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DIAGNOSTIC MICROBIOLOGY

SIXTEENTH EDITION

Patricia M. **TILLE**

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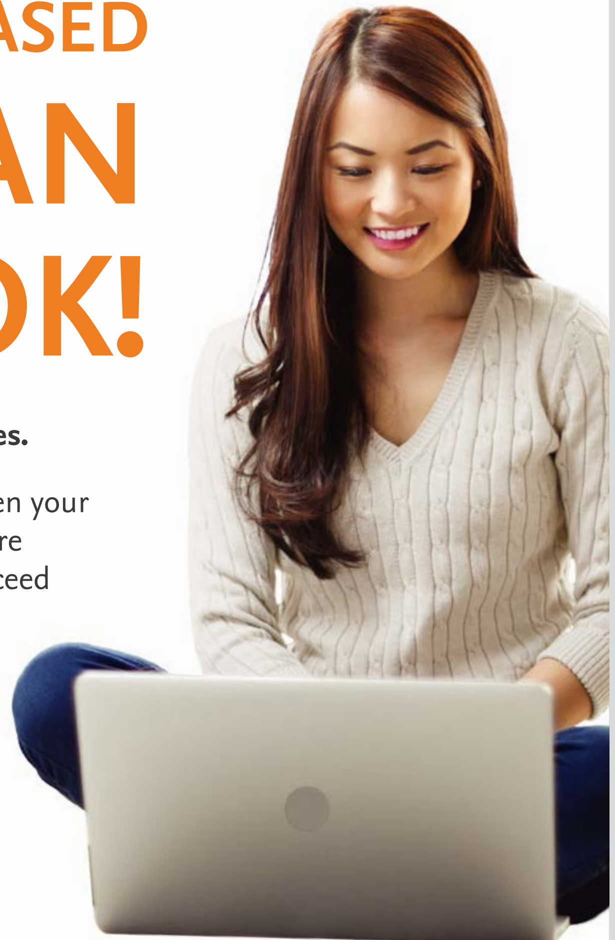

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Bailey & Scott's

DIAGNOSTIC MICROBIOLOGY

SIXTEENTH EDITION

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The world of microbiology continues to amaze me! The advances in technology, diagnostics, and health care are rapidly changing and improving patient care! An endeavor such as this edition of Bailey and Scott's would not be what it is without the review, contributions, insightful comments, and expertise of numerous colleagues, friends, professional users, and students.

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Thank you to all who contributed to the completion of this work, the emails, late night phone calls, and joy you all bring. Life is one long lesson in humility and respect for others. Love your family and friends, work really hard but most of all, live your passion! One of mine is microbiology!

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Preface

This, the sixteenth edition of *Bailey & Scott's Diagnostic Microbiology*, is the fourth edition that I have had the great pleasure to edit and author with some amazing colleagues. The dynamics of infectious disease trends, along with the technical developments available for diagnosing, treating, and controlling diseases, continues to present major challenges in the laboratory and medical care. In meeting these challenges, the primary goal for the sixteenth edition is to provide an updated and reliable reference text for practicing clinical microbiologists and technologists while also presenting this information in a format that supports the educational efforts of those responsible for preparing others for a career in medical and diagnostic microbiology. The text retains the traditional information needed to develop a solid, basic understanding of diagnostic microbiology while integrating the dynamic expansion of molecular diagnostics, automation, artificial intelligence (AI), and matrix-assisted laser desorption time-of-flight mass spectrometry.

We have kept the favorite features and adjusted in response to important critical input from users of the text. The succinct presentation of each organism group's key laboratory, clinical, epidemiologic, and therapeutic features in tables and figures has been kept and updated. Regarding content, the major changes reflect the changes that the discipline of diagnostic microbiology continues to experience. Also, although the grouping of organisms into sections according to key features (e.g., Gram reaction, catalase or oxidase reaction, growth on MacConkey agar) has remained, changes regarding the genera and species discussed in these sections have been made. These changes, along with changes in organism nomenclature, were made to accurately reflect the changes that have occurred, and continue to occur, in taxonomy. Also, throughout the text, the content has been altered to minimize the use of gender specific terminology where appropriate to recognize the unique nature and changes in population dynamics and environmental factors that contribute to the development, transmission, and treatment in infectious disease. Finally, although some classic methods for bacterial identification and characterization developed over the years (e.g., catalase, oxidase, Gram stain) continue to play a critical role in today's laboratory, others have given way to commercial identification systems. We realize that in a textbook such as this, a balance is needed for practicing and teaching diagnostic microbiology; our selection of identification methods that receive the most detailed attention may not always meet the needs of everyone. However, we have tried to be consistent in selecting those methods that reflect the common practices in clinical microbiology laboratories, along with those that present historical information required to educate others.

Finally, in terms of organization, the sixteenth edition includes a variety of instructor ancillaries available on the Evolve website, including an expanded test bank, updated PowerPoints, a laboratory manual with answers, review questions with answer keys, and an electronic image collection. Student resources include a laboratory manual, review questions, online case studies, and online procedures.

We sincerely hope that clinical microbiology practitioners and educators continue to find *Bailey & Scott's Diagnostic Microbiology*, sixteenth edition, a worthy and useful tool to support their professional activities.

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Patricia M. Tille

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1 Microbial Taxonomy

OBJECTIVES

1. Define classification, identification, species, genus, type genus, and binomial nomenclature.
2. Accurately apply binomial nomenclature in the identification of microorganisms, including syntax, capitalization, and punctuation.
3. Differentiate the major microorganism domains Eukarya, Archaea, and Bacteria (Eubacteria).
4. Identify a microorganism's characteristics as either phenotypic or genotypic.
5. Define polyphasic taxonomy and chemotaxonomic methods and how they are being applied to the classification of microorganisms.
6. Describe how the classification, naming, and identification of organisms play a role in diagnostic microbiology in the clinical setting.

The science of **taxonomy** is a systematic process applied to all living entities, providing a consistent means to classify, name (nomenclature), and identify organisms. This consistency allows biologists worldwide to use a common label for every organism studied within the multitude of biologic disciplines. The common language of taxonomy minimizes confusion about organisms' names, physiology, and biologic relatedness. Taxonomy is important in the **phylogeny** (the evolutionary history of organisms) and scientific study of all living things in virtually every biologic discipline, including microbiology.

As a result of the advances in molecular biology, traditional taxonomy based on genotypic, phenotypic, and phylogenetic or evolutionary relationships encompasses a multifaceted analysis of **epigenetic** (variations in gene expression not caused by nucleic acid sequence similarities or differences) and **chemotaxonomic methods** (chemical constituents of the cell). This method of classification, or **polyphasic taxonomy,** is a more detailed and complex system using ribosomal ribonucleic acid (rRNA) sequences, whole genome sequences, epigenetics, and mass spectrometry (MS). The "gold standard" for classification of bacterial species has historically been based on deoxyribonucleic acid (DNA), including DNA-DNA hybridization (DDH) patterns and 16S rRNA gene (16S rDNA) sequence homology. With the implementation of next-generation sequencing, a more detailed analysis of organism genomes, including the average nucleotide identity (ANI), multilocus phylogenetic, and genome-to-genome distance (GGD) analyses, permits the resolution of microorganisms from closely related subspecies to specific species. Not all parameters clearly delineate each organism to the species level. In other words, some characteristics may strengthen the organization of the genus, and some may be useful at the species level. Species identification techniques have distinct variations in cutoff values or thresholds for the differentiation of organisms at the genus and species levels. The comparative thresholds indicate the likelihood that two genomes are from the same organism (Table 1.1). When using a single sequence such as the 16S rRNA, the possibility of gene transfer may also affect genotypic classification. Although 16S rRNA sequences are evolutionarily highly conserved, ANI analysis evaluates multiple coding regions across an entire genome, making the genomic analysis more detailed and accurate. Finally, lateral gene transfer among organisms, particularly bacteria, creates difficulty in the classification of organisms according to phenotypic or biochemical traits and genotypic criteria such as guanine and cytosine (DNA G+C) content, which has historically been the hallmark of diagnostic microbiology. Molecular methods have provided a means for identifying the historical core genomes used in classification and species identification. However, it is important to recognize that phenotypic expression and classification of organisms will continue to be compounded by the variation in genomes as a result of gene transfer among organisms.

In addition to more advanced genomic analysis, **chemotaxonomic methods** are more frequently being applied to the identification and classification of microorganisms. These methods include protein studies, fatty acid analysis, and cell wall composition. Mass spectrometry (MS) and matrix-assisted laser desorption ionization time-of-flight MS (MALDI-TOF MS) use the separation and analysis of high-abundance proteins and peptides to classify and identify bacterial isolates. Techniques such as rapid evaporative ionization MS (REIMS) can identify molecules and create images of tissues and microorganisms from laboratory growth medium. Beyond genomics, this polyphasic analysis provides a mechanism to use MS data in conjunction with

TABLE 1.1 Identification Criteria and Characteristics for Microbial Classification

Criteria	Characteristics
Phenotypic	
Macroscopic morphology	The microbial growth patterns on artificial media as observed when inspected with the unaided eye. Examples include the size, texture, and pigmentation of bacterial colonies.
Microscopic morphology	The size, shape, intracellular inclusions, cellular appendages, and arrangement of cells when observed with the aid of microscopic magnification.
Staining characteristics	The ability of an organism to reproducibly stain a particular color with the application of specific dyes and reagents. Staining is used in conjunction with microscopic morphology for bacterial identification. For example, the Gram stain for bacteria is a critical criterion for differential identification.
Environmental requirements	The ability of an organism to grow at various temperatures, in the presence of oxygen and other gases, at various pH levels, or in the presence of other ions and salts, such as NaCl.
Nutritional requirements	The ability of an organism to use various carbon and nitrogen sources as nutritional substrates when grown under specific environmental conditions.
Resistance profiles	The exhibition of a characteristic inherent resistance to specific antibiotics, heavy metals, or toxins.
Antigenic properties	The profiles of microorganisms established by various serologic and immunologic methods to determine relatedness among various microbial groups (serotype or serovar).
Subcellular properties	Molecular constituents of the cell that are typical of a particular taxon, or organism group, as established by various analytic methods. Some examples include cell wall components, components of the cell membrane, and enzymatic content of the microbial cell.
Chemotaxonomic properties	The chemical constituents of the cell, such as the structure of teichoic acids, fatty acid analysis, and protein profiles, as determined by analytical methods.
Genotypic	
DNA base composition ratio	DNA comprises four bases (guanine, cytosine, adenine, and thymine). The extent to which the DNA from two organisms is made up of cytosine and guanine (i.e., G + C content) relative to their total base content can be used as an indicator of relatedness or lack thereof. For example, an organism with a G + C content of 50% is not closely related to an organism with a G + C content of 25%.
Nucleic acid (DNA and RNA) base sequence characteristics, including those determined by hybridization assays	The order of bases along a strand of DNA or RNA is known as the **base sequence**. The extent to which sequences are **homologous** (similar) between two microorganisms can be determined directly or indirectly by various molecular methods. The degree of similarity in the sequences (specifically, the rRNA sequences that remain stable in comparison to the whole genome) may be a measure of the degree of organism relatedness.
Average nucleotide identity (ANI)	This method analyzes multiple coding sequences in a microorganism's genome to determine the average nucleotide identity using genome sequencing and computer algorithms. The relatedness of microorganisms is accurate at a 95%–96% threshold for organism identification.
Genome-to-genome distance (GGD)	This is a computerized calculation that uses inference by *in silico* genome comparisons, eliminating the limitations and errors associated with wet-lab techniques. Organisms are related with a GGD threshold score of 70% or greater.

DNA, deoxyribonucleic acid; *RNA,* ribonucleic acid; *rRNA,* ribosomal RNA.

the genomic analysis and phenotypic characteristics to identify and classify organisms and monitor biochemical therapies in complex disease states.

As technology improves, the classification and identification of organisms will undoubtedly continue to evolve along with changes in the populations of organisms. In diagnostic microbiology, classification, nomenclature, and identification of microorganisms play a central role in providing an accurate, timely diagnosis and in the management of infectious disease. A brief, detailed discussion of the major components of taxonomy is important for a basic understanding of bacterial identification and its application in diagnostic microbiology.

Classification

Classification is a method for organizing microorganisms into groups, or **taxa** (plural, taxon), based on similar morphologic, physiologic, and genetic traits. The hierarchical classification system consists of the following taxa:

- Domains (Bacteria, Archaea, and Eukarya)
- Eukarya supergroups

- Kingdom (contains similar divisions, or phyla; most inclusive taxa)
- Phylum (contains similar classes; equivalent to the Division taxa in botany)
- Class (contains similar orders)
- Order (contains similar families)
- Family (contains similar genera)
- Genus (contains similar species)
- Species (specific epithet; lowercase Latin adjective or noun; most exclusive taxa)

Bacteria, or **prokaryotes** (prenucleus), are separated into two domains, the Bacteria (Eubacteria) and the Archaea (ancient bacteria). The Bacteria domain contains the environmental prokaryotes (cyanobacteria, also known as blue-green algae) and the heterotrophic medically relevant bacteria. The Archaea domain contains environmental isolates that live in extreme habitats such as high salt concentrations, jet fuel, or high temperatures. **Eukaryotes** (true nucleus) form the third domain, which also contains medically relevant organisms, including fungi and parasites. However, the evolutionary tree of eukaryotes has dramatically changed as a result of the process of **phylogenomics**, analysis using molecular methods. The eukaryotes are divided into eight **supergroups** based on molecular phylogenetics and may lack defining morphologic and cell-biologic characteristics. Metagenomics has revolutionized microbiology and the nomenclature and grouping of organisms that may never have been observed under a microscope. However, eukaryotic metagenomics is still in the early stages of development when it comes to taxonomic organization.

There are several other taxonomic sublevels below the domains, as noted previously; however, the International Code of Nomenclature for Prokaryotes (ICNP) typically includes nomenclature up to the rank of class. Changes to the ICNP have added the inclusion of phyla. Typical organism classification and naming in the diagnostic microbiology laboratory primarily uses taxa beginning at the family designation.

Family

A **family** encompasses a group of organisms that may contain multiple genera and consists of organisms with a common attribute. The name of a family is formed by adding the suffix *-aceae* to the root name of one of the group's genera, called the **type genus;** for example, the *Streptococcaceae* family type genus is *Streptococcus.* One exception to the rule in microbiology is *Enterobacteriaceae*; it is named after the "enteric" group of bacteria rather than the type species *Escherichia coli.* Bacterial- (prokaryotic-) type species or strains are determined according to guidelines published by the International Committee for the Systematics of Prokaryotes (ICSP) in the ICNP. This code provides guidelines for linking nomenclature, classification, and characterization of organisms using physiologic, biochemical, genetic, and phenotypic traits. Microorganism type species should be described in detail using diagnostic, comparable, and reproducible methods, and all authentic strains must be available for further analysis.

Genus

A **genus** (plural, genera), the next taxon, contains different species that have several important features in common. Each species within a genus differs sufficiently to maintain its status as an individual species. Placement of a species within a particular genus is based on various genetic and phenotypic characteristics shared among the species.

Microorganisms do not possess the multitude of physical features exhibited by higher organisms such as plants and animals. For instance, they rarely leave a fossil record, and they exhibit a tremendous capacity to intermix genetic material among seemingly unrelated species and genera. For these reasons, confidently establishing a microorganism's relatedness in taxa higher than the genus level is difficult. Although grouping similar genera into common families and similar families into common orders and orders into classes is used for classification of plants and animals, these higher taxa designations (i.e., division and class) are not useful for classifying bacteria in clinical practice.

Species

Species (abbreviated **sp.**, singular, or **spp.**, plural) is the most basic of the taxonomic groups and can be defined as a collection of bacterial strains that share common physiologic and genetic features and differ notably from other microbial species. Occasionally, taxonomic subgroups within a species, called **subspecies (**abbreviated **subsp.),** are recognized. Furthermore, designations such as **biotype** or **biovar, serotype** or **serovar,** or **genotype** may be given to groups below the subspecies level that share specific characteristics. For example, *Klebsiella pneumoniae* and *Klebsiella oxytoca* are two distinct species within the genus *Klebsiella.* However, *K. pneumoniae* also has three subspecies: *K. pneumoniae* subsp. *ozaenae*, *K. pneumoniae* subsp. *pneumoniae*, and *K. pneumoniae* subsp. *rhinoscleromatis. Brucella suis* biovar 2 is an example of a biotype designation. A biotype contains species with the same genetic makeup but differential physiologic characteristics identified by biochemical methods. Subspecies do not display significant enough divergence to be classified as a biotype or a new species. A serotype or serovar is distinguished by differences in antigenic structure, and a genotype is differentiated by characteristics of the nucleic acids, including sequence or gene variants.

Nomenclature

Nomenclature is the naming of microorganisms according to established rules and guidelines put forth in the ICNP. It provides the accepted labels by which organisms are universally recognized. Because genus and species are the groups commonly used by microbiologists, the discussion herein of rules governing microbial nomenclature is limited

to these two taxa. In this **binomial** (two name) system of nomenclature, every organism is assigned a genus and a species of Latin or Greek derivation. Each organism has a scientific "label" consisting of two parts: the genus designation, in which the first letter is always capitalized, and the species designation, in which the first letter is always lowercase. The two components are used simultaneously and are printed in italics or underlined in script. For example, the streptococci include *Streptococcus pneumoniae, Streptococcus pyogenes, Streptococcus agalactiae,* and *Streptococcus gallolyticus,* among others. Alternatively, the name may be abbreviated using the uppercase form of the first letter of the genus designation followed by a period (.) and the full species name (e.g., *S. pneumoniae, S. pyogenes, S. agalactiae,* and *S. gallolyticus*). Finally, when discussing a single specific organism, the species may be designated using sp., and a group of species within the genus may be designated using spp. (e.g., *Staphylococcus* sp. and *Staphylococcus* spp.). Frequently, an informal designation (e.g., staphylococci, streptococci, enterococci) may be used to label a particular group of organisms. These designations are not capitalized or italicized.

As more information is gained regarding organism classification and identification, a particular species may be moved to a different genus or assigned a new genus name. The rules and criteria for these changes are beyond the scope of this chapter, but such changes are documented in the *International Journal of Systemic and Evolutionary Microbiology.* Published nomenclature may be found at http://www.bacterio.net for bacteria, http://www.ictvonline.org for viruses, http://www.iapt-taxon.org/nomen/main.php for fungi, and http://zoobank.org for parasites. In addition, the List of Prokaryotic Names with Standing in Nomenclature (LPSN) (http://lpsn.dsmz.de) includes the Bacteria and Archaea domains and provides a continually updated resource for changes in taxonomy and identification of novel taxa. It is important to note that fungi and parasite lists are difficult to maintain and may not reflect current validity at the time of review. In the diagnostic laboratory, changes in nomenclature are phased in gradually so that providers and laboratorians have ample opportunity to recognize that a familiar pathogen has been given a new name. This is usually accomplished by using the new genus designation while continuing to provide the previous designation in parentheses; for example, *Stenotrophomonas (Xanthomonas) maltophilia* or *Burkholderia (Pseudomonas) cepacia*.

Identification

Microbial identification is the process by which a microorganism's key features are delineated. Once those features have been established, the profile is compared with those of previously characterized microorganisms. The organism can then be assigned to the most appropriate taxa and given appropriate genus and species names; both are essential aspects of taxonomy in diagnostic microbiology and the management of infectious disease (Box 1.1).

• BOX 1.1 Role of Taxonomy in Diagnostic Microbiology

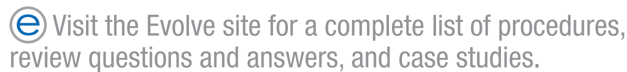
- Establishes and maintains records of key characteristics of clinically relevant microorganisms
- Facilitates communication among technologists, microbiologists, providers, and scientists by assigning universal names to clinically relevant microorganisms. This is essential for:
  - Establishing an association of particular diseases or syndromes with specific microorganisms
  - Epidemiology and tracking outbreaks
  - Accumulating knowledge regarding the management and outcome of diseases associated with specific microorganisms
  - Establishing patterns of resistance to antimicrobial agents and recognition of changing microbial resistance patterns
  - Understanding the mechanisms of antimicrobial resistance and detecting new resistance mechanisms exhibited by microorganisms
  - Recognizing new and emerging pathogenic microorganisms
  - Recognizing changes in the types of infections or diseases caused by characteristic microorganisms
  - Revising and updating available technologies for the development of new methods to optimize the detection and identification of infectious agents and the detection of resistance to antiinfective agents (microbial, viral, fungal, and parasitic)
  - Developing new antiinfective therapies (microbial, viral, fungal, and parasitic)

Identification Methods

A wide variety of methods and criteria are used to establish a microorganism's identity. These methods can be separated into two general categories: genotypic or phenotypic characteristics. **Genotypic characteristics** relate to an organism's genetic makeup, including the nature of the organism's genes and constituent nucleic acids (see Chapter 2 for more information about microbial genetics). **Phenotypic characteristics** are based on features beyond the genetic level, including both readily observable characteristics and features that may require extensive analytic procedures to be detected. Examples of characteristics used as criteria for bacterial identification and classification are provided in Table 1.1. Modern microbial taxonomy uses a combination of several methods to characterize microorganisms when classifying and naming an organism.

Although the criteria and examples in Table 1.1 are given in the context of microbial identification for classification purposes, the principles and practices of classification parallel those used in diagnostic microbiology for the identification and characterization of microorganisms encountered in the clinical setting. Fortunately, because of the previous efforts and accomplishments of microbial taxonomists, microbiologists do not have to use several burdensome classification and identification schemes to identify infectious agents. Instead, identification is based on key phenotypic

and genotypic features to provide clinically relevant information in a timely manner (see Chapter 12). This should not be taken to mean that the identification of all clinically relevant organisms is easy and straightforward. This is also not meant to imply that microbiologists can identify or recognize only organisms that have already been characterized and named by taxonomists. Indeed, the clinical microbiology laboratory is well recognized as the place where previously unknown or uncharacterized infectious agents are initially encountered; as such, it has an ever-increasing responsibility to be the source of information and reporting for emerging etiologies of infectious disease.



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Chapter Review

1. The most specific and exclusive taxon used in the classification of microorganisms is:
   a. Family
   b. Order
   c. Species
   d. Genus
2. The process consisting of a series of methods designed to provide the microbiologist with relevant and useful clinical information about a microorganism is:
   a. Classification
   b. Identification
   c. Organization
   d. Taxonomy
3. Classification and naming of organisms are useful in diagnostic microbiology for all the following **except:**
   a. Providing standardized groupings for identification
   b. Standardized groupings are always genotypically similar at 0.98%
   c. Standardized groupings share similar phenotypic traits
   d. Organisms within a standard group may be identified using similar methods
4. Which of the following is *not* a correct use of the binomial nomenclature system? (Select all that apply.)
   a. *Staphylococcus Aureus*
   b. *S. aureus*
   c. *Staphylococcus aureus*
   d. Staphylococcus aureus
5. Microorganisms are classified into three domains. The domain containing prokaryotes that are medically relevant organisms is:
   a. *Enterobacteriaceae*
   b. Archaea
   c. Eubacteria
   d. Eukarya
6. **Labeling:** *Label each of the following characteristics as either phenotypic (P) or genotypic (G).*
   _____ The color of growth on artificial media
   _____ The presence of an antibiotic-resistance DNA sequence
   _____ The shape of a bacterial cell
   _____ The arrangement of bacterial cells on a microscope slide
   _____ The ability of an organism to ferment lactose
7. Mass spectrometry is a technique used to separate and identify the spectrum of proteins and peptides that are expressed by microorganisms. This method is considered a _________method for the characterization and classification of organisms.
   a. phenotypic
   d. chemotaxonomic
   c. genotypic
   d. polyphasic
8. Which of the following methods would be considered chemotaxonomic?
   a. Fatty acid analysis
   b. Protein mass spectrometry
   c. Cell wall composition
   d. All the answers are correct

2

Bacterial Genetics, Metabolism, and Structure

OBJECTIVES

1. Describe the basic structure and organization of prokaryotic (bacterial) chromosomes, including number, relative size, and cellular location.
2. Outline the basic processes and essential components required for information transfer in replication, transcription, translation, and regulatory mechanisms.
3. Define mutation, recombination, transduction, transformation, and conjugation.
4. Describe how genetic alterations and diversity provide a mechanism for the evolution and survival of microorganisms.
5. Differentiate environmental oxygenation and final electron acceptors (aerobes, facultative anaerobes, and strict anaerobes) in the formation of energy.
6. Compare and contrast the key structural elements, cellular organization, and types of organisms classified as prokaryotic and eukaryotic.
7. State the functions and biologic significance of the following cellular structures: the outer membrane, cell wall, periplasmic space, cytoplasmic membrane, capsule, fimbriae, pili, flagella, nucleoid, and cytoplasm.
8. Differentiate the organization and chemical composition of the cell envelope (outer membrane, plasma membrane, periplasmic space, and cell wall) for a gram-negative and a gram-positive bacterium.

Microbial genetics, metabolism, and structure are the keys to microbial viability and survival. These processes involve numerous pathways that are widely varied, often complicated, and frequently interactive. Essentially, survival requires nutrients and energy to fuel the synthesis of materials necessary to grow, propagate, and carry out metabolic processes (Fig. 2.1). Although the goal of survival is the same for all organisms, the strategies microorganisms use to accomplish this vary substantially.

Knowledge regarding genetic, metabolic, and structural characteristics of microorganisms provides the basis for understanding almost every aspect of diagnostic microbiology, including:

- The mechanisms by which microorganisms cause disease
- The development and implementation of techniques for microbial detection, cultivation, identification, and characterization
- Antimicrobial action and resistance
- The development and implementation of tests for the detection of antimicrobial resistance
- Potential strategies for disease therapy and control of microorganisms

Microorganisms vary significantly in their genomic and metabolic pathways and therefore structure. A detailed consideration of these differences is beyond the scope of this textbook. Therefore a generalized description of bacterial systems is used as a model to discuss microbial physiology and structure. Information regarding characteristics of fungi, parasites, and viruses can be found in subsequent chapters for each specific taxonomic group.

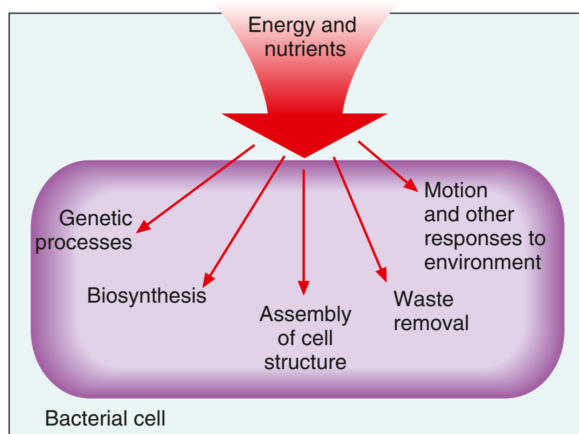
Bacterial Genetics

Genetics, the process of heredity and variation, is the starting point from which all other cellular pathways, functions, and structures originate. The ability of a microorganism to maintain viability, adapt, multiply, and cause disease is determined by the organism's genetic composition. The three major aspects of microbial genetics that require discussion include:

- The structure and organization of genetic material
- Replication and expression of genetic information
- The mechanisms by which genetic information is altered and exchanged among bacteria

Nucleic Acid Structure and Organization

For all living entities, hereditary information resides or is encoded in nucleic acids. The two major classes of nucleic acids are **deoxyribonucleic acid** (**DNA**), which is the most common macromolecule that encodes genetic information, and **ribonucleic acid** (**RNA**). In some forms, RNA encodes genetic information for various viruses; in other forms, RNA plays an essential role in several of the genetic processes in prokaryotic and eukaryotic cells, including the regulation and transfer of information. Prokaryotic, or prenuclear, organisms do not have membrane-bound



• **Fig. 2.1** General Overview of Bacterial Cellular Processes.

organelles, and the cells' genetic material is therefore not enclosed in a nucleus. Eukaryotic, or "true nucleus," organisms have the genetic material enclosed in a nuclear envelope or membrane.

Nucleotide Structure and Sequence

DNA consists of deoxyribose sugars connected by phosphodiester bonds (Fig. 2.2A). The bases that are covalently linked to each deoxyribose sugar are the key to the **genetic code** within the DNA molecule. The four nitrogenous bases include two **purines**, adenine (A) and guanine (G), and the two **pyrimidines**, cytosine (C) and thymine (T) (Fig. 2.3). In RNA, uracil replaces thymine. The combined sugar, phosphate, and a base form a single unit referred to as a **nucleotide** (adenosine triphosphate [ATP], guanine triphosphate [GTP], cytosine triphosphate [CTP], and thymine triphosphate [TTP] or uridine triphosphate [UTP]). DNA and RNA are nucleotide polymers (i.e., chains or strands), and the order of bases along a DNA or RNA strand is known as the **base sequence**. This sequence provides the information that codes for the proteins that will be synthesized by microbial cells; that is, the sequence is the genetic code.

Deoxyribonucleic Acid Molecular Structure

The intact DNA molecule is composed of two nucleotide polymers. Each strand has a 5′ (prime) phosphate and a 3′ (prime) hydroxyl terminus (Fig. 2.2A). The two strands run **antiparallel**, with the 5′ of one strand opposed to the 3′ terminal of the other. The strands are also complementary. This adherence to A-T and G-C base pairing results in a double-stranded DNA (dsDNA) molecule (double helix). The two antiparallel single strands of DNA form a "twisted ladder" structure (Fig. 2.2B). In addition, the dedicated base pairs (bps) provide the format for consistent replication and expression of the genetic code. In contrast to DNA, which carries the genetic code, RNA rarely exists as a double-stranded molecule. There are four major types of RNA (**messenger RNA [mRNA], transfer RNA [tRNA],** and **ribosomal RNA [rRNA]**) along with a variety of **noncoding RNA (ncRNA)** molecules such as microRNA (miRNA), small RNA (sRNA) and antisense RNA (asRNA) that play key roles in posttranscriptional regulation of gene expression.

Genes and the Genetic Code

A DNA sequence that encodes a specific product (RNA or protein) is defined as a **gene**. Thousands of genes in an organism encode messages or blueprints that produce one or more proteins and RNA products that play essential metabolic roles in the cell. All the genes in an organism comprise the organism's **genome**. The genome of a microorganism includes the chromosomes and the **mobilome** (extrachromosomal mobile genetic elements [MGEs]). The size of a gene and an entire genome are usually expressed in the number of bps present (e.g., kilobases [10^3 bases], megabases [10^6 bases]).

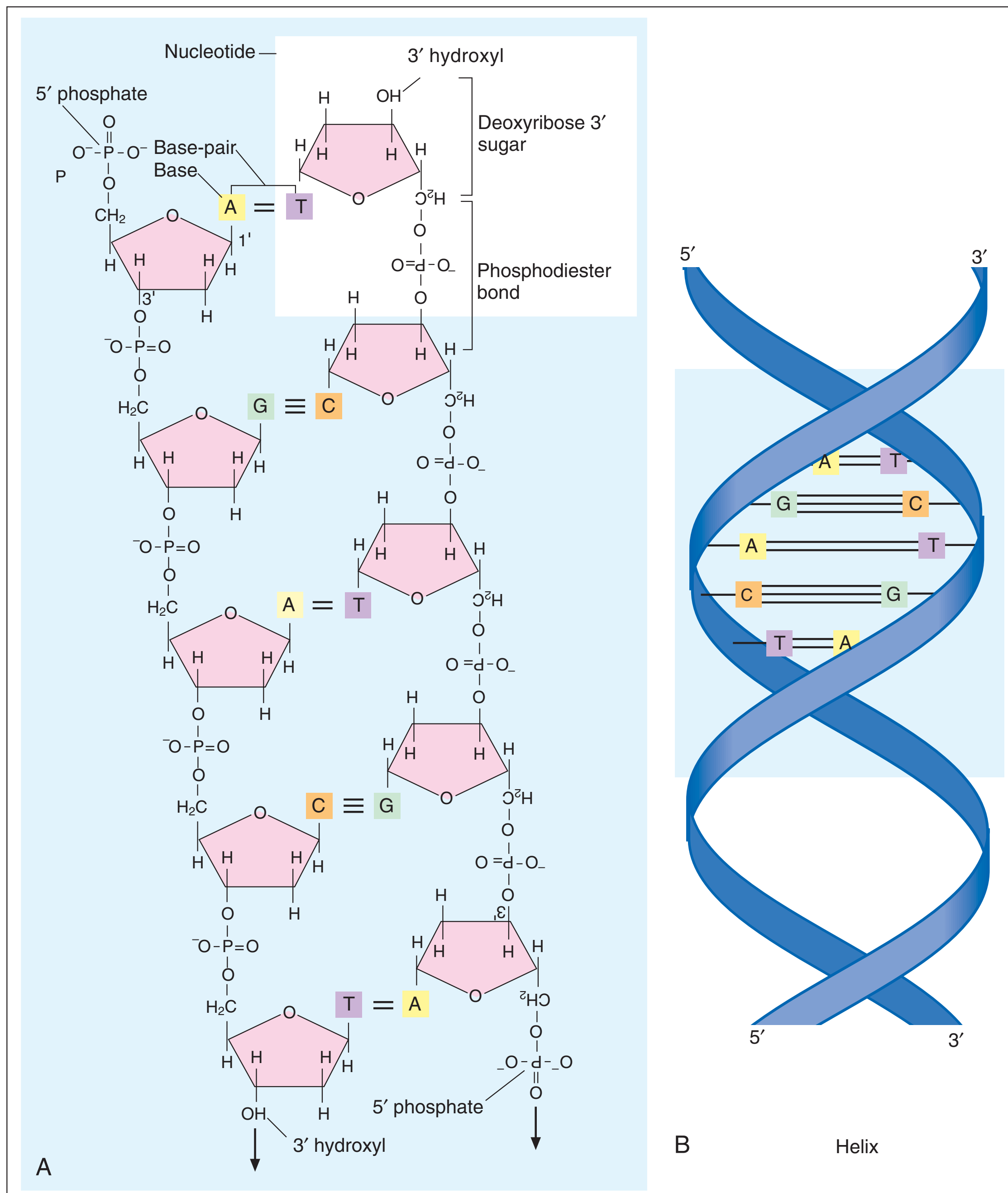
Some genes are widely distributed among multiple organisms, whereas others are limited to a particular species. In addition, the bp sequence for individual genes may be highly conserved (i.e., show limited sequence differences among different organisms) or be widely variable. As discussed in Chapter 8, the similarities and differences in genetic content and sequences are the basis for the development of molecular methods used to detect, identify, and characterize microorganisms.

Chromosomes

The genome is organized into discrete elements known as **chromosomes**. The set of genes within a given chromosome is arranged in a linear fashion, but the number of genes per chromosome is variable. Similarly, although the number of chromosomes per cell is consistent for a given species, this number varies considerably among species. For example, human cells contain 23 pairs (i.e., diploid) of chromosomes, whereas bacteria contain a single, unpaired (i.e., haploid) chromosome.

Bacteria are classified as prokaryotes; the chromosome is not located in a membrane-bound organelle (i.e., **nucleus**). The bacterial chromosome contains the genes essential for viability and exists as a double-stranded, closed, circular macromolecule. The molecule is extensively folded and twisted (i.e., supercoiled) to fit within the confined space of the bacterial cell. The linearized, unsupercoiled chromosome of the bacterium *Escherichia coli* is approximately 130 μm long, but it fits within a cell 1 × 3 μm; this attests to the extreme compact structure of the supercoiled bacterial chromosome. For genes in the compacted chromosome to be expressed and replicated, unwinding or relaxation of the molecule is required.

In contrast to the bacterial chromosome, the chromosomes of parasites and fungi number more than one per cell, are linear, and are housed within a membrane-bound organelle (the nucleus) of the cell. This difference is a major criterion for classifying bacteria as prokaryotes and fungi and parasites as eukaryotes. The genetic makeup of a virus may consist of DNA or RNA contained within a protein coat rather than a cell.

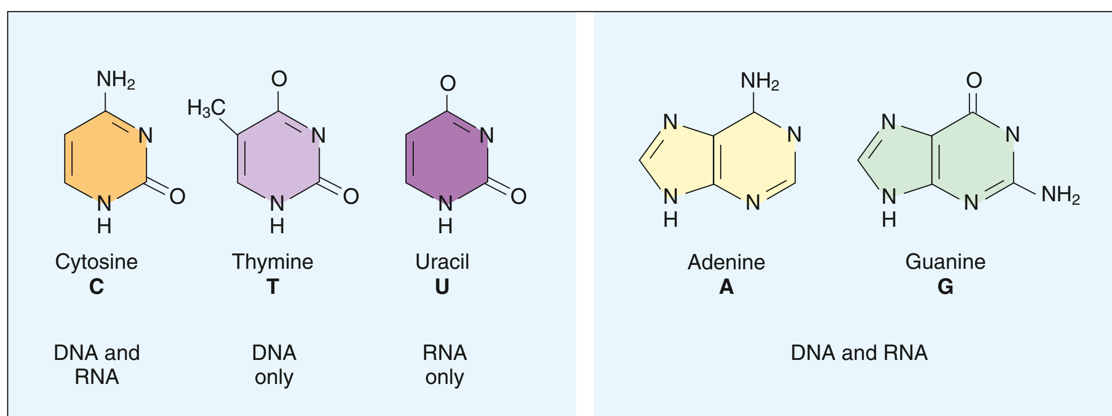


• **Fig. 2.2** (A) Molecular structure of deoxyribonucleic acid (DNA) depicting nucleotide structure, phosphodiester bonds connecting nucleotides, and complementary base pairing (*A*, adenine; *T*, thymine; *G*, guanine; *C*, cytosine) between antiparallel nucleic acid strands. (B) 5′ and 3′ antiparallel polarity and double-helix configuration of DNA.

Nonchromosomal Mobile Genetic Elements

Although the bacterial chromosome represents the majority of a cell's genome, not all genes are confined to the chromosome. Many genes may also be located on **plasmids** and **transposable elements**. Extrachromosomal elements replicate and encode information to produce various cellular products. Many of these elements replicate by integration into the host chromosome, whereas others, referred to as **episomes**, are capable of replication independently. Although considered part of the bacterial genome, they are not as stable as the chromosome and may be lost during cellular replication, often without any detrimental effects on the viability of the cell.

Plasmids exist as double-stranded, closed, circular, autonomously replicating extrachromosomal genetic elements ranging in size from 1 to 2 kilobases up to 1 megabase or more. The number of plasmids per bacterial cell varies extensively, and each plasmid is composed of several genes. Some genes encode products that mediate plasmid replication and transfer between bacterial cells, whereas



• **Fig. 2.3** Molecular Structure of Nucleic Acid Bases *DNA*, Deoxyribonucleic acid; *RNA*, ribonucleic acid. Pyrimidines: cytosine, thymine, and uracil. Purines: adenine and guanine.

others encode products that provide a specialized function, such as a determinant of antimicrobial resistance or a unique metabolic process. Unlike most chromosomal genes, plasmid genes do not usually encode for products essential for viability. Plasmids, in whole or in part, may also become incorporated into the chromosome.

Transposable elements are pieces of DNA that move from one genetic element to another, from plasmid to chromosome or vice versa within an organism. Unlike plasmids, many are unable to replicate independently and do not exist as separate entities in the bacterial cell. The two types of transposable elements are the **simple transposon** or **insertion sequence** (**IS**) and the **composite** (also termed compound) or **complex transposon**. Insertion sequences are limited to containing the genes that encode information required for movement from one site in the genome to another. Composite transposons are cassettes (grouping of genes) flanked by insertion sequences. The internal gene embedded between the ISs encode for an accessory function, such as antimicrobial resistance. In addition to transposons, other gene cassettes have been identified that are small mobile elements that consist of one or two genes inserted into an **integron**. An integron differs from a transposon structurally and mechanism for recombination. Plasmids, transposable elements, and integrons coexist with chromosomes in the cells of many bacterial species. These extrachromosomal elements play a key role in the exchange of genetic material throughout the bacterial microbiosphere, including genetic exchange among clinically relevant bacteria.

DNA Replication

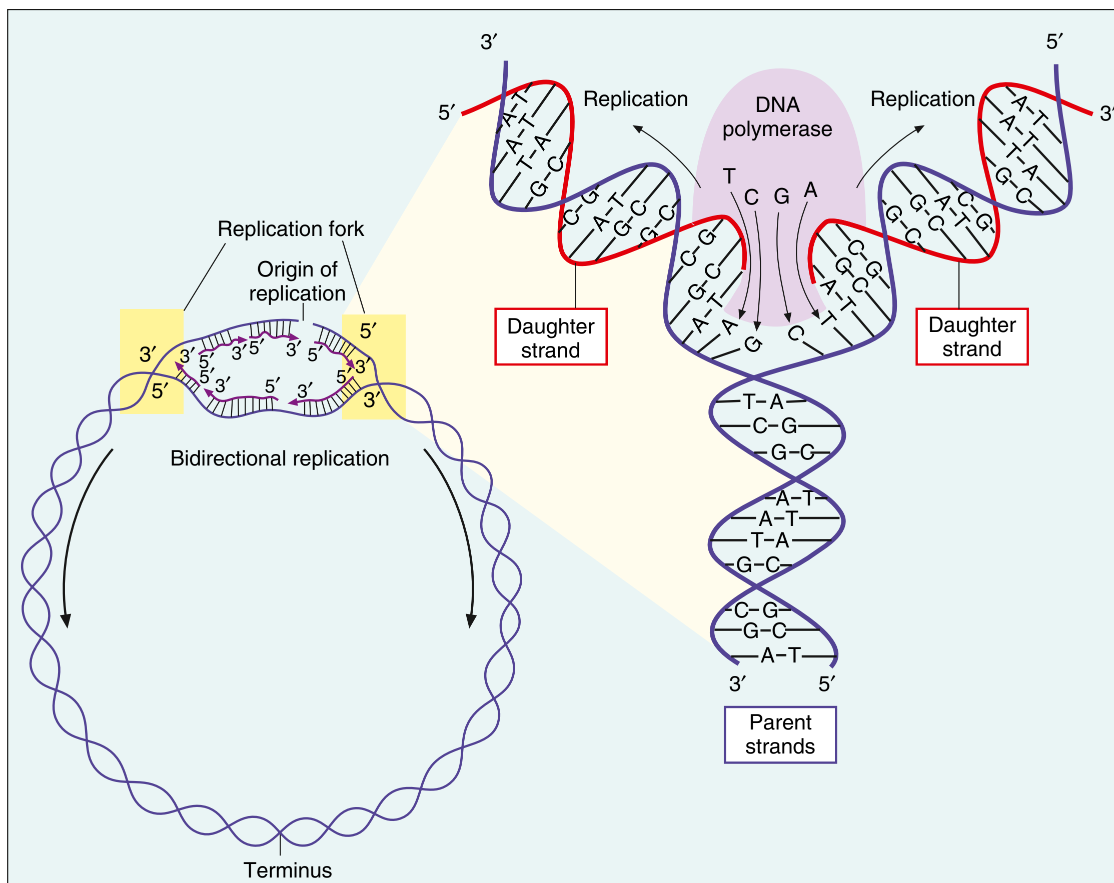
Replication

Bacteria multiply by **binary fission** (a form of cell division), resulting in the production of two daughter cells from one parent cell. As part of this process, the genome must be replicated and each daughter cell receives an identical copy of functional DNA. **Replication** is a complex process mediated by various enzymes, such as DNA polymerase and cofactors; replication must occur quickly and accurately. For descriptive purposes, replication may be considered in four stages (Fig. 2.4):

1. Unwinding or relaxation of the chromosome's supercoiled DNA
2. Separation of the complementary strands of the parental DNA. Each strand may serve as a **template** (i.e., pattern) for synthesis of new DNA strands, referred to as **semiconservative replication**
3. Synthesis of the new (i.e., daughter) DNA strands
4. Termination of replication, releasing two identical chromosomes, one for each daughter cell

Relaxation of supercoiled chromosomal DNA is required, which permits the enzymes and cofactors involved in replication access to the DNA molecule at the site where the replication process will originate (i.e., origin of replication). The **origin of replication** (a specific sequence of approximately 300 bp) is recognized by several initiation proteins, followed by the separation of the complementary strands of parental DNA. Each parental strand serves as a template for the synthesis of a new complementary daughter strand. The site of active replication is referred to as the **replication fork**; two bidirectional forks are involved in the replication process. Each replication fork moves through the parent DNA molecule in opposite directions as a bidirectional process. Activity at each replication fork involves different cofactors and enzymes, with **DNA polymerase** playing a central role. Using each parental strand as a template, DNA polymerase adds nucleotide bases to each growing daughter strand in a sequence that is complementary to the base sequence of the template (parent) strand. The complementary bases of each strand are then held together by hydrogen bonding between nucleotides and the hydrophobic nature of the nitrogenous bases. The new nucleotides can be added only to the 3′ hydroxyl end of the growing strand. The synthesis for each daughter strand occurs in the 5′ to 3′ direction.

Termination of replication occurs when the replication forks meet. The result is two complete chromosomes, each containing two complementary strands, one of parental origin and one newly synthesized daughter strand. Although the time required for replication can vary among bacteria,



• **Fig. 2.4** Bacterial deoxyribonucleic acid (DNA) replication with bidirectional movement of two replication forks from the origin of replication. Each parent strand serves as a template for production of a complementary daughter strand and, eventually, two identical chromosomes.

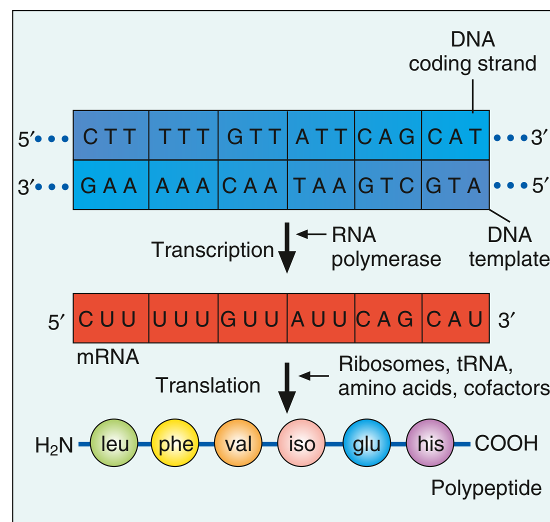
the process generally takes approximately 20 to 40 minutes in rapidly growing bacteria such as *E. coli.* The replication time for a particular bacterial strain can vary depending on environmental conditions, such as the availability of nutrients or the presence of toxic substances (e.g., antimicrobial agents).

Expression of Genetic Information

Gene **expression** is the processing of information encoded in genetic elements (i.e., chromosomes, plasmids, and transposons) that results in the production of biochemically functional molecules, including RNA and proteins. The overall process of gene expression is composed of two steps, **transcription** and **translation**. Gene expression requires various components, including a DNA template representing a single gene or cluster of genes, various enzymes and cofactors, and RNA molecules of specific structure and function.

Transcription

Gene expression begins with transcription. During transcription the DNA base sequence of the gene (i.e., the genetic code) is copied creating an RNA molecule that is complementary to the gene's DNA sequence (Fig. 2.5). One of the two DNA strands (**sense strand**) encodes the functional gene product. This same strand is the template for RNA synthesis.



• **Fig. 2.5** Overview of Gene Expression Components Transcription for production of messenger ribonucleic acid (mRNA) and translation for production of a polypeptide (protein). *DNA*, Deoxyribonucleic acid; *RNA*, ribonucleic acid; *tRNA*, transfer RNA.

RNA polymerase is the enzyme central to the transcription process. The enzyme is composed of four protein

subunits and a sigma (σ) factor. **Sigma factors** are required for the RNA polymerase to identify the appropriate site on the DNA template where transcription of RNA is initiated. This initiation site is also known as the **promoter sequence**. The remainder of the enzyme functions to unwind the dsDNA at the promoter sequence and use the DNA strand as a template to sequentially add ribonucleotides (ATP, GTP, UTP, and CTP) to form the growing RNA strand.

Transcription proceeds in a 5′ to 3′ direction. However, in RNA, the TTP of DNA is replaced with UTP. TTP contains thymine, and UTP contains uracil. Both molecules contain a heterocyclic ring and are classified as pyrimidines. During synthesis and modification of these molecules, a portion of the molecules are dehydroxylated, forming a 2′-deoxynucleotide monophosphate. The dehydroxylated uracil monophosphate (dUMP) is then methylated, forming dehydroxylated thymine monophosphate (dTMP). After phosphorylation, thymine is found only in the final state as deoxythymidine and therefore cannot be incorporated into an RNA molecule. Synthesis of the single-stranded RNA product ends when specific nucleotide base sequences on the DNA template are encountered. Termination of transcription may be facilitated by a rho (a prokaryotic protein) cofactor or an intrinsic termination sequence. Both mechanisms disrupt the RNA-RNA polymerase template DNA complex.

In bacteria, the mRNA molecules that result from the transcription process are **polycistronic**; that is, they encode for several gene products (proteins). Polycistronic mRNA may encode several genes whose proteins are involved in a single or closely related cellular function. When a cluster of genes is under the control of a single promoter sequence, the gene group is referred to as an **operon**.

The transcription process produces mRNA but also tRNA, rRNA, and regulatory noncoding (ncRNA) molecules. All types of RNA molecules have key roles in protein synthesis. To initiate transcription, accessory factors are needed to localize the RNA polymerase to the promoter upstream of the coding sequence. In bacteria, the sigma factor binds to the RNA polymerase and recognizes the gene-specific promotor. In some bacteria a small regulatory RNA (sRNA), 6S RNA, binds the sigma factor to repress transcription in the late stationary phase of bacterial growth. The 6S RNA binds and forms a bulge or loop. The loop serves as an RNA-dependent site for RNA synthesis. The RNA synthesized from the loop is referred to as pRNA. When sufficient pRNA is produced, it causes the 6S RNA to detach from the promotor, permitting transcription to continue.

Transfer RNA (tRNA) binds to the A site in the ribosome and delivers the appropriate amino acid during elongation. However, tRNAs exist in many more diverse forms than once thought. In bacteria, the initiation codon codes for an *N*-formylmethionine. This modified amino acid is never placed inside the coding sequence of a bacterial protein. In other words, there are two forms of tRNA that are produced in bacteria that are capable of carrying methionine. One is the initiator $tRNA^{Met}$ and the other is the elongation $tRNA^{Met}$. The elongation $tRNA^{Met}$ binds to the A site of the ribosome, whereas the initiation $tRNA^{Met}$ is capable of binding only to the P site within the ribosome. The binding of the elongation-specific tRNA is controlled by transcription elongation factor 1.

Ribosomal RNA, specifically the 16S rRNA, has historically been associated with classification of organisms based on evolutionary relatedness. The 16S rRNA is present in all organisms and is responsible for catalyzing the peptidyl transferase reaction during protein synthesis. A very small portion of the molecule undergoes genetic changes without deleterious effects to the transcription process, providing a means to monitor the evolutionary development of bacterial species.

In addition to the differences in tRNA specificity, bacteria have developed numerous mechanisms to regulate gene transcription and respond to the environment, including transcriptional and posttranscriptional regulation. Many sensory and regulatory RNA molecules have been identified that serve as RNA thermosensors and riboswitches. These molecules may undergo structural alterations during temperature changes or serve as asRNAs and sRNAs that bind to either nucleic acid–binding proteins modulating activity or directly to mRNA sequences to suppress and alter gene expression. This reversible regulation is evident in the expression of virulence genes in many pathogens, including *E. coli*, *Shigella* spp., and *Yersinia* spp. The global changes of RNA expression within the transcriptome of a pathogenic bacteria allows the organism to rapidly adjust to changes in the environment associated with temperature, ionic conditions, oxygen conditions, pH, calcium, iron, and other metals to maintain growth and survival.

Translation

The next phase in gene expression, translation, involves protein synthesis. Through this process the genetic code in mRNA molecules is translated into specific amino acid sequences that are responsible for protein structure and function (Fig. 2.5).

The process of protein translation requires the use of a genetic alphabet or code. The code consists of triplets of nucleotide bases, referred to as **codons**; each codon encodes for a specific amino acid. Because there are 64 different codons for 20 amino acids, an amino acid can be encoded by more than one codon (Table 2.1). Each codon is specific for a single amino acid. The codon sequences in mRNA direct which amino acids are added and in what order. Translation ensures that proteins with proper structure and function are produced. Errors in the process can result in aberrant proteins that are nonfunctional, emphasizing the need for translation to be well controlled and accurate.

To accomplish the task of translation, intricate interactions between mRNA, tRNA, and rRNA are required. Sixty different standard types of tRNA molecules are responsible for transferring different amino acids from intracellular locations to the site of protein synthesis. These molecules,

TABLE 2.1 The Genetic Code as Expressed by Triplet-Base Sequences of Messenger Ribonucleic Acid[a]

Codon	Amino Acid	Codon	Amino Acid	Codon	Amino Acid	Codon	Amino Acid
UUU	Phenylalanine	CUU	Leucine	GUU	Valine	AUU	Isoleucine
UUC	Phenylalanine	CUC	Leucine	GUC	Valine	AUC	Isoleucine
UUG	Leucine	CUG	Leucine	GUG	Valine	AUG (start)[b]	Methionine
UUA	Leucine	CUA	Leucine	GUA	Valine	AUA	Isoleucine
UCU	Serine	CCU	Proline	GCU	Alanine	ACU	Threonine
UCC	Serine	CCC	Proline	GCC	Alanine	ACC	Threonine
UCG	Serine	CCG	Proline	GCG	Alanine	ACG	Threonine
UCA	Serine	CCA	Proline	GCA	Alanine	ACA	Threonine
UGU	Cysteine	CGU	Arginine	GGU	Glycine	AGU	Serine
UGC	Cysteine	CGC	Arginine	GGC	Glycine	AGC	Serine
UGG	Tryptophan	CGG	Arginine	GGG	Glycine	AGG	Arginine
UGA	None (stop signal)	CGA	Arginine	GGA	Glycine	AGA	Arginine
UAU	Tyrosine	CAU	Histidine	GAU	Aspartic	AAU	Asparagine
UAC	Tyrosine	CAC	Histidine	GAC	Aspartic	AAC	Asparagine
UAG	None (stop signal)	CAG	Glutamine	GAG	Glutamic	AAG	Lysine
UAA	None (stop signal)	CAA	Glutamine	GAA	Glutamic	AAA	Lysine

[a]The codons in deoxyribonucleic acid (DNA) are complementary to those given here. Thus U is complementary to the A in DNA, C is complementary to G, G to C, and A to T. The nucleotide on the left is at the 5′ end of the triplet.
[b]AUG codes for *N*-formylmethionine at the beginning of messenger ribonucleic acid (mRNA) in bacteria.
Modified from Brock TD, Madigan M, Martinko J, et al., editors: *Biology of microorganisms,* 2009, Prentice Hall.

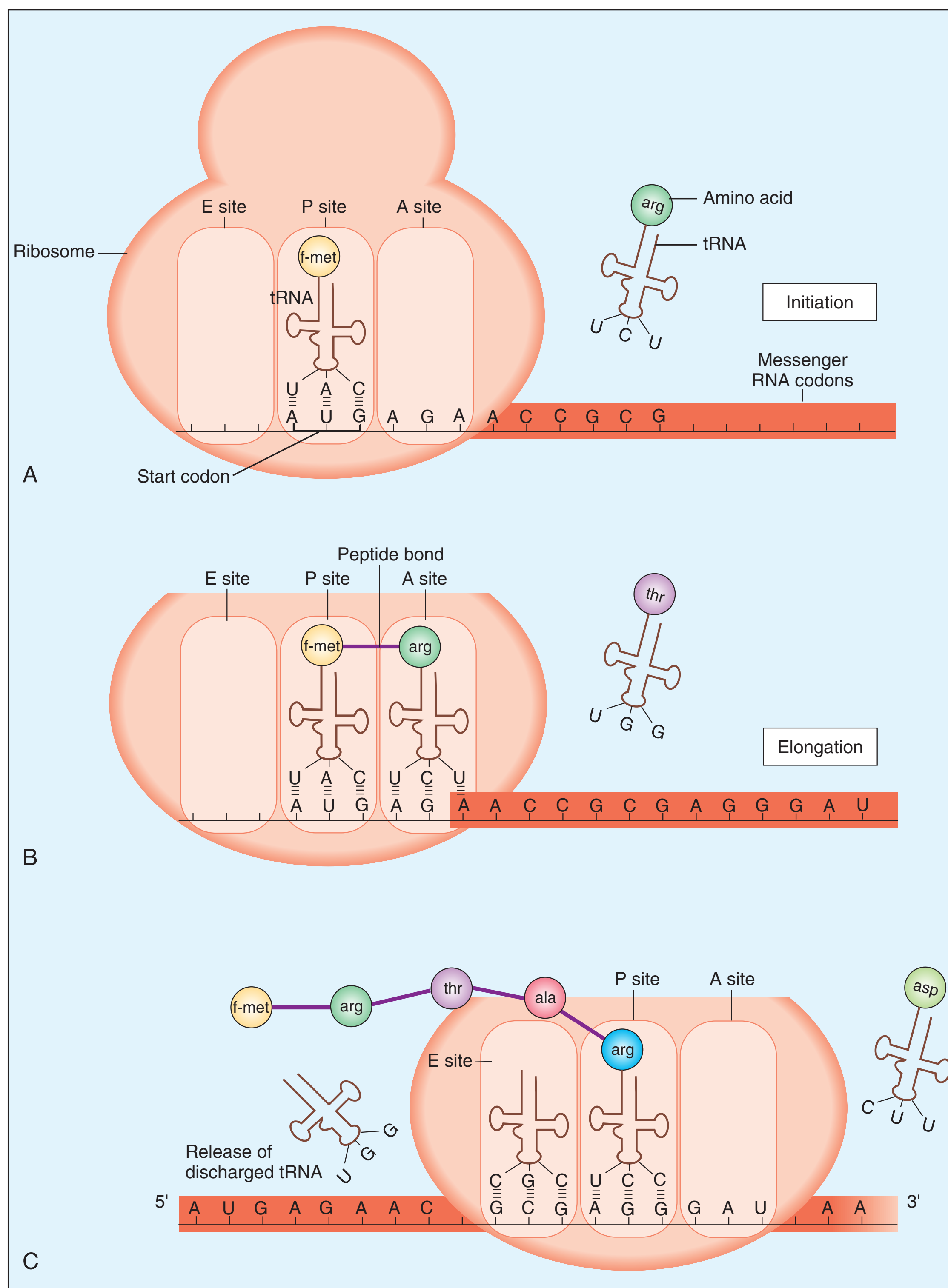
which have a structure that resembles an inverted *t*, contain one **anticodon** (sequence recognition site) for binding to specific codons (3-base sequences) on the mRNA molecule (Fig. 2.6). A second site binds specific amino acids, the building blocks of proteins. Each amino acid is joined to a specific tRNA molecule through the enzymatic activity of aminoacyl-tRNA synthetases. Transfer RNA molecules use the codons of the mRNA molecule as the template for precisely delivering a specific amino acid for polymerization. This process occurs in **ribosomes**, which are compact nucleoproteins, composed of rRNA and proteins. They are central to translation, assisting with the coupling of all required components and controlling the translational process.

Translation, diagrammatically shown in Fig. 2.6, involves three steps: **initiation**, **elongation**, and **termination**. After termination, bacterial proteins often undergo posttranslational modifications as a final step in protein synthesis.

Initiation begins with the association of ribosomal subunits, mRNA, formylmethionine (f-met) tRNA (carrying the initial amino acid of the protein to be synthesized), and various initiation factors (Fig. 2.6A). Assembly of the complex begins at a specific 3- to 9-base sequence (Shine-Dalgarno sequence) on the mRNA approximately 10 bp upstream of the AUG start codon. After the initial complex has been formed, addition of individual amino acids begins.

Elongation involves tRNAs and a host of elongation factors that mediate the addition of amino acids in a specific sequence dictated by the codon on the mRNA molecule (Fig. 2.6B and C and Table 2.1). As the mRNA molecule threads through the ribosome in a 5′ to 3′ direction, peptide bonds are formed between adjacent amino acids, still bound by the respective tRNA molecule in the peptide (P) and acceptor (A) sites of the ribosome. During the process, the forming peptide is moved to the P site, and the 5′ tRNA is released from the exit (E) site. This movement vacates the A site, which contains the codon specific for the next amino acid, so that the incoming tRNA–amino acid can join the complex (Fig. 2.6C).

Because multiple proteins encoded on an mRNA strand can be translated at the same time, multiple ribosomes may be simultaneously associated with one mRNA molecule. Such an arrangement is referred to as a **polysome**; its appearance resembles a string of pearls.



• **Fig. 2.6** Overview of Translation Messenger ribonucleic acid (mRNA) serves as the template for the assembly of amino acids into polypeptides. The three steps include initiation (A), elongation (B and C), and termination (not shown). *tRNA*, transfer RNA.

Termination, the final step in translation, occurs when the ribosomal A site encounters a stop or nonsense codon that does not specify an amino acid (i.e., a "stop signal"; Table 2.1). At this point, the protein synthesis complex disassociates and the ribosomes are available for another round of translation. After termination, most proteins must undergo modification, such as folding or enzymatic trimming, so that protein function, transportation, or incorporation into various cellular structures can be accomplished. This process is referred to as **posttranslational modification**.

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