

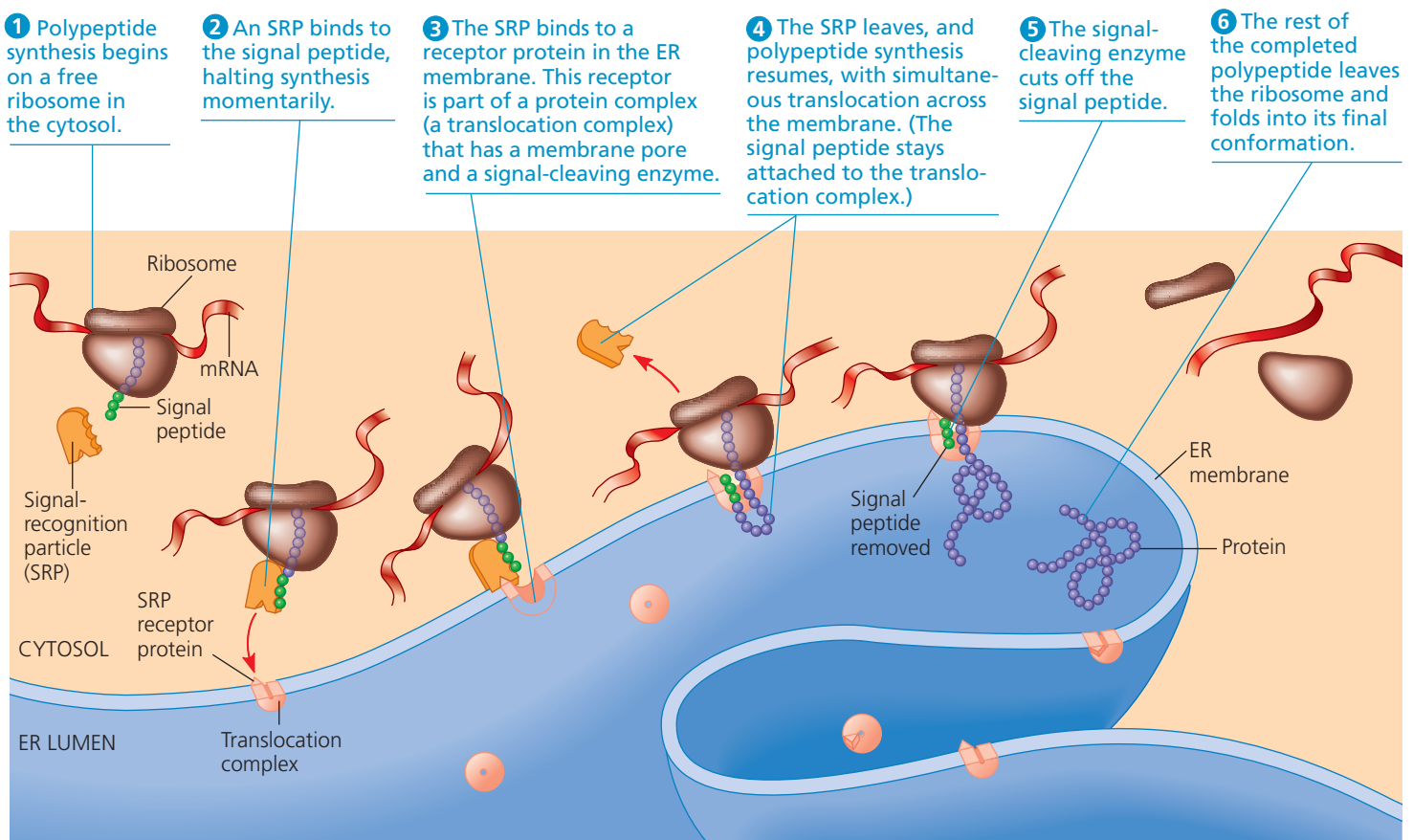
## Targeting Polypeptides to Specific Locations

In electron micrographs of eukaryotic cells active in protein synthesis, two populations of ribosomes (and polyribosomes) are evident: free and bound (see Figure 6.10). Free ribosomes are suspended in the cytosol and mostly synthesize proteins that stay in the cytosol and function there. In contrast, bound ribosomes are attached to the cytosolic side of the endoplasmic reticulum (ER) or to the nuclear envelope. Bound ribosomes make proteins of the endomembrane system (the nuclear envelope, ER, Golgi apparatus, lysosomes, vacuoles, and plasma membrane) as well as proteins secreted from the cell, such as insulin. It is important to note that the ribosomes themselves are identical and can switch their status from free to bound.

What determines whether a ribosome is free in the cytosol or bound to rough ER? Polypeptide synthesis always begins in the cytosol as a free ribosome starts to translate an mRNA molecule. There the process continues to completion—*unless* the growing polypeptide itself cues the ribosome to attach to the ER. The polypeptides of proteins destined for the endomembrane system or for secretion are marked by a **signal peptide**, which targets the protein to the ER (Figure 17.22). The signal peptide, a sequence of about 20 amino acids at or near the

leading end (N-terminus) of the polypeptide, is recognized as it emerges from the ribosome by a protein-RNA complex called a **signal-recognition particle (SRP)**. This particle functions as an escort that brings the ribosome to a receptor protein built into the ER membrane. The receptor is part of a multiprotein translocation complex. Polypeptide synthesis continues there, and the growing polypeptide snakes across the membrane into the ER lumen via a protein pore. The signal peptide is usually removed by an enzyme. The rest of the completed polypeptide, if it is to be secreted from the cell, is released into solution within the ER lumen (as in Figure 17.22). Alternatively, if the polypeptide is to be a membrane protein, it remains partially embedded in the ER membrane.

Other kinds of signal peptides are used to target polypeptides to mitochondria, chloroplasts, the interior of the nucleus, and other organelles that are not part of the endomembrane system. The critical difference in these cases is that translation is completed in the cytosol before the polypeptide is imported into the organelle. The mechanisms of translocation also vary, but in all cases studied to date, the “postal zip codes” that address proteins for secretion or to cellular locations are signal peptides of some sort. Bacteria also employ signal peptides to target proteins to the plasma membrane for secretion.



▲ **Figure 17.22 The signal mechanism for targeting proteins to the ER.** A polypeptide destined for the endomembrane system or for secretion from the cell begins

with a signal peptide, a series of amino acids that targets it for the ER. This figure shows the synthesis of a secretory protein and its simultaneous import into the ER. In the ER and

then in the Golgi, the protein will be processed further. Finally, a transport vesicle will convey it to the plasma membrane for release from the cell (see Figure 7.12).

## CONCEPT CHECK 17.4

1. What two processes ensure that the correct amino acid is added to a growing polypeptide chain?
2. Discuss the ways in which rRNA structure likely contributes to ribosomal function.
3. Describe how a polypeptide to be secreted is transported to the endomembrane system.
4. **WHAT IF? DRAW IT** Draw a tRNA with the anticodon 3'-CGU-5'. What two different codons could it bind to? Draw each codon on an mRNA, labeling all 5' and 3' ends. Add the amino acid carried by this tRNA.

For suggested answers, see Appendix A.

## CONCEPT 17.5

### Mutations of one or a few nucleotides can affect protein structure and function

Now that you have explored the process of gene expression, you are ready to understand the effects of changes to the genetic information of a cell (or virus). These changes, called **mutations**, are responsible for the huge diversity of genes found among organisms because mutations are the ultimate source of new genes. In Figure 15.14, we considered chromosomal rearrangements that affect long segments of DNA, which can be considered large-scale mutations. Here we examine small-scale mutations of one or a few nucleotide pairs, including **point mutations**, changes in a single nucleotide pair of a gene.

If a point mutation occurs in a gamete or in a cell that gives rise to gametes, it may be transmitted to offspring and to a succession of future generations. If the mutation has an adverse effect on the phenotype of an organism, the mutant condition is referred to as a genetic disorder or hereditary disease. For example, we can trace the genetic basis of sickle-cell disease to the mutation of a single nucleotide pair in the gene that encodes the  $\beta$ -globin polypeptide of hemoglobin. The change of a single nucleotide in the DNA's template strand leads to the production of an abnormal protein (Figure 17.23; also see Figure 5.21). In individuals who are homozygous for the mutant allele, the sickling of red blood cells caused by the altered hemoglobin produces the multiple symptoms associated with sickle-cell disease (see Chapter 14). Another disorder caused by a

point mutation is a heart condition, familial cardiomyopathy, that is responsible for some incidents of sudden death in young athletes. Point mutations in several genes have been identified, any of which can lead to this disorder.

### Types of Small-Scale Mutations

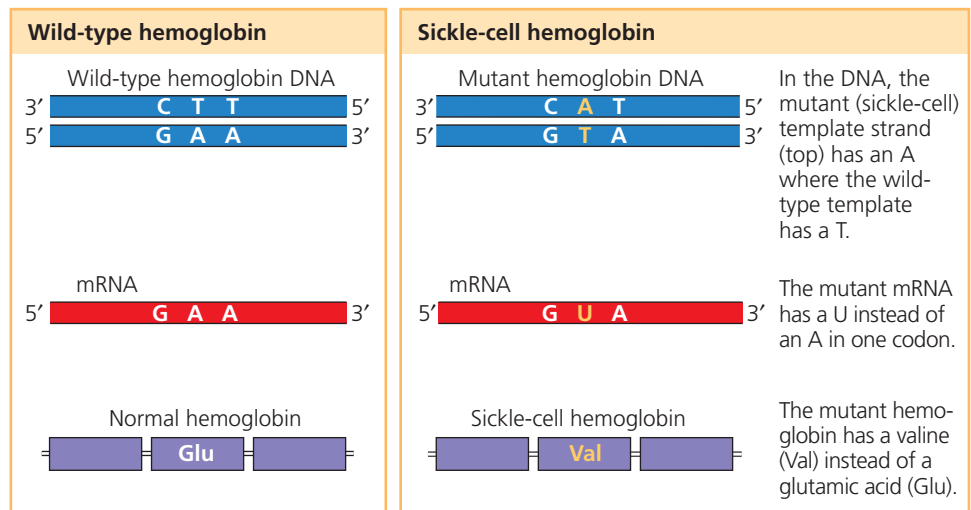
Let's now consider how small-scale mutations affect proteins. Point mutations within a gene can be divided into two general categories: (1) single nucleotide-pair substitutions and (2) nucleotide-pair insertions or deletions. Insertions and deletions can involve one or more nucleotide pairs.

#### Substitutions

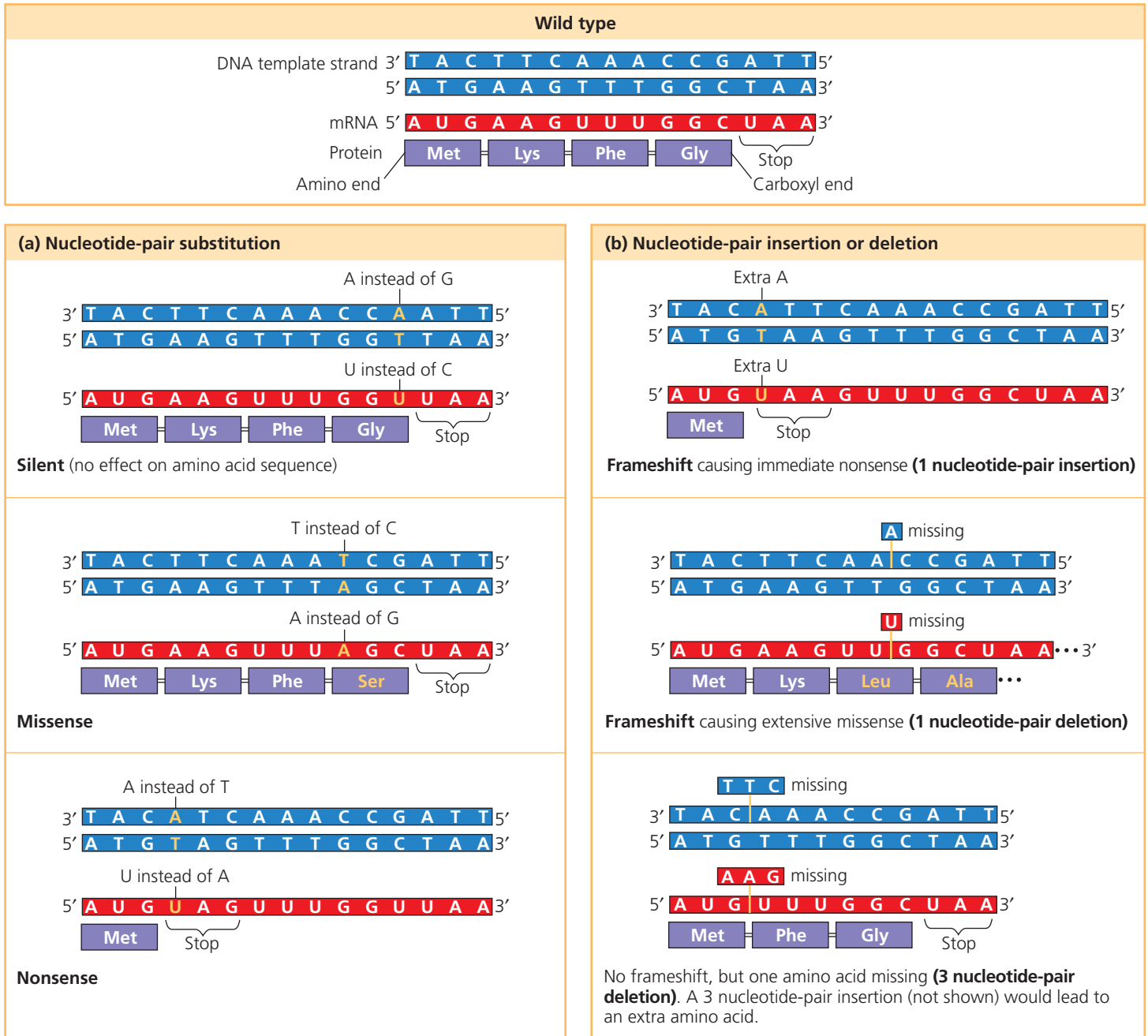
A **nucleotide-pair substitution** is the replacement of one nucleotide and its partner with another pair of nucleotides (Figure 17.24a). Some substitutions have no effect on the encoded protein, owing to the redundancy of the genetic code. For example, if 3'-CCG-5' on the template strand mutated to 3'-CCA-5', the mRNA codon that used to be GGC would become GGU, but a glycine would still be inserted at the proper location in the protein (see Figure 17.5). In other words, a change in a nucleotide pair may transform one codon into another that is translated into the same amino acid. Such a change is an example of a **silent mutation**, which has no observable effect on the phenotype. (Silent mutations can occur outside genes as well.) Substitutions that change one amino acid to another one are called **missense mutations**. Such a mutation may have little effect on the protein: The new amino acid may have properties similar to those of the amino acid it replaces, or it may be in a region of the protein where the exact sequence of amino acids is not essential to the protein's function.

#### ▼ Figure 17.23 The molecular basis of sickle-cell disease: a point mutation.

The allele that causes sickle-cell disease differs from the wild-type (normal) allele by a single DNA nucleotide pair.



▼ **Figure 17.24** Types of small-scale mutations that affect mRNA sequence. All but one of the types shown here also affect the amino acid sequence of the encoded polypeptide.



However, the nucleotide-pair substitutions of greatest interest are those that cause a major change in a protein. The alteration of a single amino acid in a crucial area of a protein—such as in the part of hemoglobin shown in Figure 17.23 or in the active site of an enzyme as shown in Figure 8.18—will significantly alter protein activity. Occasionally, such a mutation leads to an improved protein or one with novel capabilities, but much more often such mutations are detrimental, leading to a useless or less active protein that impairs cellular function.

Substitution mutations are usually missense mutations; that is, the altered codon still codes for an amino acid and

thus makes sense, although not necessarily the *right* sense. But a point mutation can also change a codon for an amino acid into a stop codon. This is called a **nonsense mutation**, and it causes translation to be terminated prematurely; the resulting polypeptide will be shorter than the polypeptide encoded by the normal gene. Nearly all nonsense mutations lead to nonfunctional proteins.

### Insertions and Deletions

**Insertions** and **deletions** are additions or losses of nucleotide pairs in a gene (Figure 17.24b). These mutations have

a disastrous effect on the resulting protein more often than substitutions do. Insertion or deletion of nucleotides may alter the reading frame of the genetic message, the triplet grouping of nucleotides on the mRNA that is read during translation. Such a mutation, called a **frameshift mutation**, will occur whenever the number of nucleotides inserted or deleted is not a multiple of three. All the nucleotides that are downstream of the deletion or insertion will be improperly grouped into codons, and the result will be extensive missense, usually ending sooner or later in nonsense and premature termination. Unless the frameshift is very near the end of the gene, the protein is almost certain to be nonfunctional.

## Mutagens

Mutations can arise in a number of ways. Errors during DNA replication or recombination can lead to nucleotide-pair substitutions, insertions, or deletions, as well as to mutations affecting longer stretches of DNA. If an incorrect nucleotide is added to a growing chain during replication, for example, the base on that nucleotide will then be mismatched with the nucleotide base on the other strand. In many cases, the error will be corrected by systems you learned about in Chapter 16. Otherwise, the incorrect base will be used as a template in the next round of replication, resulting in a mutation. Such mutations are called *spontaneous mutations*. It is difficult to calculate the rate at which such mutations occur. Rough estimates have been made of the rate of mutation during DNA replication for both *E. coli* and eukaryotes, and the numbers are similar: About one nucleotide in every  $10^{10}$  is altered, and the change is passed on to the next generation of cells.

A number of physical and chemical agents, called **mutagens**, interact with DNA in ways that cause mutations. In the 1920s, Hermann Muller discovered that X-rays caused genetic changes in fruit flies, and he used X-rays to make *Drosophila* mutants for his genetic studies. But he also recognized an alarming implication of his discovery: X-rays and other forms of high-energy radiation pose hazards to the genetic material of people as well as laboratory organisms. Mutagenic radiation, a physical mutagen, includes ultraviolet (UV) light, which can cause disruptive thymine dimers in DNA (see Figure 16.19).

Chemical mutagens fall into several categories. Nucleotide analogs are chemicals that are similar to normal DNA nucleotides but that pair incorrectly during DNA replication. Some other chemical mutagens interfere with correct DNA replication by inserting themselves into the DNA and distorting the double helix. Still other mutagens cause chemical changes in bases that change their pairing properties.

Researchers have developed a variety of methods to test the mutagenic activity of chemicals. A major application of these tests is the preliminary screening of chemicals to identify those that may cause cancer. This approach makes sense because most carcinogens (cancer-causing chemicals) are mutagenic, and conversely, most mutagens are carcinogenic.

## CONCEPT CHECK 17.5

1. What happens when one nucleotide pair is lost from the middle of the coding sequence of a gene?
2. **MAKE CONNECTIONS** Individuals heterozygous for the sickle-cell allele are generally healthy but show phenotypic effects of the allele under some circumstances; see Concept 14.4, pages 277–278. Explain in terms of gene expression.
3. **WHAT IF? DRAW IT** The template strand of a gene includes this sequence:  
3'-TACTTGTCCGATATC-5'. It is mutated to  
3'-TACTTGTCCAATATC-5'. For both normal and mutant sequences, draw the double-stranded DNA, the resulting mRNA, and the amino acid sequence each encodes. What is the effect of the mutation on the amino acid sequence?

For suggested answers, see Appendix A.

## CONCEPT 17.6

### While gene expression differs among the domains of life, the concept of a gene is universal

Although bacteria and eukaryotes carry out transcription and translation in very similar ways, we have noted certain differences in cellular machinery and in details of the processes in these two domains. The division of organisms into three domains was established about 40 years ago, when archaea were recognized as distinct from bacteria. Like bacteria, archaea are prokaryotes. However, archaea share many aspects of the mechanisms of gene expression with eukaryotes, as well as a few with bacteria.

### Comparing Gene Expression in Bacteria, Archaea, and Eukarya

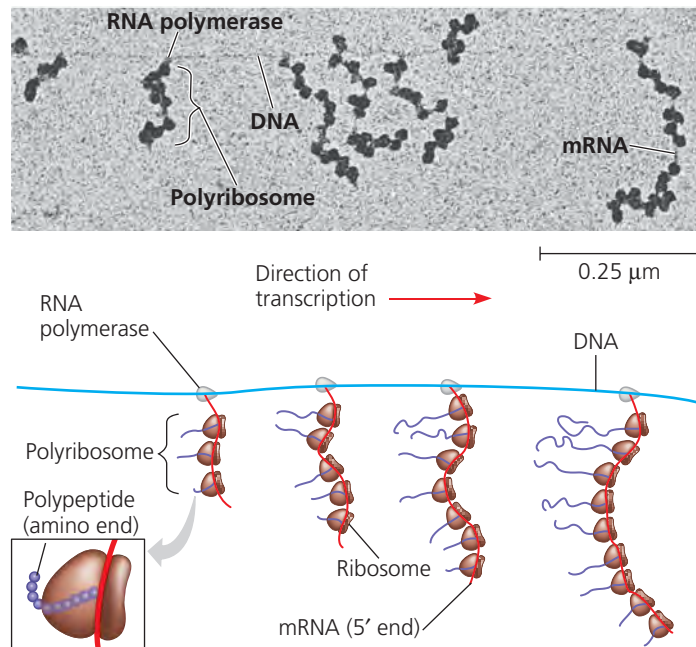
Recent advances in molecular biology have enabled researchers to determine the complete nucleotide sequences of hundreds of genomes, including many genomes from each domain. This wealth of data allows us to compare gene and protein sequences across domains. Foremost among genes of interest are those that encode components of such fundamental biological processes as transcription and translation.

Bacterial and eukaryotic RNA polymerases differ significantly from each other, while the single archaeal RNA polymerase resembles the three eukaryotic ones. Archaea and eukaryotes use a complex set of transcription factors, unlike the smaller set of accessory proteins in bacteria. Transcription is terminated differently in bacteria and eukaryotes. The little that is known about archaeal transcription termination suggests that it is similar to the eukaryotic process.

As far as translation is concerned, archaeal ribosomes are the same size as bacterial ribosomes, but their sensitivities to chemical inhibitors more closely match those of eukaryotic ribosomes. We mentioned earlier that initiation of translation is slightly different in bacteria and eukaryotes. In this respect, the archaeal process is more like that of bacteria.

The most important differences between bacteria and eukaryotes with regard to gene expression arise from the bacterial cell's lack of compartmental organization. Like a one-room workshop, a bacterial cell ensures a streamlined operation. In the absence of a nucleus, it can simultaneously transcribe and translate the same gene (Figure 17.25), and the newly made protein can quickly diffuse to its site of function. Most researchers suspect that transcription and translation are coupled like this in archaeal cells as well, since archaea lack a nuclear envelope. In contrast, the eukaryotic cell's nuclear envelope segregates transcription from translation and provides a compartment for extensive RNA processing. This processing stage includes additional steps whose regulation can help coordinate the eukaryotic cell's elaborate activities (see Chapter 18).

Learning more about the proteins and RNAs involved in archaeal transcription and translation will tell us much about the evolution of these processes in all three domains. In spite of the differences in gene expression cataloged here, however, the idea of the gene itself is a unifying concept among all forms of life.



**▲ Figure 17.25 Coupled transcription and translation in bacteria.** In bacterial cells, the translation of mRNA can begin as soon as the leading (5') end of the mRNA molecule peels away from the DNA template. The micrograph (TEM) shows a strand of *E. coli* DNA being transcribed by RNA polymerase molecules. Attached to each RNA polymerase molecule is a growing strand of mRNA, which is already being translated by ribosomes. The newly synthesized polypeptides are not visible in the micrograph but are shown in the diagram.

**?** Which one of the mRNA molecules started transcription first? On that mRNA, which ribosome started translating first?

## What Is a Gene? Revisiting the Question

Our definition of a gene has evolved over the past few chapters, as it has through the history of genetics. We began with the Mendelian concept of a gene as a discrete unit of inheritance that affects a phenotypic character (Chapter 14). We saw that Morgan and his colleagues assigned such genes to specific loci on chromosomes (Chapter 15). We went on to view a gene as a region of specific nucleotide sequence along the length of the DNA molecule of a chromosome (Chapter 16). Finally, in this chapter, we have considered a functional definition of a gene as a DNA sequence that codes for a specific polypeptide chain. (Figure 17.26, on the next page, summarizes the path from gene to polypeptide in a eukaryotic cell.) All these definitions are useful, depending on the context in which genes are being studied.

Clearly, the statement that a gene codes for a polypeptide is too simple. Most eukaryotic genes contain noncoding segments (such as introns), so large portions of these genes have no corresponding segments in polypeptides. Molecular biologists also often include promoters and certain other regulatory regions of DNA within the boundaries of a gene. These DNA sequences are not transcribed, but they can be considered part of the functional gene because they must be present for transcription to occur. Our definition of a gene must also be broad enough to include the DNA that is transcribed into rRNA, tRNA, and other RNAs that are not translated. These genes have no polypeptide products but play crucial roles in the cell. Thus, we arrive at the following definition: *A gene is a region of DNA that can be expressed to produce a final functional product that is either a polypeptide or an RNA molecule.*

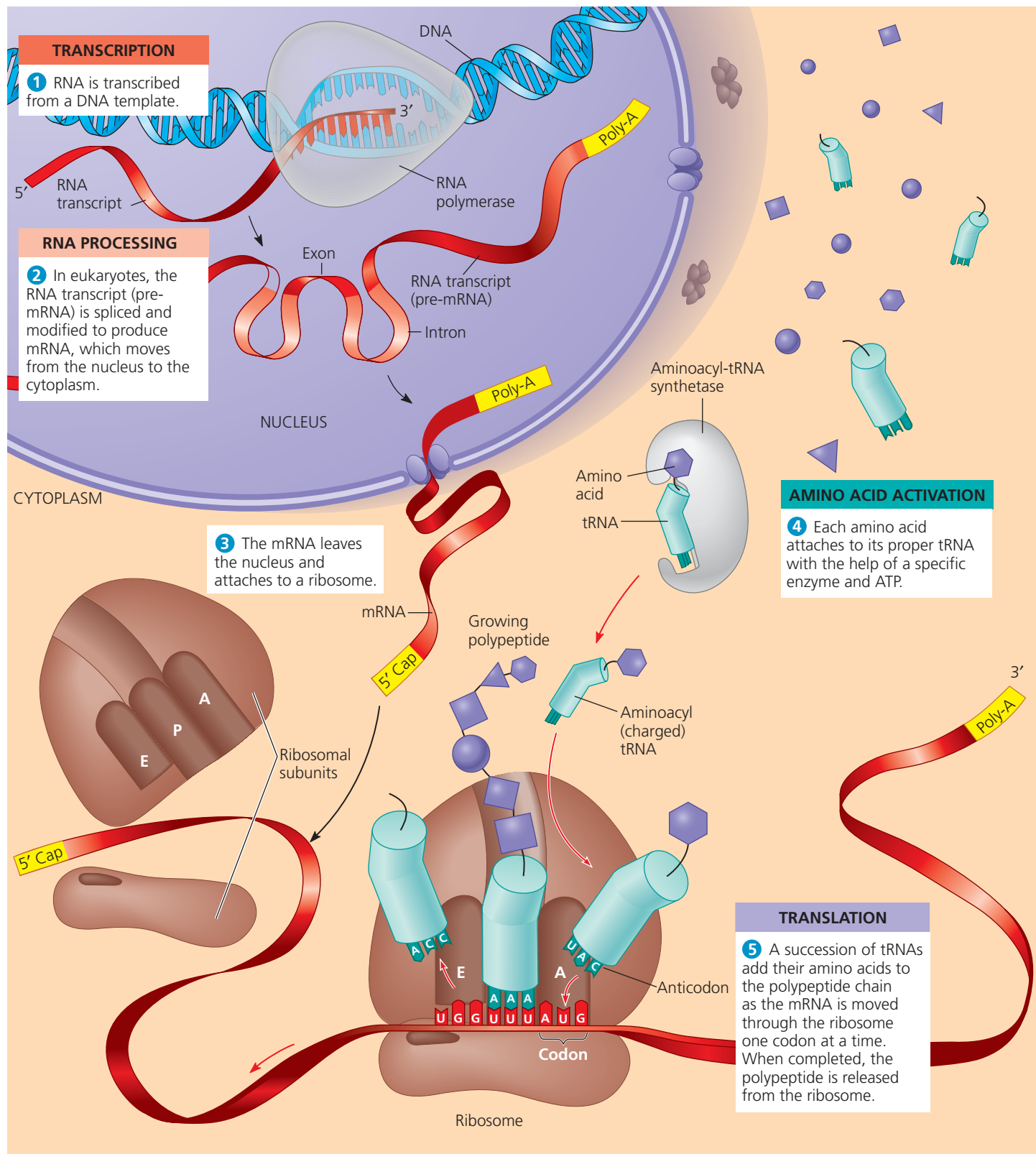
When considering phenotypes, however, it is often useful to start by focusing on genes that code for polypeptides. In this chapter, you have learned in molecular terms how a typical gene is expressed—by transcription into RNA and then translation into a polypeptide that forms a protein of specific structure and function. Proteins, in turn, bring about an organism's observable phenotype.

A given type of cell expresses only a subset of its genes. This is an essential feature in multicellular organisms: You'd be in trouble if the lens cells in your eyes started expressing the genes for hair proteins, which are normally expressed only in hair follicle cells! Gene expression is precisely regulated. We'll explore gene regulation in the next chapter, beginning with the simpler case of bacteria and continuing with eukaryotes.

### CONCEPT CHECK 17.6

1. Would the coupling of processes shown in Figure 17.25 be found in a eukaryotic cell? Explain.
2. **WHAT IF?** In eukaryotic cells, mRNAs have been found to have a circular arrangement in which proteins hold the poly-A tail near the 5' cap. How might this increase translation efficiency?

For suggested answers, see Appendix A.



▲ **Figure 17.26 A summary of transcription and translation in a eukaryotic cell.** This diagram shows the path from one gene to one polypeptide. Keep in mind that each gene in the DNA can be transcribed repeatedly into many identical RNA molecules and that each mRNA can be

translated repeatedly to yield many identical polypeptide molecules. (Also, remember that the final products of some genes are not polypeptides but RNA molecules, including tRNA and rRNA.) In general, the steps of transcription and translation are similar in bacterial, archaeal, and eukaryotic cells. The

major difference is the occurrence of RNA processing in the eukaryotic nucleus. Other significant differences are found in the initiation stages of both transcription and translation and in the termination of transcription.

# 17 CHAPTER REVIEW

## SUMMARY OF KEY CONCEPTS

### CONCEPT 17.1

#### Genes specify proteins via transcription and translation (pp. 325–331)

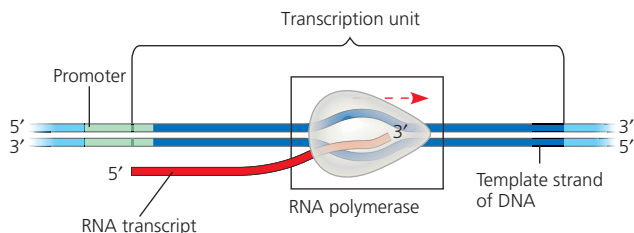
- DNA controls metabolism by directing cells to make specific enzymes and other proteins, via the process of **gene expression**. Beadle and Tatum's studies of mutant strains of *Neurospora* led to the one gene–one polypeptide hypothesis. Genes code for polypeptide chains or specify RNA molecules.
- Transcription** is the synthesis of RNA complementary to a **template strand** of DNA, providing a nucleotide-to-nucleotide transfer of information. **Translation** is the synthesis of a polypeptide whose amino acid sequence is specified by the nucleotide sequence in **mRNA**; this informational transfer thus involves a change of language, from that of nucleotides to that of amino acids.
- Genetic information is encoded as a sequence of nonoverlapping nucleotide triplets, or **codons**. A codon in messenger RNA (mRNA) either is translated into an amino acid (61 of the 64 codons) or serves as a stop signal (3 codons). Codons must be read in the correct **reading frame**.

? Describe the process of gene expression, by which a gene affects the phenotype of an organism.

### CONCEPT 17.2

#### Transcription is the DNA-directed synthesis of RNA: a closer look (pp. 331–334)

- RNA synthesis is catalyzed by **RNA polymerase**, which links together RNA nucleotides complementary to a DNA template strand. This process follows the same base-pairing rules as DNA replication, except that in RNA, uracil substitutes for thymine.



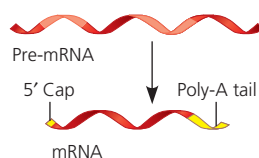
- The three stages of transcription are initiation, elongation, and termination. A **promoter**, often including a **TATA box** in eukaryotes, establishes where RNA synthesis is initiated. **Transcription factors** help eukaryotic RNA polymerase recognize promoter sequences, forming a **transcription initiation complex**. The mechanisms of termination are different in bacteria and eukaryotes.

? What are the similarities and differences in the initiation of gene transcription in bacteria and eukaryotes?

### CONCEPT 17.3

#### Eukaryotic cells modify RNA after transcription (pp. 334–336)

- Before leaving the nucleus, eukaryotic mRNA molecules undergo **RNA processing**, which includes RNA splicing, the addition of a modified nucleotide **5' cap** to the 5' end, and the addition of a **poly-A tail** to the 3' end.



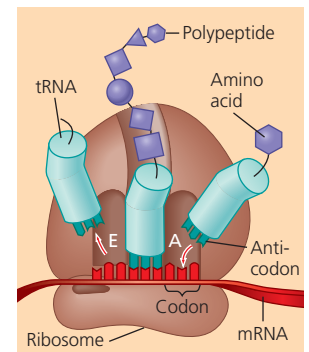
- Most eukaryotic genes are split into segments: They have **introns** interspersed among the **exons** (the regions included in the mRNA). In **RNA splicing**, introns are removed and exons joined. RNA splicing is typically carried out by **spliceosomes**, but in some cases, RNA alone catalyzes its own splicing. The catalytic ability of some RNA molecules, called **ribozymes**, derives from the inherent properties of RNA. The presence of introns allows for **alternative RNA splicing**.

? What function do the 5' cap and the poly-A tail serve on a eukaryotic mRNA?

### CONCEPT 17.4

#### Translation is the RNA-directed synthesis of a polypeptide: a closer look (pp. 337–344)

- A cell translates an mRNA message into protein using **transfer RNAs (tRNAs)**. After being bound to a specific amino acid by an **aminoacyl-tRNA synthetase**, a tRNA lines up via its **anticodon** at the complementary codon on mRNA. A **ribosome**, made up of **ribosomal RNAs (rRNAs)** and proteins, facilitates this coupling with binding sites for mRNA and tRNA.
- Ribosomes coordinate the three stages of translation: initiation, elongation, and termination. The formation of peptide bonds between amino acids is catalyzed by rRNA as tRNAs move through the **A** and **P sites** and exit through the **E site**.
- A single mRNA molecule can be translated simultaneously by a number of ribosomes, forming a **polyribosome**.
- After translation, modifications to proteins can affect their three-dimensional shape. Free ribosomes in the cytosol initiate synthesis of all proteins, but proteins destined for the endomembrane system or for secretion are transported into the ER. Such proteins have a **signal peptide** to which a **signal-recognition particle (SRP)** binds, enabling the translating ribosome to bind to the ER.



? What function do tRNAs serve in the process of translation?

### CONCEPT 17.5

#### Mutations of one or a few nucleotides can affect protein structure and function (pp. 344–346)

- Small-scale **mutations** include **point mutations**, changes in one DNA nucleotide pair, which may lead to production of nonfunctional proteins. **Nucleotide-pair substitutions** can cause **missense** or **nonsense mutations**. Nucleotide-pair **insertions** or **deletions** may produce **frameshift mutations**.
- Spontaneous mutations can occur during DNA replication, recombination, or repair. Chemical and physical **mutagens** cause DNA damage that can alter genes.

? What will be the results of chemically modifying one nucleotide base of a gene? What role is played by DNA repair systems in the cell?

## CONCEPT 17.6

While gene expression differs among the domains of life, the concept of a gene is universal (pp. 346–348)

- There are some differences in gene expression among bacteria, archaea, and eukaryotes. Because bacterial cells lack a nuclear envelope, translation can begin while transcription is still in progress. Archaeal cells show similarities to both eukaryotic and bacterial cells in their processes of gene expression. In a eukaryotic cell, the nuclear envelope separates transcription from translation, and extensive RNA processing occurs in the nucleus.
- A gene is a region of DNA whose final functional product is either a polypeptide or an RNA molecule.

**?** How does the presence of a nuclear envelope affect gene expression in eukaryotes?

### TEST YOUR UNDERSTANDING

#### LEVEL 1: KNOWLEDGE/COMPREHENSION

1. In eukaryotic cells, transcription cannot begin until
  - a. the two DNA strands have completely separated and exposed the promoter.
  - b. several transcription factors have bound to the promoter.
  - c. the 5' caps are removed from the mRNA.
  - d. the DNA introns are removed from the template.
  - e. DNA nucleases have isolated the transcription unit.
2. Which of the following is *not* true of a codon?
  - a. It consists of three nucleotides.
  - b. It may code for the same amino acid as another codon.
  - c. It never codes for more than one amino acid.
  - d. It extends from one end of a tRNA molecule.
  - e. It is the basic unit of the genetic code.
3. The anticodon of a particular tRNA molecule is
  - a. complementary to the corresponding mRNA codon.
  - b. complementary to the corresponding triplet in rRNA.
  - c. the part of tRNA that bonds to a specific amino acid.
  - d. changeable, depending on the amino acid that attaches to the tRNA.
  - e. catalytic, making the tRNA a ribozyme.
4. Which of the following is *not* true of RNA processing?
  - a. Exons are cut out before mRNA leaves the nucleus.
  - b. Nucleotides may be added at both ends of the RNA.
  - c. Ribozymes may function in RNA splicing.
  - d. RNA splicing can be catalyzed by spliceosomes.
  - e. A primary transcript is often much longer than the final RNA molecule that leaves the nucleus.
5. Which component is *not* directly involved in translation?
  - a. mRNA
  - b. DNA
  - c. tRNA
  - d. ribosomes
  - e. GTP

#### LEVEL 2: APPLICATION/ANALYSIS

6. Using Figure 17.5, identify a 5' → 3' sequence of nucleotides in the DNA template strand for an mRNA coding for the polypeptide sequence Phe-Pro-Lys.
  - a. 5'-UUUGGAAA-3'
  - b. 5'-GAACCCCTT-3'
  - c. 5'-AAAACCTT-3'
  - d. 5'-CTTCGGGAA-3'
  - e. 5'-AAACCCUUU-3'
7. Which of the following mutations would be *most* likely to have a harmful effect on an organism?
  - a. a nucleotide-pair substitution
  - b. a deletion of three nucleotides near the middle of a gene
  - c. a single nucleotide deletion in the middle of an intron

- d. a single nucleotide deletion near the end of the coding sequence
- e. a single nucleotide insertion downstream of, and close to, the start of the coding sequence

8. **DRAW IT** Fill in the following table:

Type of RNA	Functions
Messenger RNA (mRNA)	
Transfer RNA (tRNA)	
	Plays catalytic (ribozyme) roles and structural roles in ribosomes
Primary transcript	
Small nuclear RNA (snRNA)	

#### LEVEL 3: SYNTHESIS/EVALUATION

9. **EVOLUTION CONNECTION** Most amino acids are coded for by a set of similar codons (see Figure 17.5). What evolutionary explanations can you give for this pattern? (*Hint*: There is one explanation relating to ancestry, and some less obvious ones of a “form-fits-function” type.)
10. **SCIENTIFIC INQUIRY**  
Knowing that the genetic code is almost universal, a scientist uses molecular biological methods to insert the human  $\beta$ -globin gene (shown in Figure 17.11) into bacterial cells, hoping the cells will express it and synthesize functional  $\beta$ -globin protein. Instead, the protein produced is nonfunctional and is found to contain many fewer amino acids than does  $\beta$ -globin made by a eukaryotic cell. Explain why.
11. **WRITE ABOUT A THEME**  
**Evolution and The Genetic Basis of Life** Evolution accounts for the unity and diversity of life, and the continuity of life is based on heritable information in the form of DNA. In a short essay (100–150 words), discuss how the fidelity with which DNA is inherited is related to the processes of evolution. (Review the discussion of proofreading and DNA repair in Concept 16.2, pp. 316–318.)

For selected answers, see Appendix A.

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