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5TH EDITION

Leslie P. Gartner

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CELL BIOLOGY AND HISTOLOGY

5TH EDITION

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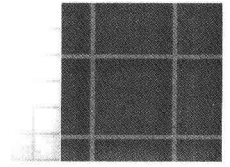
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CELL BIOLOGY AND HISTOLOGY

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Preface

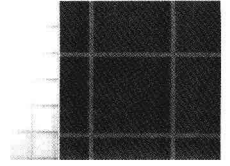
We were very pleased with the reception of the fourth edition of this book, as well as with the many favorable comments we received from students who used it in preparation for the USMLE Step 1 or as an outline and study guide for their histology and/or cell biology courses in professional schools or undergraduate colleges.

All of the chapters have been revised and updated to incorporate current information, and we have attempted to refine the content of the text to present National Board-driven material as succinctly as possible but still retain the emphasis on the relationship between cell structure and function through the vehicle of cell and molecular biology. A tremendous amount of material has been compressed into a concise but highly comprehensive presentation using some new and revised illustrations. The relevancy of cell biology and histology to clinical practice is illustrated by the presence of clinical considerations at the end of each chapter.

The greatest change that occurred in the evolution of this book from its previous edition is that we have provided references for each question, allowing the reader to return to the relevant section of the book to reinforce his or her grasp of the material there. We have also added 57 new images and relevant questions to the CD-ROM. The major impetus for the inclusion of the electronic medium continues to be the ability to present the student with color photomicrographs and with a number of additional USMLE Step 1-type questions without an exorbitant increase in the cost of the book. We believe that the included CD-ROM serves a very important purpose in preparing the student not only for the USMLE Step 1 but also for didactic and practical examinations in the histology and/or cell biology course.

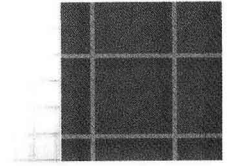
As always, we welcome comments, suggestions, and constructive criticism of this book. These may be addressed to our editors at Lippincott Williams & Wilkins or directly to us by e-mail to lgartner@umaryland.edu.

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Contents

Preface v

Acknowledgments vii

1. Plasma Membrane	1
I. Overview—The Plasma Membrane	1
II. Fluid Mosaic Model of the Plasma Membrane	1
III. Plasma Membrane Transport Processes	4
IV. Cell-to-Cell Communication	5
V. Plasmalemma—Cytoskeleton Association	7
Clinical Considerations	9
Review Test	10
2. Nucleus	13
I. Overview—The Nucleus	13
II. Nuclear Envelope	13
III. Nucleolus	16
IV. Nucleoplasm	16
V. Chromatin	17
VI. Chromosomes	17
VII. DNA	19
VIII. RNA	19
IX. Cell Cycle	21
X. Apoptosis (Programmed Cell Death)	25
XI. Meiosis	26
Clinical Considerations	28
Review Test	29
3. Cytoplasm and Organelles	31
I. Overview—The Cytoplasm	31
II. Structural Components	31
III. Interactions among Organelles	44
Clinical Considerations	49
Review Test	51
4. Extracellular Matrix	54
I. Overview—The Extracellular Matrix	54
II. Ground Substance	54
III. Fibers	58
Clinical Considerations	61
Review Test	62

5. Epithelia and Glands	65
I. Overview—Epithelia	65
II. Lateral Epithelial Surfaces	66
III. Basal Epithelial Surfaces	69
IV. Apical Epithelial Surfaces	70
V. Glands	71
Clinical Considerations	72
Review Test	74
6. Connective Tissue	77
I. Overview—Connective Tissue	77
II. Extracellular Matrix	77
III. Connective Tissue Cells	78
IV. Classification of Connective Tissue	83
Clinical Considerations	84
Review Test	86
7. Cartilage and Bone	89
I. Overview—Cartilage	89
II. Bone	92
III. Joints	99
Clinical Considerations	100
Review Test	101
8. Muscle	104
I. Overview—Muscle	104
II. Structure of Skeletal Muscle	104
III. Contraction of Skeletal Muscle	108
IV. Innervation of Skeletal Muscle	110
V. Cardiac Muscle	111
VI. Smooth Muscle	113
VII. Contractile Nonmuscle Cells	115
Clinical Considerations	115
Review Test	117
9. Nervous System	120
I. Overview—Nervous System	120
II. Histogenesis of the Nervous System	120
III. Cells of Nervous System	121
IV. Synapses	126
V. Nerve Fibers	127
VI. Nerves	129
VII. Ganglia	130
VIII. Histophysiology of Nervous System	130
IX. Somatic Nervous System and Autonomic Nervous System (ANS)	132
X. CNS	132
XI. Degeneration and Regeneration of Nerve Tissue	134
Clinical Considerations	134
Review Test	137

10. Blood and Hemopoiesis	141
I. Overview—Blood	141
II. Blood Constituents	141
III. Blood Coagulation	144
IV. Bone Marrow	145
V. Prenatal Hemopoiesis	146
VI. Postnatal Hemopoiesis	146
VII. Hemopoietic Growth Factors [Colony Stimulating Factors (CSF)]	150
Clinical Considerations	152
Review Test	153
11. Circulatory System	156
I. Overview—Blood Vascular System	156
II. Overview—Lymphatic Vascular System	162
Clinical Considerations	163
Review Test	165
12. Lymphoid Tissue	169
I. Overview—The Lymphoid (Immune) System	169
II. Cells of the Immune System	169
III. Antigen Presentation and the Role of MHC Molecules	175
IV. Immunoglobulins	176
V. Diffuse Lymphoid Tissue	176
VI. Lymphoid Organs	177
Clinical Considerations	181
Review Test	182
13. Endocrine System	185
I. Overview—The Endocrine System	185
II. Hormones	185
III. Overview—Pituitary Gland (Hypophysis)	186
IV. Overview—Thyroid Gland	190
V. Parathyroid Glands	191
VI. Overview—Adrenal (Suprarenal) Glands	192
VII. Pineal Gland (Pineal Body; Epiphysis)	194
Clinical Considerations	195
Review Test	196
14. Skin	199
I. Overview—The Skin	199
II. Epidermis	199
III. Dermis	202
IV. Glands in the Skin	203
V. Hair Follicle and Arrector Pili Muscle	204
VI. Nails	205
Clinical Considerations	205
Review Test	207

- 15. Respiratory System 210**
 - I. Overview—The Respiratory System 210
 - II. Conducting Portion of the Respiratory System 210
 - III. Overview—Respiratory Portion of the Respiratory System 214
 - IV. Lung Lobules 217
 - V. Pulmonary Vascular Supply 217
 - VI. Pulmonary Nerve Supply 218
 - Clinical Considerations 218**
 - Review Test 220**

- 16. Digestive System: Oral Cavity and Alimentary Tract 223**
 - I. Overview—The Digestive System 223
 - II. Oral Region 223
 - III. Divisions of the Alimentary Canal 225
 - IV. Digestion and Absorption 233
 - Clinical Considerations 235**
 - Review Test 237**

- 17. Digestive System: Glands 240**
 - I. Overview—Extrinsic Glands of the Digestive System 240
 - II. Major Salivary Glands 240
 - III. Overview—Pancreas 241
 - IV. Liver 242
 - V. Gallbladder 246
 - Clinical Considerations 247**
 - Review Test 249**

- 18. The Urinary System 251**
 - I. Overview—The Urinary System 251
 - II. Kidneys 251
 - III. Uriniferous Tubules 252
 - IV. Renal Blood Circulation 258
 - V. Regulation of Urine Concentration 259
 - VI. Excretory Passages 261
 - Clinical Considerations 264**
 - Review Test 265**

- 19. Female Reproductive System 268**
 - I. Overview—Female Reproductive System 268
 - II. Ovaries 268
 - III. Oviducts (Fallopian Tubes) 273
 - IV. Uterus 274
 - V. Cervix 276
 - VI. Fertilization and Implantation 276
 - VII. Placenta 276
 - VIII. Vagina 277
 - IX. External Genitalia (Vulva) 277
 - X. Mammary Glands 278
 - Clinical Considerations 279**
 - Review Test 281**

20. Male Reproductive System	283
I. Overview—Male Reproductive System	283
II. Testes	283
III. Genital Ducts	288
IV. Accessory Genital Glands	291
V. Penis	292
Clinical Considerations	292
Review Test	294
21. Special Senses	297
I. Overview—Special Sense Receptors	297
II. Specialized Diffuse Receptors	297
III. Eye	299
IV. Ear (Vestibulocochlear Apparatus)	305
Clinical Considerations	310
Review Test	312
Comprehensive Examination	315
Index	335

Plasma Membrane

I. Overview—The Plasma Membrane (plasmalemma; cell membrane)

A. **Structure.** The plasma membrane is approximately 7.5 nm thick and consists of a **lipid bilayer** and associated **proteins**.

1. The **inner leaflet** of the plasma membrane faces the cytoplasm, and the **outer leaflet** faces the extracellular environment.
2. The plasma membrane displays a trilaminar (**unit membrane**) structure that is evident when examined by transmission electron microscopy (TEM).

B. Function

1. The plasma membrane envelops the cell and maintains its structural and functional integrity.
2. It acts as a **semipermeable** membrane between the cytoplasm and the external environment.
3. It permits the cell to recognize macromolecules and other cells and to be recognized by other cells.
4. It participates in the transduction of extracellular signals into intracellular events.

II. Fluid Mosaic Model of the Plasma Membrane

A. The **lipid bilayer** (Fig. 1-1) is freely permeable to small, lipid-soluble, nonpolar molecules but is impermeable to ions.

1. **Molecular structure.** The lipid bilayer is composed of phospholipids, glycolipids, and cholesterol.
 - a. **Phospholipids** are **amphipathic** molecules consisting of one polar (**hydrophilic**) head and two nonpolar (**hydrophobic**) fatty acyl tails.
 - b. The two leaflets are not identical; instead the distribution of the various types of phospholipids is asymmetrical.
 - (1) The **polar head** of each molecule faces the membrane surface, whereas the **tails** project into the interior of the membrane, facing each other.
 - (2) The **tails** of the two leaflets form weak bonds that attach the two leaflets to each other.

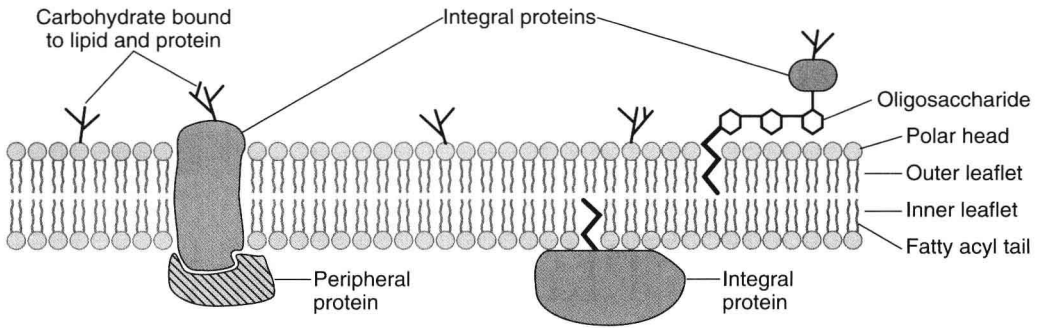


Figure 1-1 The plasma membrane showing the outer (*top*) and inner (*bottom*) leaflets of the unit membrane. The hydrophobic fatty acyl tails and the polar heads of the phospholipids constitute the lipid bilayer. Integral proteins are embedded in the lipid bilayer. Peripheral proteins are located primarily on the cytoplasmic aspect of the inner leaflet and are attached by noncovalent interactions to integral proteins.

- c. **Glycolipids** are restricted to the extracellular aspect of the outer leaflet. **Polar carbohydrate residues** of glycolipids extend from the outer leaflet into the extracellular space and form part of the **glycocalyx**.
 - d. Cholesterol, constituting 2% of plasmalemma lipids, is present in both leaflets and helps maintain the structural integrity of the membrane.
 - e. Cholesterol and phospholipids can form microdomains, known as rafts, which can affect the movement of integral proteins of the plasmalemma.
2. **Fluidity** of the lipid bilayer is crucial to **exocytosis**, **endocytosis**, **membrane trafficking**, and **membrane biogenesis**.
- a. Fluidity **increases** with increased temperature and with decreased saturation of the fatty acyl tails.
 - b. Fluidity **decreases** with an increase in the membrane's cholesterol content.

B. Membrane proteins (Fig. 1-1) include integral proteins and peripheral proteins and constitute approximately 50% of the plasma membrane composition.

1. **Integral proteins** are dissolved in the lipid bilayer.
 - a. **Transmembrane proteins** span the entire thickness of the plasma membrane and function as membrane **receptors** and **transport proteins**.
 - (1) Most transmembrane proteins are **glycoproteins**.
 - (2) Transmembrane proteins are **amphipathic** and contain **hydrophilic** and **hydrophobic** amino acids, some of which interact with the hydrocarbon tails of the membrane phospholipids.
 - (3) Most transmembrane proteins are folded so that they pass back and forth across the plasmalemma; therefore, they are also known as **multipass proteins**.
 - b. Integral proteins may also be anchored to the inner (or occasionally outer) leaflet via fatty acyl or prenyl groups.
 - c. In freeze-fracture preparations, integral proteins remain preferentially attached to the **P-face**, the outer (protoplasmic face) surface of the inner leaflet, rather than the **E-face** (extracellular face) (Fig. 1-2).
2. **Peripheral proteins** do not extend into the lipid bilayer.
 - a. These proteins are located on the cytoplasmic aspect of the inner leaflet.
 - b. The outer leaflets of some cells possess covalently linked glycolipids to which peripheral proteins are anchored; these peripheral proteins thus project into the **extracellular space**.

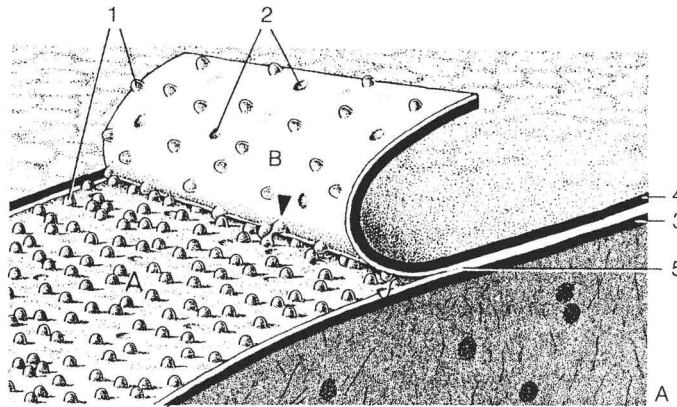


Figure 1-2 Freeze-fracturing cleaves the plasma membrane (5). The impressions (2) of the transmembrane proteins are evident on the E-face between the inner (3) and outer leaflets (4). The integral proteins (1) remain preferentially attached to the P-face (A), the external surface of the inner leaflet; fewer proteins remain associated with the E-face (B), the internal surface of the outer leaflet. The arrowhead indicates a transmembrane protein attached to both E-face and P-face. (Reprinted with permission from Krstic RV: *Ultrastruktur der Saugertierzelle*. Berlin, Springer Verlag, 1976, p 177.)

- c. Peripheral proteins bind to the phospholipid polar groups or integral proteins of the membrane via noncovalent interactions.
 - d. They usually function as part of the **cytoskeleton** or as part of an **intracellular second messenger system**.
 - e. They include a group of anionic, calcium-dependent, lipid-binding proteins known as **annexins**, which act to modify the relationships of other peripheral proteins with the lipid bilayer.
3. **Functional characteristics of membrane proteins**
- a. **The lipid-to-protein ratio** (by weight) in plasma membranes ranges from 1:1 in most cells to as much as 4:1 in myelin.
 - b. Some membrane proteins **diffuse laterally** in the lipid bilayer; others are **immobile** and are held in place by cytoskeletal components.
- C. **Glycocalyx (cell coat)**, located on the outer surface of the outer leaflet of the plasmalemma, varies in appearance (fuzziness) and thickness (up to 50 nm).
1. **Composition.** The glycocalyx consists of polar oligosaccharide side chains linked covalently to most proteins and some lipids (glycolipids) of the plasmalemma. It also contains **proteoglycans (glycosaminoglycans bound to integral proteins)**.
 2. **Function**
 - a. The glycocalyx aids in **attachment** of some cells (e.g., fibroblasts but not epithelial cells) to extracellular matrix components.
 - b. It **binds** antigens and enzymes to the cell surface.
 - c. It facilitates **cell-cell recognition and interaction**.
 - d. It **protects cells** from injury by preventing contact with inappropriate substances.
 - e. It assists T cells and antigen-presenting cells in **aligning** with each other in the proper fashion and aids in preventing inappropriate enzymatic cleavage of receptors and ligands.

III. Plasma Membrane Transport Processes

These processes include transport of a single molecule (uniport) or cotransport of two different molecules in the same (symport) or opposite (antiport) direction.

A. Passive transport (Fig. 1-3) includes **simple** and **facilitated diffusion**. Neither of these processes requires energy because molecules move across the plasma membrane **down a concentration or electrochemical gradient**.

1. **Simple diffusion** transports small nonpolar molecules (e.g., oxygen and nitrogen) and small, uncharged, polar molecules (e.g., water, carbon dioxide, and glycerol). It exhibits little specificity, and the diffusion rate is proportional to the concentration gradient of the diffusing molecule.
2. **Facilitated diffusion** occurs via **ion channels** and/or **carrier proteins**, structures that exhibit **specificity** for the transported molecules. Not only is it faster than simple diffusion, but it is also responsible for providing a pathway for ions and large polar molecules to traverse membranes that would otherwise be impermeable to them.
 - a. **Ion channel proteins** are multipass transmembrane proteins that form small aqueous pores across membranes through which specific small water-soluble molecules and ions pass down an electrochemical gradient (**passive transport**).
 - b. **Aquaporins** are channels designed for the rapid transport of water across the cell membrane without permitting an accompanying flow of protons to pass through the channels. They accomplish this by forcing the water molecules to flip-flop halfway down the channel, so that water molecules enter aquaporins with their oxygen leading into the channel and leave with their oxygen trailing the hydrogen atoms.
 - c. **Carrier proteins** are multipass transmembrane proteins that undergo reversible conformational changes to transport specific molecules across the membrane; these proteins function in both passive transport and **active transport**.

B. Active transport is an **energy-requiring process** that transports a molecule **against** an electrochemical gradient via carrier proteins.

1. $\text{Na}^+\text{-K}^+$ pump

- a. **Mechanism.** The $\text{Na}^+\text{-K}^+$ pump involves the **antiport** transport of Na^+ and K^+ mediated by the carrier protein, **$\text{Na}^+\text{-K}^+$ adenosine triphosphatase (ATPase)**.

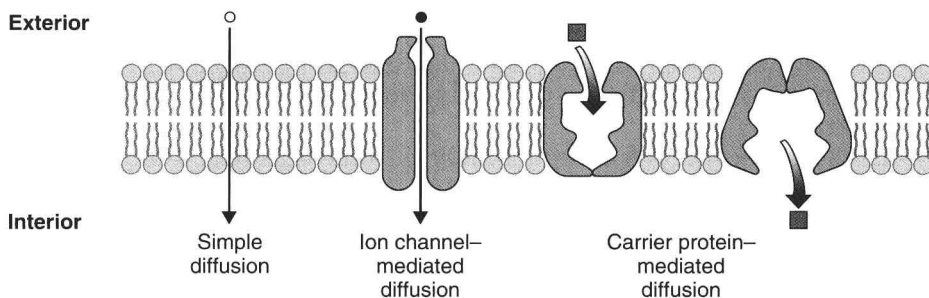


Figure 1-3 Passive transport of molecules across plasma membranes by simple diffusion (*left*) and by either of the two types of facilitated diffusion mediated by ion channel proteins (*center*) and carrier proteins (*right*).

- (1) Three sodium ions are pumped **out** of the cell and two potassium ions are pumped **into** the cell.
 - (2) The hydrolysis of a single ATP molecule by the Na⁺-K⁺ ATPase is required to transport five ions.
- b. Function**
- (1) The primary function is to **maintain constant cell volume** by decreasing the intracellular ion concentration (and thus the osmotic pressure) and increasing the extracellular ion concentration, thus decreasing the flow of water into the cell.
 - (2) The Na⁺-K⁺ pump also plays a minor role in the maintenance of a **potential difference** across the plasma membrane.
2. **Glucose transport** involves the **symport** movement of glucose across an epithelium (**transepithelial transport**). Transport is frequently powered by an electrochemical Na⁺ gradient, which drives carrier proteins located at specific regions of the cell surface.
- C. Facilitated diffusion of ions** can occur via ion channel proteins or ionophores.
1. Selective ion channel proteins permit only certain ions to traverse them.
 - a. **K⁺ leak channels** are the most common ion channels. These channels are ungated and leak K⁺, the ions most responsible for establishing a potential difference across the plasmalemma.
 - b. **Gated ion channels** open only transiently in response to various stimuli. They include the following types:
 - (1) **Voltage-gated channels** open when the potential difference across the membrane changes (e.g., voltage-gated Na⁺ channels, which function in the generation of action potentials; see Chapter 9 VIII B 1 e).
 - (2) **Mechanically gated channels** open in response to a mechanical stimulus (e.g., the tactile response of the hair cells in the inner ear).
 - (3) **Ligand-gated channels** open in response to the binding of a **signaling molecule or ion**. These channels include neurotransmitter-gated channels, nucleotide-gated channels, and G protein-gated K⁺ channels of cardiac muscle cells.
 2. **Ionophores** are molecules that form a complex with ions and insert into the lipid bilayer to transport those ions across the membrane.

IV. Cell-to-Cell Communication

A. Signaling molecules, secreted by signaling cells, are directed to target cells, and in this fashion these molecules function in cell-to-cell communication. Examples include neurotransmitters, which are released into the synaptic cleft (see Chapter 8 IV A 1 b and Chapter 9 IV B 5); endocrine hormones, which are carried in the bloodstream and act on distant target cells; and hormones released into the intercellular space, which act on nearby cells (**paracrine hormones**) or on the releasing cell itself (**autocrine hormones**).

1. **Lipid-soluble signaling molecules** penetrate the plasma membrane and bind to *receptors within the cytoplasm* or inside the **nucleus**, activating intracellular messengers. Examples include hormones that influence gene transcription.
2. **Hydrophilic signaling molecules** bind to and activate **cell-surface receptors** (as do some lipid-soluble signaling molecules) and have diverse physiologic effects

(see Chapter 13). Examples include neurotransmitters and numerous hormones (e.g., serotonin, thyroid-stimulating hormone, insulin).

B. Membrane receptors are primarily glycoproteins. They are located on the cell surface, and specific signaling molecules bind to them.

1. *Function*

- a. Membrane receptors **control plasmalemma permeability** by regulating the conformation of ion channel proteins.
- b. They **regulate the entry of molecules** into the cell (e.g., the delivery of cholesterol via low-density lipoprotein receptors).
- c. They **bind extracellular matrix molecules** to the cytoskeleton via **integrins**, which are essential for cell–matrix interactions.
- d. They **act as transducers** to translate extracellular events into an intracellular response via the second messenger systems.
- e. They permit pathogens that mimic normal ligands to enter cells.

2. *Types of membrane receptors*

- a. **Channel-linked receptors** bind a signaling molecule that temporarily opens or closes the gate, permitting or inhibiting the movement of ions across the cell membrane. Examples include **nicotinic acetylcholine receptors** on the muscle-cell sarcolemma at the myoneural junction (see Chapter 8 IV A).
- b. **Catalytic receptors** are single-pass transmembrane proteins.
 - (1) Their extracellular moiety is a receptor, and their **cytoplasmic component** is a protein kinase.
 - (2) Some catalytic receptors lack an extracytoplasmic moiety and as a result are continuously activated; such defective receptors are coded for by some **oncogenes**.
 - (3) Examples of catalytic receptors include the following:
 - (a) **Insulin** binds to its receptor, which **autophosphorylates**. The cell then takes up the insulin–receptor complex by **endocytosis**, enabling the complex to function within the cell.
 - (b) **Growth factors** (e.g., epidermal growth factor, platelet-derived growth factor) bind to specific catalytic receptors and induce mitosis.
- c. **G protein–linked receptors are** transmembrane proteins associated with an ion channel or with an enzyme that is bound to the cytoplasmic surface of the cell membrane.
 - (1) These receptors interact with **heterotrimeric G protein** (guanosine triphosphate [GTP] binding regulatory protein) after binding of a signaling molecule. This interaction results in the activation of **intracellular second messengers**, the most common of which are cyclic adenosine monophosphate (cAMP) and Ca^{2+} .
 - (2) Examples include the following:
 - (a) **Heterotrimeric G proteins** (Table 1-1), which are folded in such a fashion that they make seven passes as they penetrate the cell membrane. They include stimulatory G protein (G_s) (Fig. 1-4), inhibitory G protein (G_i), phospholipase C activator G protein (G_p), olfactory-specific G protein (G_{olf}), and transducin (G_t).
 - (b) **Monomeric G proteins (low-molecular-weight G proteins)**, are small single-chain proteins that also function in signal transduction.
 - (i) Various subtypes resemble Ras, Rho, Rab, and ARF proteins.