialists. Their collective contributions are reflected in the final outcome.

Deborah Brooker (Freelance Developmental Editor) meticulously read the new material, analyzed every figure, and offered extensive feedback. Her attention to detail in this edition and previous editions has profoundly contributed to the accuracy and clarity of this textbook. I would also like to thank Jane Hoover (Freelance Copy Editor) for understanding the material and working extremely hard to improve the text's clarity. Her efforts are truly appreciated.

I would particularly like to acknowledge the many people at McGraw-Hill Education whose skills and insights are amazing. My highest praise goes to Elizabeth Sievers (Lead Product Developer), who carefully checks all aspects of textbook development and makes sure that all of the pieces of the puzzle are in place. I am also grateful to Justin Wyatt (Brand Manager) for overseeing this project. I would like to thank other people at McGraw-Hill who have played key roles in producing an actual book and the supplements that go along with it. In particular, Jayne Klein (Senior Content Project Manager), has done a superb job of managing the components that need to be assembled to produce a book. I would also like to thank Carrie Burger (Content Licensing Specialist), who acted as an interface between me and the photo company. In addition, my gratitude goes to David Hash (Designer), who provided much input into the internal design of the book as well as created an awesome cover. Finally, I would like to thank Patrick Reidy (Executive Marketing Manager), whose major efforts begin when the sixth edition comes out!

I would also like to extend my thanks to everyone at Aptara who worked with great care in the paging of the book, making sure that the figures and relevant text are as close to each other as possible. Likewise, the people at Photo Affairs, Inc. have done a great job of locating many of the photographs that have been used in the sixth edition.

Finally, I want to thank the many scientists who reviewed the chapters of this textbook with special attention to the new Chapter 17, Non-coding RNAs. Their broad insights and constructive suggestions were an overriding factor that shaped its final content and organization. I am truly grateful for their time and compassion.

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CHAPTER OUTLINE

CC (for "carbon copy" or "copy cat"), the first cloned pet. *In 2002, the cat shown here was produced by cloning, a procedure described in Chapter 22.*

1 OVERVIEW OF GENETICS

Hardly a week goes by without a major news story involving a genetic breakthrough. The increasing pace of genetic discoveries has become staggering. The Human Genome Project is a case in point. This project began in the United States in 1990, when the National Institutes of Health and the Department of Energy joined forces with international partners to decipher the massive amount of information contained in our **genome**—the DNA found within all of our chromosomes (**Figure 1.1**). Remarkably, in only a decade, they determined the DNA sequence (the order of the bases A, T, G, and C) of over 90% of the human genome. The completed sequence, published in 2003, has an accuracy greater than 99.99%; less than one mistake was made in every 10,000 base pairs!

In 2008, a more massive undertaking, called the 1000 Genomes Project, was launched to establish a detailed understanding of human genetic variation. In this international project, researchers set out to determine the DNA sequence of at least 1000 anonymous participants from around the globe. In 2015, the sequencing of over 2500 genomes was described in the journal *Nature*.

Studying the human genome allows us to explore fundamental details about ourselves at the molecular level. The results of the Human Genome Project and the 1000 Genomes Project have shed considerable light on basic questions, like how many genes we have, how genes direct the activities of living cells, how species evolve, how single cells develop into complex tissues, and how defective genes cause disease. Furthermore, such understanding may lend itself to improvements in modern medicine by leading to better diagnoses of diseases and the development of new treatments for them.

The journey to unravel the mysteries within our genes has involved the invention of many new technologies. For example, researchers have developed genetic techniques to produce medicines, such as human insulin, that would otherwise be difficult or impossible to make. Human insulin is synthesized in strains of *Escherichia coli* bacteria that have been genetically altered by the addition of genes that encode the polypeptides that form this hormone. The bacteria are grown in a laboratory and make large amounts of human insulin. As discussed in Chapter 22, the insulin is purified and administered to many people with insulin-dependent diabetes.

DNA, the molecule of life

The adult human body is composed of trillions of cells.

Most human cells contain the following:

- 46 human chromosomes, found in 23 pairs
- 2 meters of DNA
- Approximately 22,000 genes coding for proteins that perform most life functions
- Approximately 3 billion DNA base pairs per set of chromosomes, containing the bases A, T, G, and C

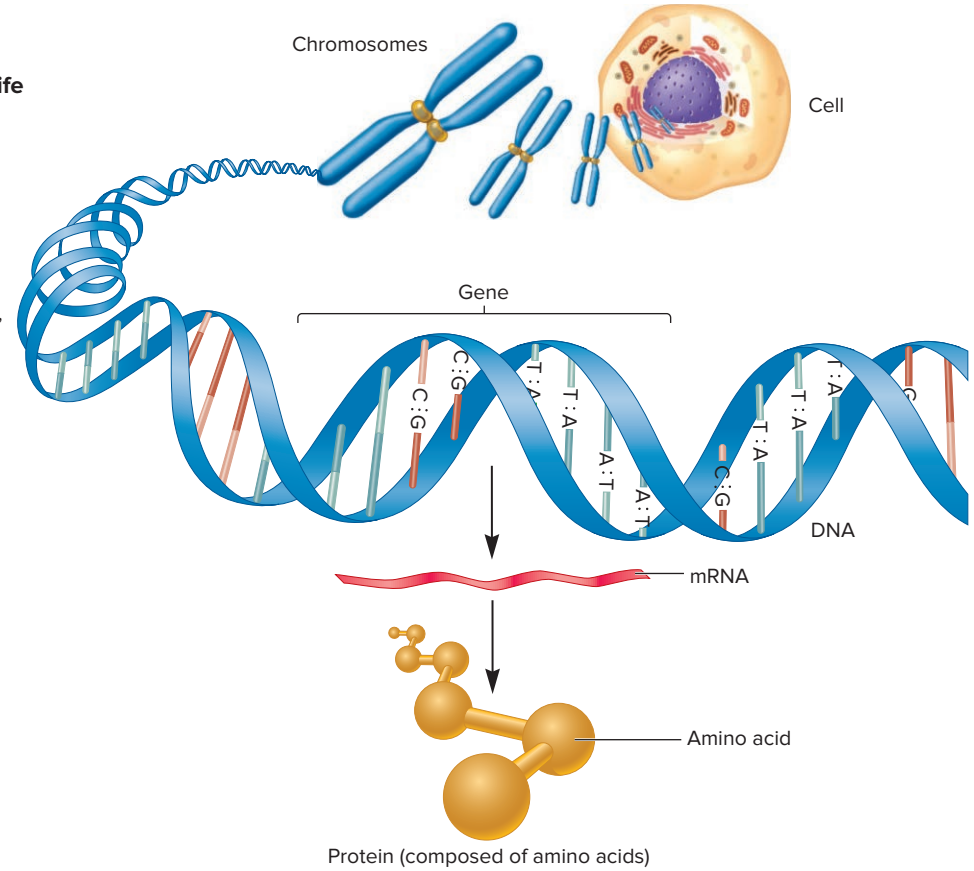


FIGURE 1.1 The human genome. The human genome is a complete set of human chromosomes. People have two sets of chromosomes—one set from each parent—which are found in the cell nucleus. The Human Genome Project revealed that each set of chromosomes is composed of a DNA sequence that is approximately 3 billion nucleotide base pairs long. Estimates suggest that each set contains about 22,000 different genes that encode proteins. As discussed later, most genes are first transcribed into mRNA and then the mRNA is used to make proteins. This figure emphasizes the DNA found in the cell nucleus. Humans also have a small amount of DNA in their mitochondria, which has also been sequenced.

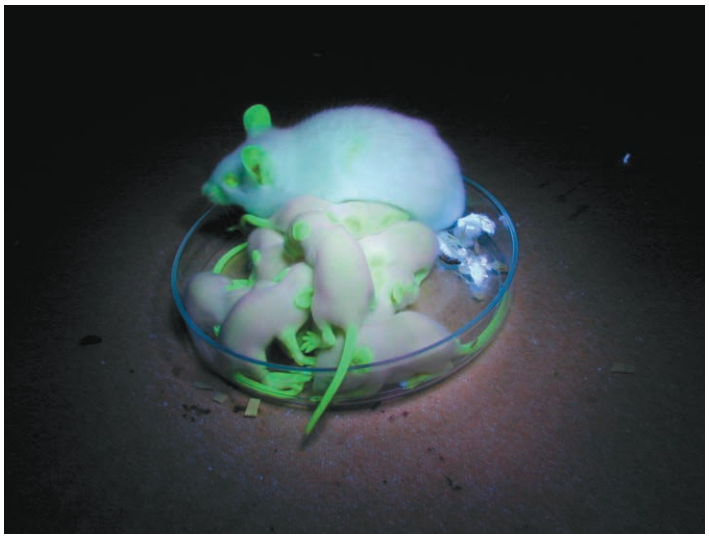
CONCEPT CHECK: How might a better understanding of our genes be used in the field of medicine?

New genetic technologies are often met with skepticism and sometimes even with disdain. An example is mammalian cloning. In 1997, Ian Wilmut and his colleagues created clones of sheep, using mammary cells from an adult animal (**Figure 1.2**). More recently, such cloning has been achieved in several mammalian species, including cows, mice, goats, pigs, and cats. In 2002, the first pet was cloned, a cat named CC (for "carbon copy" or "copy cat"; see photo at the beginning of the chapter). The cloning of mammals provides the potential for many practical applications. With regard to livestock, cloning would enable farmers to use cells from their best individuals to create genetically homogeneous herds. This could be advantageous in terms of agricultural yield, although such a genetically homogeneous herd may be more susceptible to certain diseases. However, people have become greatly concerned with the possibility of human cloning. This prospect has raised serious ethical questions. Within the past few years, legislation has been introduced that involves bans on human cloning.

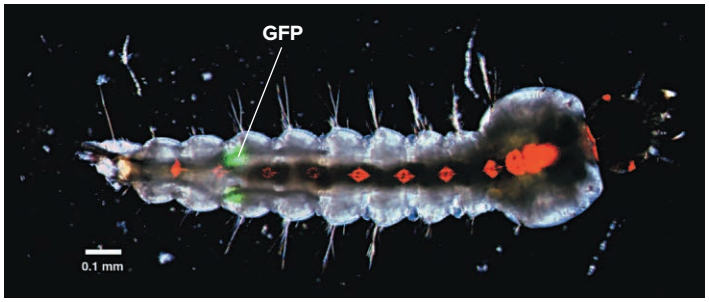
Finally, genetic technologies provide the means to modify the traits of animals and plants in ways that would have been unimaginable just a few decades ago. **Figure 1.3a** illustrates a striking example in which scientists introduced a gene from

FIGURE 1.2 The cloning of a mammal. The lamb in the front is Dolly, the first mammal to be cloned. She was cloned from the cells of a Finn Dorset (a white-faced sheep). The sheep in the back is Dolly's surrogate mother, a Blackface ewe. A description of how Dolly was produced is presented in Chapter 22.

CONCEPT CHECK: What ethical issues may be associated with human cloning?



(a) GFP expressed in mice



(b) GFP expressed in the gonads of a male mosquito

FIGURE 1.3 The introduction of a jellyfish gene into laboratory mice and mosquitoes. **(a)** A gene that naturally occurs in jellyfish encodes a protein called green fluorescent protein (GFP). The *GFP* gene was cloned and introduced into mice. When these mice are exposed to UV light, GFP emits a bright green color. These mice glow green, just like the jellyfish! **(b)** The *GFP* gene was introduced next to a gene sequence that causes the expression of GFP only in the gonads of male mosquitoes. This allows researchers to identify and sort males from females.

(a): © Advanced Cell Technology, Inc., Worcester, Massachusetts; (b): Photo taken by Flaminia Catteruccia, Jason Benton and Andrea Crisanti, and assembled by www.luciariccidesign.com

CONCEPT CHECK: Why is it useful to sort male mosquitoes from females?

jellyfish into mice. Certain species of jellyfish emit a "green glow" produced by a gene that encodes a bioluminescent protein called green fluorescent protein (GFP). When exposed to blue or ultraviolet (UV) light, the protein emits a striking green-colored light. Scientists were able to clone the *GFP* gene from a sample of jellyfish cells and then introduce this gene into laboratory mice. The green fluorescent protein is made throughout the cells of their bodies. As a result, their skin, eyes, and organs give off an eerie green glow when exposed to UV light. Only their fur does not glow.

The expression of green fluorescent protein allows researchers to identify particular proteins in cells or specific body parts. For example, Andrea Crisanti and colleagues have altered mosquitoes to express GFP only in the gonads of males (**Figure 1.3b**). This enables the researchers to identify and sort males from females. Why is this useful? Researchers can produce a population of mosquitoes and then sterilize the males. The ability to rapidly sort males and females makes it possible to release the sterile males without the risk of releasing additional females. The release of sterile males may be an effective means of controlling mosquito populations because females mate only once before they die. Mating with a sterile male prevents a female from producing offspring. In 2008, Osamu Shimomura, Martin Chalfie, and Roger Tsien received the Nobel Prize in chemistry for the discovery and the development of GFP, which has become a widely used tool in biology.

Overall, as we move forward in the twenty-first century, the excitement level in the field of genetics is high, perhaps higher than it has ever been. Nevertheless, new genetic knowledge and technologies will also create many ethical and societal challenges. In this chapter, we begin with an overview of genetics and then explore the various fields of genetics and their experimental approaches.

1.1 THE MOLECULAR EXPRESSION OF GENES

Learning Outcomes:

1. Describe the biochemical composition of cells.
2. Explain how proteins are largely responsible for cell structure and function.
3. Outline how DNA stores the information to make proteins.

Genetics is the branch of biology that deals with heredity and variation. It stands as the unifying discipline in biology by allowing us to understand how life can exist at all levels of complexity, ranging from the molecular to the population level. Genetic variation is the root of the natural diversity that we observe among members of the same species and among different species.

Genetics is centered on the study of genes. A gene is classically defined as a unit of heredity. At the molecular level, a **gene** is a segment of DNA that produces a functional product. The functional product of most genes is a polypeptide, which is a linear sequence of amino acids that folds into units that constitute proteins. In addition, genes are commonly described according to the way they affect **traits,** which are the characteristics of an organism. In humans, for example, we speak of traits such as eye color, hair texture, and height. The ongoing theme of this textbook is the relationship between genes and traits. As an organism grows and develops, its collection of genes provides a blueprint that determines its traits.

In this section, we examine the general features of life, beginning with the molecular level and ending with populations of organisms. As will become apparent, genetics is the

common thread that explains the existence of life and its continuity from generation to generation. For most students, this chapter should serve as an overview of topics they have learned in other introductory courses such as General Biology. Even so, it is usually helpful to see the "big picture" of genetics before delving into the finer details that are covered in Chapters 2 through 29.

Living Cells Are Composed of Biochemicals

To fully understand the relationship between genes and traits, we need to begin with an examination of the composition of living organisms. Every cell is constructed from intricately organized chemical substances. Small organic molecules such as glucose and amino acids are produced from the linkage of atoms via chemical bonds. The chemical properties of organic molecules are essential for cell vitality in two key ways. First, the breaking of chemical bonds during the degradation of small molecules provides energy to drive cellular processes. A second important function of these small organic molecules is their role as the building blocks for the synthesis of larger molecules. Four important categories of larger molecules are **nucleic acids** (i.e., DNA and RNA), **proteins, carbohydrates,** and **lipids.** Three of these—nucleic acids, proteins, and carbohydrates—form **macromolecules** that are composed of many repeating units of smaller building blocks. RNA, proteins, and some carbohydrates are made from hundreds or even thousands of repeating building blocks. DNA is the largest macromolecule found in living cells. A single DNA molecule can be composed of a linear sequence of hundreds of millions of building blocks called nucleotides!

The formation of cellular structures relies on the interactions of molecules and macromolecules. For example, nucleotides are connected together to make DNA, which is a constituent of chromosomes (**Figure 1.4**). In addition, DNA is associated with many proteins that provide organization to the structure of chromosomes. Within a eukaryotic cell, the chromosomes are contained in a compartment called the cell nucleus. The nucleus is bounded by a double membrane composed of lipids and proteins that shields the chromosomes from the rest of the cell. The organization of chromosomes within a cell nucleus protects the chromosomes from mechanical damage and provides a single compartment for genetic activities such as gene transcription. As a general theme, the formation of large cellular structures arises from interactions among different molecules and macromolecules. These cellular structures, in turn, are organized to make a complete living cell.

Each Cell Contains Many Different Proteins That Determine Cell Structure and Function

To a great extent, the characteristics of a cell depend on the types of proteins that it makes. The entire collection of proteins that a cell makes at a given time is called its **proteome.** The range of functions among different types of proteins is truly remarkable. Some proteins help determine the shape and structure of a given

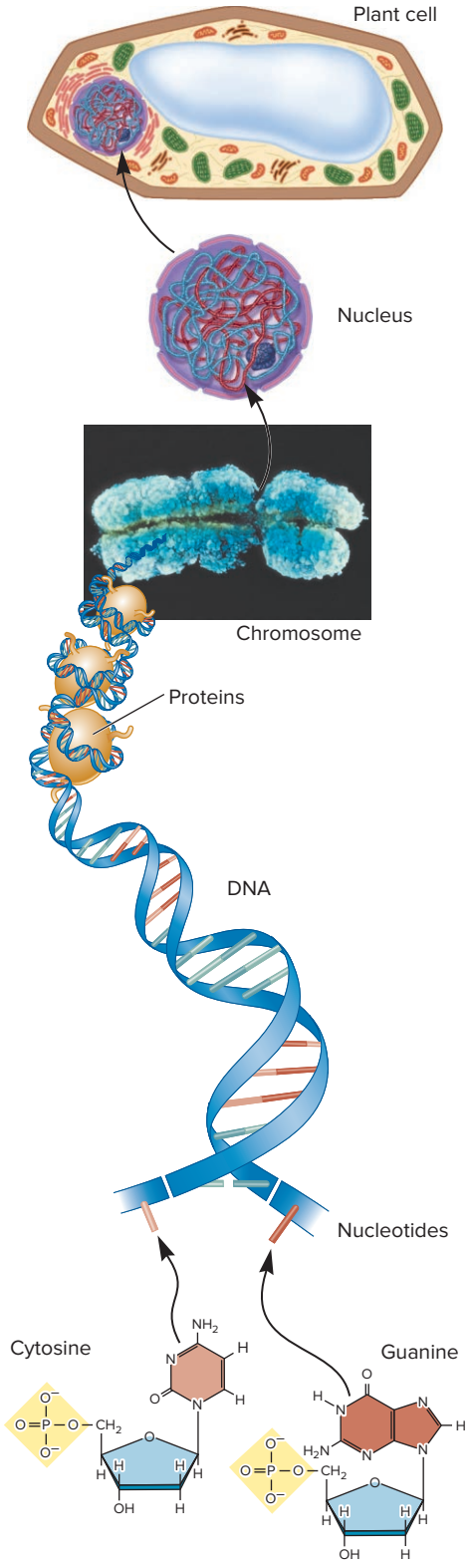


FIGURE 1.4 Molecular organization of a living cell. Cellular structures are constructed from smaller building blocks. In this example, DNA is formed from the linkage of nucleotides to produce a very long macromolecule. The DNA associates with proteins to form a chromosome. The chromosomes are located within a membrane-bound organelle called the nucleus, which, along with many different types of organelles, is found within a complete cell.

photo: © Biophoto Associates/Science Source

CONCEPT CHECK: Is DNA a small molecule, a macromolecule, or an organelle?

cell. For example, the protein known as tubulin assembles into large structures known as microtubules, which provide the cell with internal structure and organization. Other proteins are inserted into cell membranes and aid in the transport of ions and small molecules across the membrane. **Enzymes,** which accelerate chemical reactions, are a particularly important category of proteins. Some enzymes play a role in the breakdown of molecules or macromolecules into smaller units. These are known as catabolic enzymes and are important in the utilization of energy. Alternatively, anabolic enzymes and accessory proteins function in the synthesis of molecules and macromolecules throughout the cell. The construction of a cell greatly depends on its proteins that are involved in anabolism because these are required to synthesize all cellular macromolecules.

Molecular biologists have come to realize that the functions of proteins underlie the cellular characteristics of every organism. At the molecular level, proteins can be viewed as the active participants in the enterprise of life.

DNA Stores the Information for Protein Synthesis

The genetic material of living organisms is composed of a substance called **deoxyribonucleic acid,** abbreviated **DNA.** The DNA stores the information needed for the synthesis of all cellular proteins. In other words, the main function of the genetic blueprint is to code for the production of proteins in the correct cell, at the proper time, and in suitable amounts. This is an extremely complicated task because living cells make thousands of different proteins. Genetic analyses have shown that a typical bacterium can make a few thousand different proteins, and estimates for the numbers produced by complex eukaryotic species range in the tens of thousands.

DNA's ability to store information is based on its structure. DNA is composed of a linear sequence of **nucleotides.** Each nucleotide contains one of four nitrogen-containing bases: adenine (A), thymine (T), guanine (G), or cytosine (C). The linear order of these bases along a DNA molecule contains information similar to the way that groups of letters of the alphabet represent words. For example, the "meaning" of the sequence of bases ATGGGCCTTAGC differs from that of TTTAAGCTTGCC. DNA sequences within most genes contain the information to direct the order of amino acids within **polypeptides** according to the **genetic code.** In the code, a three-base sequence specifies one particular **amino acid** among the 20 possible choices. One or more polypeptides form a functional protein. In this way, the DNA can store the information to specify the proteins made by an organism.

DNA Sequence	Amino Acid Sequence
ATG GGC CTT AGC	Methionine Glycine Leucine Serine
TTT AAG CTT GCC	Phenylalanine Lysine Leucine Alanine

In living cells, the DNA is found within large structures known as **chromosomes.** Figure 1.5 is a micrograph of the 46 chromosomes contained in a cell from a human male; this type of image is known as a **karyotype.** The DNA of an average human chromosome is an extraordinarily long, linear, double-stranded structure that contains well over a hundred million nucleotides. Along the immense length of a chromosome, the genetic information is parceled into functional units known as genes. An average-sized human chromosome is expected to contain about 1000 different protein-encoding genes.

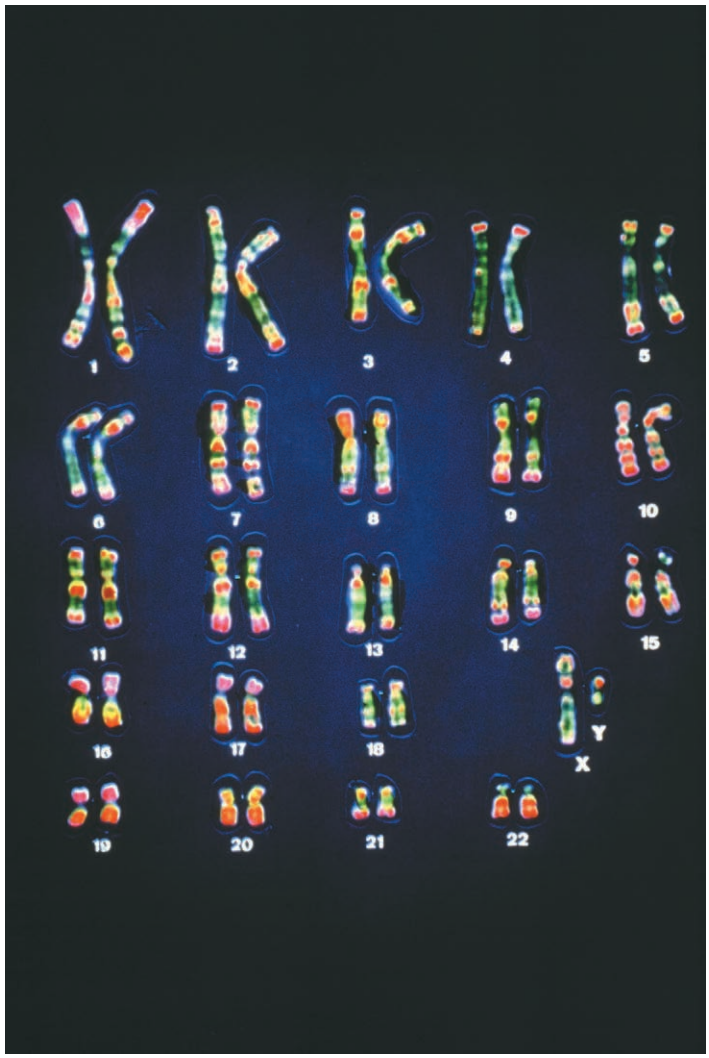
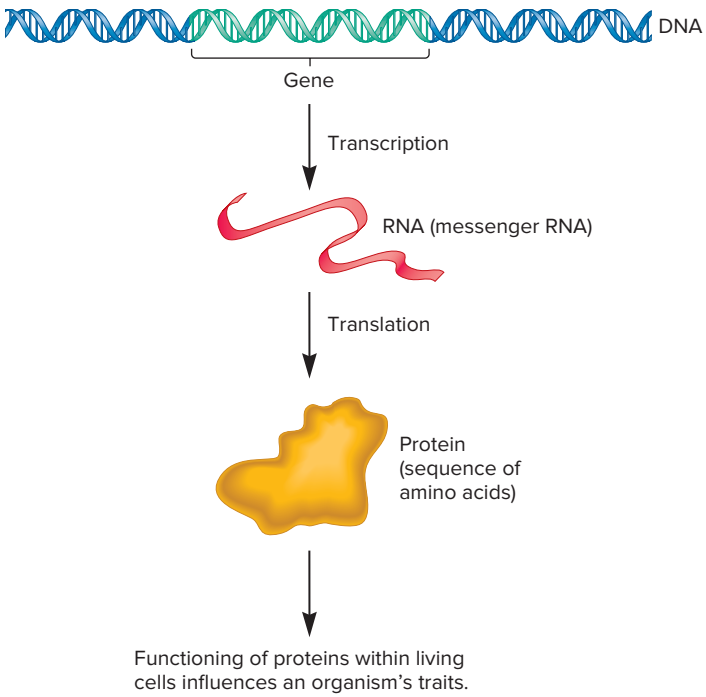


FIGURE 1.5 A micrograph of the 46 chromosomes found in a cell from a human male.

CONCEPT CHECK: Which types of macromolecules are found in chromosomes?

The Information in DNA Is Accessed During the Process of Gene Expression

To synthesize its proteins, a cell must be able to access the information that is stored within its DNA. The process of using a gene sequence to affect the characteristics of cells and organisms is referred to as **gene expression.** At the molecular level, the information



ONLINE ANIMATION

FIGURE 1.6 Gene expression at the molecular level. The expression of a gene is a multistep process. During transcription, one of the DNA strands is used as a template to make an RNA strand. During translation, the RNA strand is used to specify the sequence of amino acids within a polypeptide. One or more polypeptides produce a protein that functions within the cell, thereby influencing an organism's traits.

CONCEPT CHECK: Where is the information to make a polypeptide stored?

within genes is accessed in a stepwise process (**Figure 1.6**). In the first step, known as **transcription,** the DNA sequence within a gene is copied into a nucleotide sequence of **ribonucleic acid (RNA). Protein-encoding genes** (also called **structural genes**) carry the information for the amino acid sequence of a polypeptide. When a protein-encoding gene is transcribed, the first product is an RNA molecule known as **messenger RNA (mRNA).** During polypeptide synthesis—a process called **translation**—the sequence of nucleotides within the mRNA determines the sequence of amino acids in a polypeptide. One or more polypeptides then fold and assemble into a functional protein. The synthesis of functional proteins ultimately determines an organism's traits. As discussed further in Chapter 12 (look ahead to Figure 12.1), the pathway of gene expression from DNA to RNA to protein is called the **central dogma of genetics** (also called the central dogma of molecular biology). It forms a cornerstone of our understanding of genetics at the molecular level.

1.1 COMPREHENSION QUESTIONS

1. Which of the following is *not* a constituent of a cell's proteome?
   a. An enzyme
   b. A cytoskeletal protein
   c. A transport protein in the plasma membrane
   d. An mRNA
2. A gene is a segment of DNA that has the information to produce a functional product. The functional product of most genes is
   a. DNA.
   b. mRNA.
   c. a polypeptide.
   d. all of the above.
3. The function of the genetic code is to
   a. promote transcription.
   b. specify the amino acids within a polypeptide.
   c. alter the sequence of DNA.
   d. none of the above.
4. The process of transcription directly results in the synthesis of
   a. DNA.
   b. RNA.
   c. a polypeptide.
   d. all of the above.

1.2 THE RELATIONSHIP BETWEEN GENES AND TRAITS

Learning Outcomes:

1. Outline how the expression of genes leads to an organism's traits.
2. Define *genetic variation.*
3. Discuss the relationship between genes and traits.
4. Describe how genes are transmitted in sexually reproducing species.
5. Explain the process of evolution.

A trait is any characteristic that an organism displays. In genetics, we often focus our attention on **morphological traits,** those that affect the appearance, form, and structure of an organism. The color of a flower and the height of a pea plant are morphological traits. Geneticists frequently study these types of traits because they are easy to evaluate. For example, an experimenter can simply look at a plant and tell if it has red or white flowers. However, not all traits are morphological. **Physiological traits** affect the ability of an organism to function. For example, the rate at which a bacterium metabolizes a sugar such as lactose is a physiological trait. Like morphological traits, physiological traits are controlled, in part, by the expression of genes. **Behavioral traits** affect the ways an organism responds to its environment. An example is the mating calls of bird species. In animals, the nervous system plays a key role in governing such traits. In this section, we will examine the relationship between the expression of genes and an organism's traits.

The Molecular Expression of Genes Leads to an Organism's Traits

A complicated, yet very exciting, aspect of genetics is that our observations and theories span four levels of biological organization:

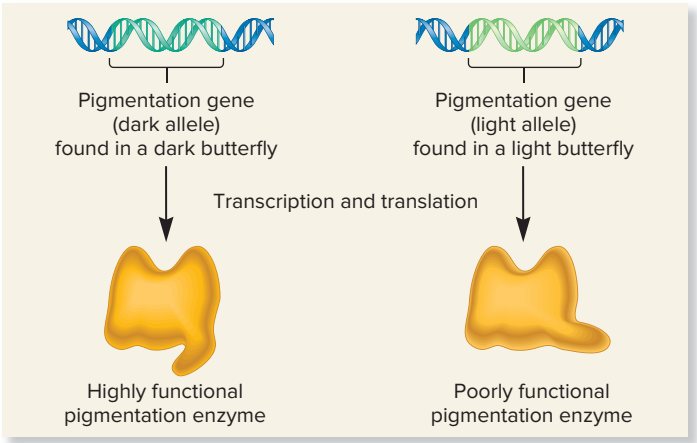
molecules, cells, organisms, and populations. This can make it difficult to appreciate the relationship between genes and traits. To understand this connection, we need to relate the following phenomena:

1. Genes are expressed at the **molecular level.** In other words, gene transcription and translation lead to the production of a particular protein, which is a molecular process.
2. Proteins often function at the **cellular level.** The function of a protein within a cell affects the structure and workings of that cell.
3. An organism's traits are determined by the characteristics of its cells. We do not have microscopic vision, yet when we view morphological traits, we are really observing the properties of an individual's cells. For example, a red flower has its color because its cells make a red pigment. The trait of red flower color is an observation at the **organism level.** Yet the trait is rooted in the molecular characteristics of the organism's cells.
4. A **species** is a group of organisms that maintains a distinctive set of attributes in nature. The occurrence of a trait within a species is an observation at the **population level.** Along with learning how a trait occurs, we also want to understand why a trait becomes prevalent in a particular species. In many cases, researchers discover that a trait predominates within a population because it promotes the reproductive success of the members of the population. This leads to the evolution of beneficial traits.

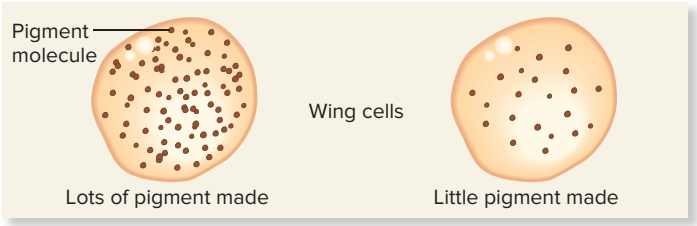
As a schematic example to illustrate the four levels of genetics, **Figure 1.7** shows the trait of pigmentation in butterflies. One member of this species is dark-colored and the other is very light. Let's consider how we can explain this trait at the molecular, cellular, organism, and population levels.

At the molecular level, we need to understand the nature of the gene or genes that govern this trait. As shown in Figure 1.7a, a gene, which we will call the pigmentation gene, is responsible for the amount of pigment produced. The pigmentation gene exists in two different versions. Alternative versions of a specific gene are called **alleles.** In this example, one allele confers a dark pigmentation and the other causes a light pigmentation. Each of these alleles encodes a protein that functions as a pigment-synthesizing enzyme. However, the DNA sequences of the two alleles differ slightly from each other. This difference in the DNA sequence leads to a variation in the structure and function of the respective pigmentation enzymes.

At the cellular level (Figure 1.7b), the functional differences between the two pigmentation enzymes affect the amount of pigment produced. The allele causing dark pigmentation, which is shown on the left, encodes an enzyme that functions very well. Therefore, when this gene is expressed in the cells of the wings, a large amount of pigment is made. By comparison, the allele causing light pigmentation encodes an enzyme that functions poorly. Therefore, when this allele is the only pigmentation gene expressed, little pigment is made.

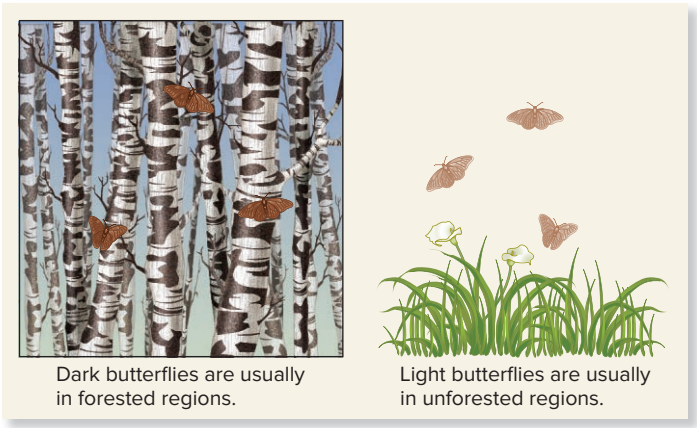


(a) Molecular level



(b) Cellular level

(c) Organism level



(d) Population level

FIGURE 1.7 **The relationship between genes and traits at the (a) molecular, (b) cellular, (c) organism, and (d) population levels.**

CONCEPT CHECK: Which butterfly has a more active pigment-producing enzyme, the dark- or light-colored one?

At the organism level (Figure 1.7c), the amount of pigment in the wing cells governs the color of the wings. If the pigment cells produce high amounts of pigment, the wings are dark-colored. If the pigment cells produce little pigment, the wings are light.

Finally, at the population level (Figure 1.7d), geneticists would like to know why a species of butterfly would contain some members with dark wings and other members with light wings. One possible explanation is differential predation. The butterflies with dark wings might avoid being eaten by birds if they happen to live within the dim light of a forest. The dark wings would help to camouflage the butterfly if it were perched on a dark surface such as a tree trunk. In contrast, the lightly colored wings would be an advantage if the butterfly inhabited a brightly lit meadow. Under these conditions, a bird may be less likely to notice a light-colored butterfly that is perched on a sunlit surface. A population geneticist might study this species of butterfly and find that the dark-colored members usually live in forested areas and the light-colored members reside in unforested regions.

Inherited Differences in Traits Are Due to Genetic Variation

In Figure 1.7, we considered how gene expression leads to variation in a trait of organisms, using the example of dark- versus light-colored wings in butterflies. Variation in traits among members of the same species is very common. For example, some people have brown hair and others have blond hair; some petunias have white flowers and others have purple flowers. These are examples of **genetic variation.** This term describes the differences in inherited traits among individuals within a population.

In large populations that occupy a wide geographic range, genetic variation can be quite striking. Morphological differences have often led geneticists to misidentify two members of the same species as belonging to separate species. As an example, **Figure 1.8** shows two dyeing poison frogs that are members of the same species, *Dendrobates tinctorius.* They display dramatic differences in their markings. Such contrasting forms within a single species are termed **morphs.** You can easily imagine how someone might mistakenly conclude that these frogs are not members of the same species.

Changes in the nucleotide sequence of DNA underlie the genetic variation that we see among individuals. Throughout this textbook, we will routinely examine how variation in the genetic material results in changes in an organism's traits. At the molecular level, genetic variation can be attributed to different types of modifications.

1. Small or large differences can occur within gene sequences. When such changes initially occur, they are called **gene mutations.** Mutations result in genetic variation in which a gene is found in two or more alleles, as previously described in Figure 1.7. In many cases, gene mutations alter the expression or function of a protein that a gene encodes.

FIGURE 1.8 Two dyeing poison frogs (*Dendrobates tinctorius*) showing different morphs within a single species.

(Top): © Mark Smith/Science Source; (Bottom): © Dante Fenolio/Science Source

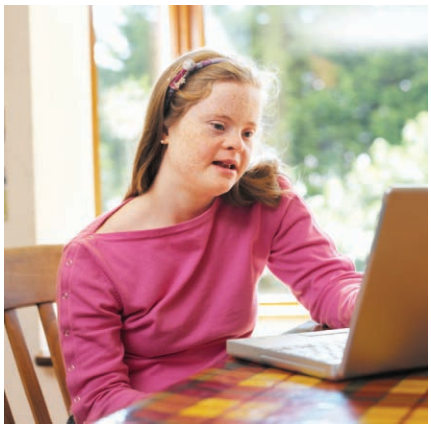
CONCEPT CHECK: Why do these two frogs look so different?

2. Major alterations can also occur in the structure of a chromosome. A large segment of a chromosome can be lost, rearranged, or reattached to another chromosome.
3. Variation may also occur in the total number of chromosomes. In some cases, an organism may inherit one too many or one too few chromosomes. In other cases, it may inherit an extra set of chromosomes.

Variations of sequences within genes are a common source of genetic variation among members of the same species. In humans, familiar examples of variation involve genes for eye color, hair texture, and skin pigmentation. Chromosome variation—a change in chromosome structure or number (or both)—is also found, but this type of change is often detrimental. Many human genetic disorders are the result of chromosomal alterations. The most common example is Down syndrome, which is due to the presence of an extra chromosome (**Figure 1.9a**). By comparison, chromosome variation in plants is common and often leads to plants with superior characteristics, such as increased resistance to disease. Plant breeders have frequently exploited this observation. Cultivated varieties of wheat, for example, have many more chromosomes than the wild species (**Figure 1.9b**).

Traits Are Governed by Genes and by the Environment

In our discussion thus far, we have considered the role that genes play in determining an organism's traits. Another critical factor is



(a)

(b)

FIGURE 1.9 Examples of chromosome variation. **(a)** A person with Down syndrome. She has 47 chromosomes rather than the common number of 46, because she has an extra copy of chromosome 21. **(b)** A wheat plant. Cultivated wheat is derived from the contributions of three wild species with two sets of chromosomes each, producing an organism with six sets of chromosomes.

CONCEPT CHECK: Do these examples constitute variation in chromosome structure or variation in chromosome number?

the **environment**—the surroundings in which an organism exists. A variety of factors in an organism's environment profoundly affect its morphological and physiological features. For example, a person's diet greatly influences many traits such as height, weight, and even intelligence. Likewise, the amount of sunlight a plant receives affects its growth rate and the color of its flowers.

An interesting example of the interplay between genes and the environment involves the human genetic disease **phenylketonuria (PKU).** Humans have a gene that encodes an enzyme known as phenylalanine hydroxylase. Most people have two functional copies of this gene. People with one or two functional copies of the gene can eat foods containing the amino acid phenylalanine and metabolize it properly. A rare variation in the gene that encodes phenylalanine hydroxylase results in a nonfunctional version of this enzyme. Individuals with two copies of this rare, inactive allele cannot metabolize phenylalanine properly. When given a standard diet containing phenylalanine, individuals with this disorder are unable to break down this amino acid. Phenylalanine accumulates and is converted into phenylketones, which are detected in the urine. Individuals with PKU can manifest a variety of detrimental traits, including mental impairment, underdeveloped teeth, and foul-smelling urine. Fortunately, through routine newborn screening in the United States, PKU is now diagnosed early. Part of the treatment is a diet that restricts phenylalanine, which is present in high-protein foods such as eggs, meat, and dairy products. Restricting phenylalanine allows the affected child to develop normally. PKU provides a dramatic example of how the environment and an individual's genes can interact to influence the traits of the organism.

During Reproduction, Genes Are Passed from Parent to Offspring

Now that we have considered how genes and the environment govern the outcome of traits, we can turn to the issue of inheritance. How are traits passed from parents to offspring? The foundation for our understanding of inheritance came from Gregor Mendel's study of pea plants in the nineteenth century. His work revealed that the genetic determinants that govern traits, which we now call genes, are passed from parent to offspring as discrete units. We can predict the outcome of many genetic crosses based on Mendel's laws of inheritance.

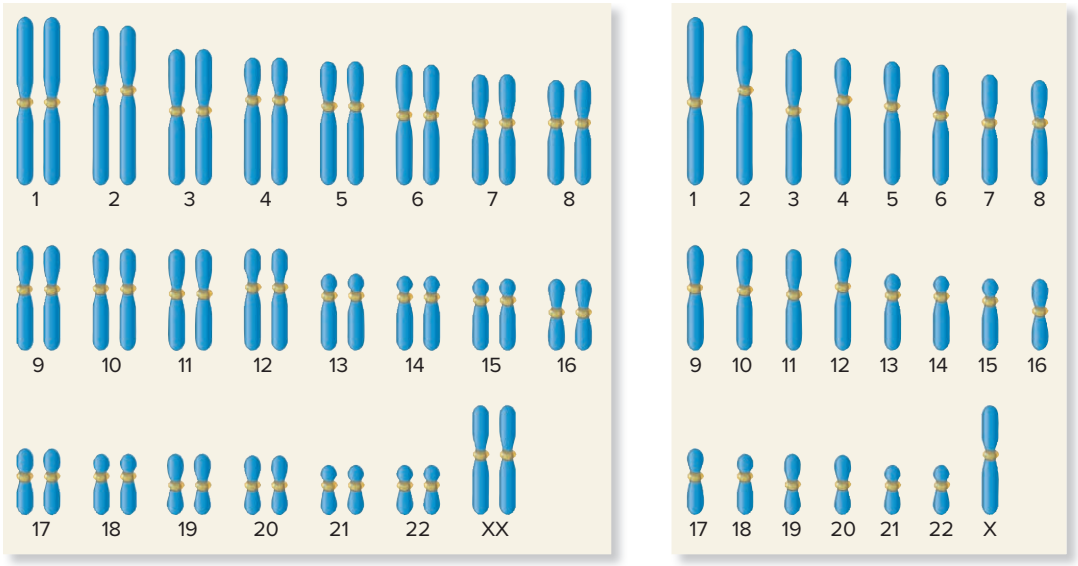
The inheritance patterns identified by Mendel can be explained by the existence of chromosomes and their behavior during cell division. Like Mendel's pea plants, sexually reproducing species are commonly **diploid.** This means they contain two copies of each chromosome, one from each parent. The two copies are called **homologs** of each other. Because genes are located within chromosomes, diploid organisms have two copies of most genes. Humans, for example, have 46 chromosomes, which are found in homologous pairs (**Figure 1.10a**). With the exception of the sex chromosomes (X and Y), each homologous pair contains the same kinds of genes. For example, both copies of human chromosome 12 carry the gene that encodes phenylalanine hydroxylase, which was discussed previously. Therefore, an individual has two copies of this gene, which may or may not be identical alleles.

Most cells of the human body that are not directly involved in sexual reproduction contain 46 chromosomes. These cells are called **somatic cells.** In contrast, the **gametes**—sperm and egg cells—contain half that number (23) and are termed **haploid** (**Figure 1.10b**). The union of gametes during fertilization restores the diploid number of chromosomes. The primary advantage of sexual reproduction is that it enhances genetic variation. For example, a tall person with blue eyes and a short person with brown eyes may have short offspring with blue eyes or tall offspring with brown eyes. Therefore, sexual reproduction can result in new combinations of two or more traits that differ from those of either parent.

The Genetic Composition of a Species Evolves over the Course of Many Generations

As we have just seen, sexual reproduction has the potential to enhance genetic variation. This can be an advantage for a population of individuals as they struggle to survive and compete within their natural environment. The term **biological evolution,** or simply, **evolution,** refers to the phenomenon that the genetic makeup of a population changes from one generation to the next.

As suggested by Charles Darwin, the members of a species are in competition with one another for essential resources. Random genetic changes (i.e., mutations) occasionally occur



(a) Chromosomal composition found in human somatic cells of females (46 chromosomes)

(b) Chromosomal composition found in a human gamete (23 chromosomes)

FIGURE 1.10 The complement of human chromosomes in somatic cells and gametes. **(a)** A schematic drawing of the 46 chromosomes of a human. With the exception of the sex chromosomes, these are always found in homologous pairs. **(b)** The chromosomal composition of a gamete, which contains only 23 chromosomes, one from each pair. This gamete contains an X chromosome. Half of the gametes from human males contain a Y chromosome instead of the X chromosome.

CONCEPT CHECK: The leaf cells of a corn plant contain 20 chromosomes each. How many chromosomes are found in a gamete made by a corn plant?

within an individual's genes, and sometimes these changes lead to a modification of traits that promote reproductive success. For example, over the course of many generations, random gene mutations have lengthened the snout and extended the tongue of the anteater, enabling it to probe into the ground and feed on ants. When a mutation creates a new allele that is beneficial, the allele may become prevalent in future generations because the individuals carrying the allele are more likely to reproduce and pass the beneficial allele to their offspring. This process is known as **natural selection.** In this way, a species becomes better adapted to its environment.

Over a long period of time, the accumulation of many genetic changes may lead to rather striking modifications in a species' characteristics. As an example, **Figure 1.11** depicts the evolution of the modern-day horse. Over time, a variety of morphological changes occurred, including an increase in size, fewer toes, and modified jaw structure. The changes can be attributed to natural selection. Over North America, where much of horse evolution occurred, large areas of dense forests were replaced with grasslands. The increase in size and changes in foot structure enabled horses to escape predators more easily and travel greater distances in search of food. Natural selection favored the changes seen in horses' teeth, because such changes allowed them to eat grasses and other types of vegetation that are more abrasive and require more chewing.

1.2 COMPREHENSION QUESTIONS

1. Gene expression can be viewed at which of the following levels?
   a. Molecular and cellular levels
   b. Organism level
   c. Population level
   d. All of the above
2. Variation in the traits of organisms may be attributable to
   a. gene mutations.
   b. alterations in chromosome structure.
   c. variation in chromosome number.
   d. all of the above.
3. A human skin cell has 46 chromosomes. A human sperm cell has
   a. 23.
   b. 46.
   c. 92.
   d. none of the above.
4. Evolutionary change caused by natural selection results in species with
   a. greater complexity.
   b. less complexity.
   c. greater reproductive success in their native environment.
   d. the ability to survive longer.