BIOLOGY

ANIMAL SYSTEMS

LEVINE / MILLER

BIOLOGY

Discovering Life

VOLUME 4: *Animal Systems*

Joseph S. Levine

Kenneth R. Miller
Brown University

D. C. HEATH AND COMPANY
Lexington, Massachusetts   Toronto

Authors' Dedication
To Carol and Bob, Marion and Ray, our parents, who gave us our lives, the best of our values, our love of learning, and our appreciation for the importance of education in a complex world.

Publisher's Dedication
All of us involved with this project will remember with affection Mary Le Quesne, our editor, mentor, and friend. Her enthusiasm, laughter, and love of publishing will remain an inspiration to all who worked with her.

Acquisitions Editors: Mary Le Quesne, Elizabeth Coolidge-Stolz
Editorial Director: Kent Porter Hamann
Developmental Editor: Barbara Withington Meglis
Production Editors: Cormac Joseph Morrissey, Marret McCorkle, Jill Hobbs
Editorial Assistants: Jennifer Raymond, Joanne M. Williams
Copyeditor: Connie Day
Proofreader: Phyllis Coyne
Indexer: Michael Loo
Designer: Cornelia Boynton
Art Editors: Laurel Smith, Gary Crespo
Design Assistants: Penny Peters, Tama Hochbaum, Laura Fredericks, Marsha Goldberg
Production Coordinator: Michael O'Dea
Photo Researchers: Billie Ingram, Carole Frolich, Linda Finnegan, Mary Lang, Sharon Donahue
Text Permissions Editor: Margaret Roll
Artists: Patrice Rossi, Mickey Senkarik, Marlene DenHouter, Arleen Frasca, Lynette Cook, Marcia Smith, Horvath & Cuthbertson, Lyrl Ahern, Charles Boyter, Andrew Robinson, Michael Woods, Illustrious Inc., Sanderson Associates
Compositor: Graphic Typesetting Service, Inc.
Film Preparation: Colotone Separations
Printer: R.R. Donnelley and Sons
Cover: (*front*) Wildlife Photography/Michael L. Smith, (*back*) Greg Wenzel

recycled paper

Recycled paper is used for the interior stock of this book.

Published simultaneously in Canada.

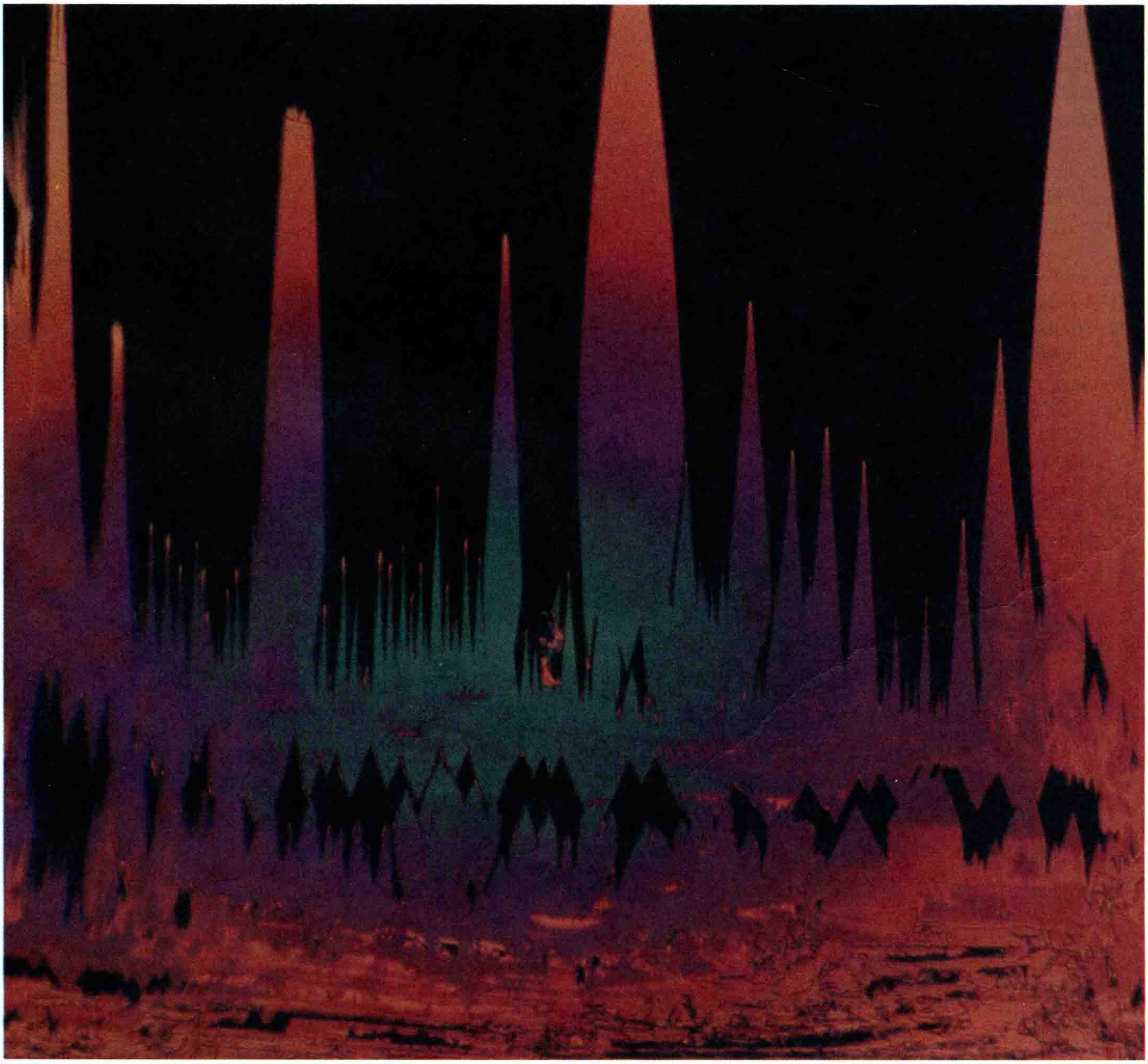
Printed in the United States of America.

International Standard Book Number: 0–669–28843–8

10 9 8 7 6 5 4 3 2 1

BIOLOGY
Discovering Life

Animal Systems



CONTENTS

CHAPTER 10 *Nervous Control* 217

CHAPTER 11 *The Sensory System* 245

We must not conceal from ourselves the fact that the causal investigation of the organism is one of the most difficult, if not the most difficult problem which the human intellect has attempted to solve, and that this investigation, like every causal science, can never reach completeness, since every new cause ascertained only gives rise to fresh questions concerning the cause of this cause.

—Wilhelm Roux (1894)

Roux's famous statement echoes a complaint that has been heard from many generations of students: "The more we learn the less we seem to know!" To be sure, many scientists would take issue with the tone of this quotation. Although it is often true that answering one question results in our posing two or three new ones, it is also true that each question that science is able to answer enriches our understanding of nature. A scientist works with the inner belief that all knowledge is worth having and therefore that the newer, deeper questions that our studies raise will be that much more profound and satisfying to answer.

Anatomy and physiology—fields devoted to the structure and function of the systems of living organisms—are excellent examples of the sources of Roux's complaint. Thousands of years ago, students of biology recognized that it was appropriate to consider a living organism as a number of systems that could be studied separately. As time passed, the classic Roman and Greek texts were updated by workers in the Middle Ages who compared the writings of the ancients with what they were able to discover on their own. With few exceptions, however, it was impossible to discover a link between any of these systems and the chemicals of which living things are made.

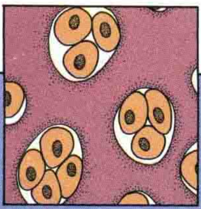
Even so, there were hints of the processes at work within the organism. The electrical activity of nerve and muscle tissue, as well as the acids found in the digestive system, suggested that basic principles of physics and chemistry were at work within living organisms. Engineers pointed out that hydraulics could be used to explain the flow of fluid in the circulatory system, and, little by little, the field of physiology evolved in an effort to link each action of a particular system with a series of cellular and molecular events.

Today, the science of physiology has fully developed the connections with chemistry and physics that were only suspected a century ago. Each of the chapters in this volume explores one or more of the systems of the body. Where appropriate, we will examine how similar systems in other animals function and how each system has been shaped by evolution. You may find that Wilhelm Roux's complaint is still quite valid today—that we have learned a great deal only to confront new questions. But we believe that you will also find that such questions have now advanced to the point where our very ability to pose them has made the last few years of the twentieth century a very exciting time to be alive and a very exciting time to study science.

◀ The dual role of the compound epinephrine, captured here in crystalline form, symbolizes the complexity found in regulatory systems of humans and other vertebrates. Epinephrine facilitates communication throughout the body, serving as both a neurotransmitter and a hormone.

CHAPTER 1

Multicellular Organization and Homeostasis



Imagine that you are visiting Africa's Serengeti Plains in late May. The grasslands are parched and brown, and more than a million wildebeest are on the move, plodding toward greener pastures in Kenya.

Imagine now that you are watching a single animal in this huge herd. He moves mechanically, as if in a trance. Internally, unconsciously, his actions and metabolic processes are geared to scarcity. His measured steps expend the least possible energy. With no food in his gut, his body mobilizes and burns stored energy from fat deposits, distributing it to organs and muscles. Lacking water on today's long march, he retains body fluids by producing as little urine as possible.

Suddenly, a lioness springs from the underbrush. Alarmed, the wildebeest rouses from his stupor, all senses on alert. Energy in the form of glucose pours into his muscles. He gallops away with a grace and speed startling for an animal his size. The lioness strikes and tears his skin with her claws but fails to knock him down. She cannot keep up with his frantic pace.

Several minutes later, once out of danger, the wildebeest relaxes. His metabolism returns to normal, and he lapses into the steady pace of his migratory style. Already, blood in damaged tissues around his wound has thickened enough to stop dripping. Already, bacteria that entered the wound are being surrounded and destroyed by his body's defenses. And already, he has resumed his 200-mile journey toward the northwest.

MAINTAINING THE BALANCE

If you could somehow have watched these events from the perspective of individual cells, you would have seen dozens of remarkable acts of communication, coordination, and control among cells belonging to different tissues. Those acts are neither more nor less remarkable than similar phenomena that occur within your own body or, for that matter, within the body of an ant.

The cells of every organism are at once independent entities and interdependent parts of a larger whole. Each and every cell, whether a nerve cell, a muscle cell, or a skin cell, must respond to changes in its immediate environment within the body. Each must successfully balance the inputs and outputs on which its metabolic activity depends. Yet despite cells' individual requirements, they must also function together as members of the greater cellular community that is the entire organism.

One of the remarkable accomplishments of multicellular organisms is the creation of an internal environment that is carefully controlled. Cells in the wildebeest's brain, for example, must be kept at constant temperature, supplied with energy in the form of glucose, bathed in fluid with a constant concentration of water, and cleansed of their waste products. Those conditions must not change, regardless of droughts, floods, famines, heat waves, or cold snaps. Failure at any of these tasks, even for a few minutes, would lead to permanent injury or death of the entire organism.

Maintaining constant internal conditions in the face of rapidly changing external environments is no small accomplishment. The major systems of the body must rely on a foolproof system of checks and balances that monitors and guides the activities of every cell.

Starting in this chapter, we will examine how the major body systems of animals succeed at this daunting task.

We will begin here by providing a brief overview of the tissues and major body systems of multicellular animals. In volume 2 of this text (Chapters 2–5), we examine some of the basic differences in structure and physiology in the many diverse groups of the animal kingdom. Although we will include a number of different species in our treatment of animal physiology here, we will most often focus on that species of particular interest to us, *Homo sapiens* (Figure 1.1).

THE RANGE OF CELLS AND TISSUES

The Diversity of Cells

Humans begin life as a single cell, a zygote formed by the fusion of sperm and egg. Over the course of a few weeks, that single cell divides into thousands and ultimately millions of cells in the developing embryo. The embryo develops three cell layers (called **germ layers**), the **ectoderm, mesoderm,** and **endoderm,** and from these the rest of the body is produced. Gradually, the cells in these three layers undergo a process called *differentiation* ("becoming different") in which they are transformed into the astonishing variety of cells found in the adult.

- **Ectoderm** develops into the cells of skin and the nervous system.
- **Mesoderm** develops into the cells of the organs found in between ectoderm and endoderm, including muscles, blood vessels, the reproductive tract, and the kidneys. The mesoderm also provides the outer layers of the organs of the digestive and respiratory systems.
- **Endoderm** produces the cells that form the lining of the digestive and respiratory systems and the glands (liver and pancreas) that are outgrowths of these systems.

As different cell types are produced, they do not take up random locations within the embryo. Rather, they become organized into groups that perform specialized functions. These groups of similar cells, which are called **tissues,** are found throughout the body, and they represent a basic level of organization just above the cell itself.

Traditionally, anatomists (biologists who study the organization of the body) have divided tissues into four types: **epithelial, connective, nervous,** and **muscle.** These categories are based on the characteristics of the tissue itself, not on the germ layer from which it was formed. Within each of these four categories there is a great range of diversity. Cells as diverse as blood cells and bone cells, for example, are considered different types of connective tissue.

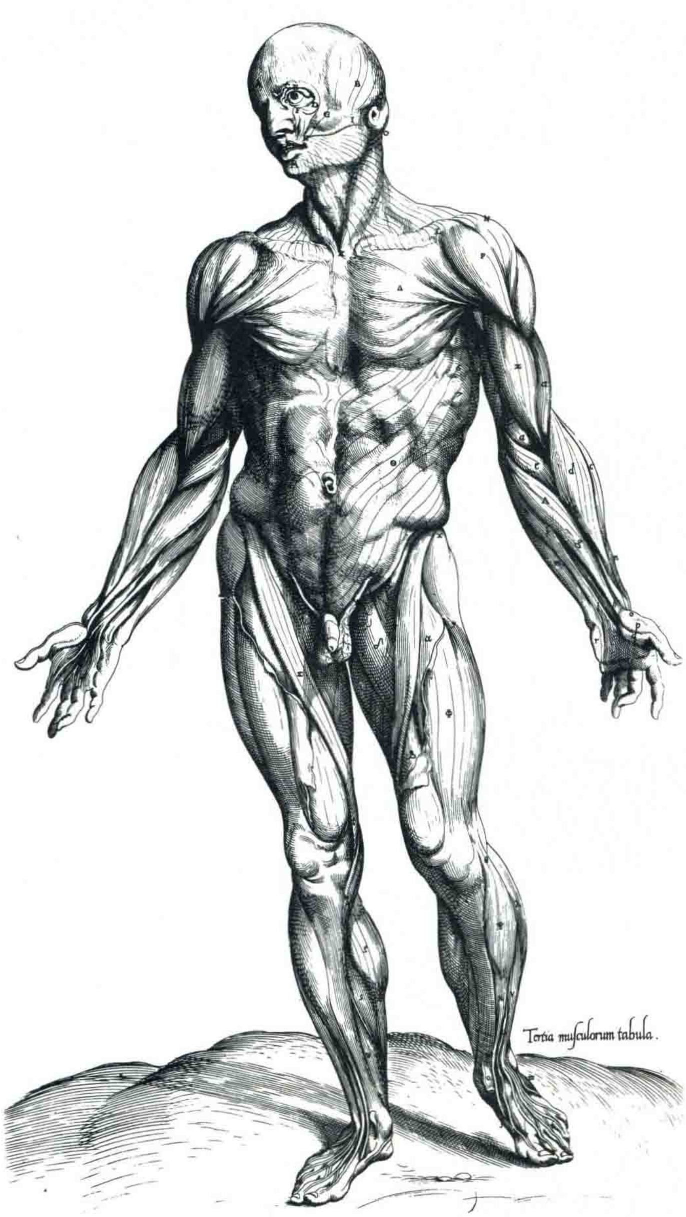


Figure 1.1 A remarkable rendering of the human muscular system, by Vesalius.

Epithelial Tissue

Epithelial tissues form surfaces around and within the body and often act as barriers that divide the body into distinct compartments. The most obvious epithelial tissue is *skin,* which covers the body and serves as its first line of defense against the outside world. Epithelial tissues that are derived from endoderm form the linings of the digestive and respiratory systems, while mesoderm produces the epithelial tissues that cover body organs and line body cavities and blood vessels. *Secretory glands,*

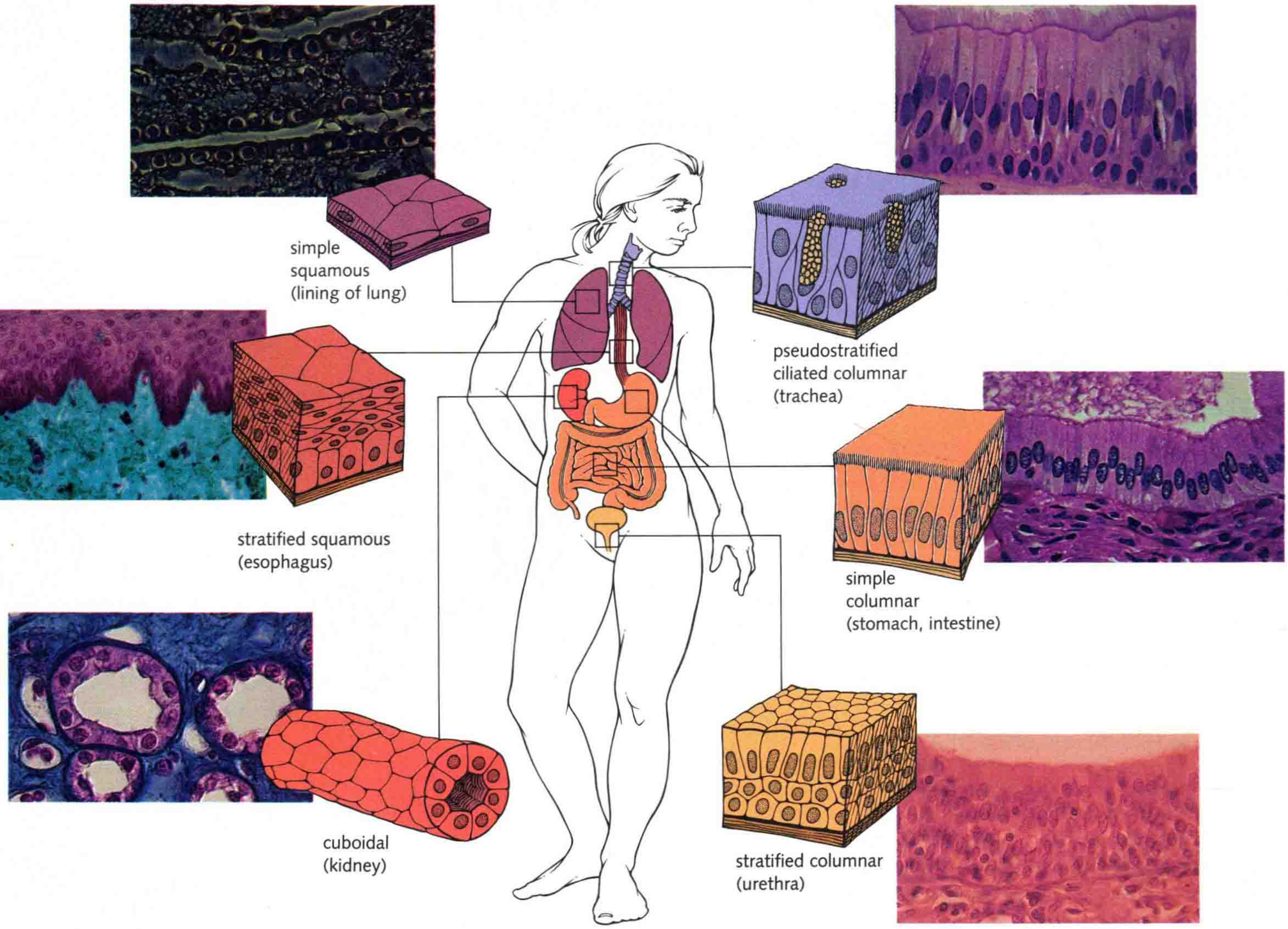


Figure 1.2 Epithelial tissues are found throughout the body. They are placed into categories based on the structural organization of the cells of which they are made. Photomicrographs of six major types of epithelial tissue. Clockwise (from the upper left), simple squamous epithelium (from the lung), pseudostratified columnar epithelium (trachea), simple columnar epithelium (stomach), stratified columnar epithelium (urethra), simple cuboidal epithelium (from kidney), and stratified squamous epithelium (esophagus).

found in tissues derived from ectoderm, endoderm, and mesoderm, are usually formed by invaginations (infoldings) of epithelial tissue.

Epithelial tissues are classified according to the shapes of the cells that form them. Figure 1.2 shows examples of *squamous, cuboidal,* and *columnar* epithelia. A **simple epithelium** consists of a single layer of cells; a **stratified epithelium** consists of two or more layers of cells. **Pseudostratified epithelium** appears to have layers of cells, yet all the cells actually touch a basement membrane.

Cell junctions In order for tissues to form, the cells that compose them must be held together by some means. The cells of many tissues must also have some means of communication with the cells adjacent to them. **Cell**

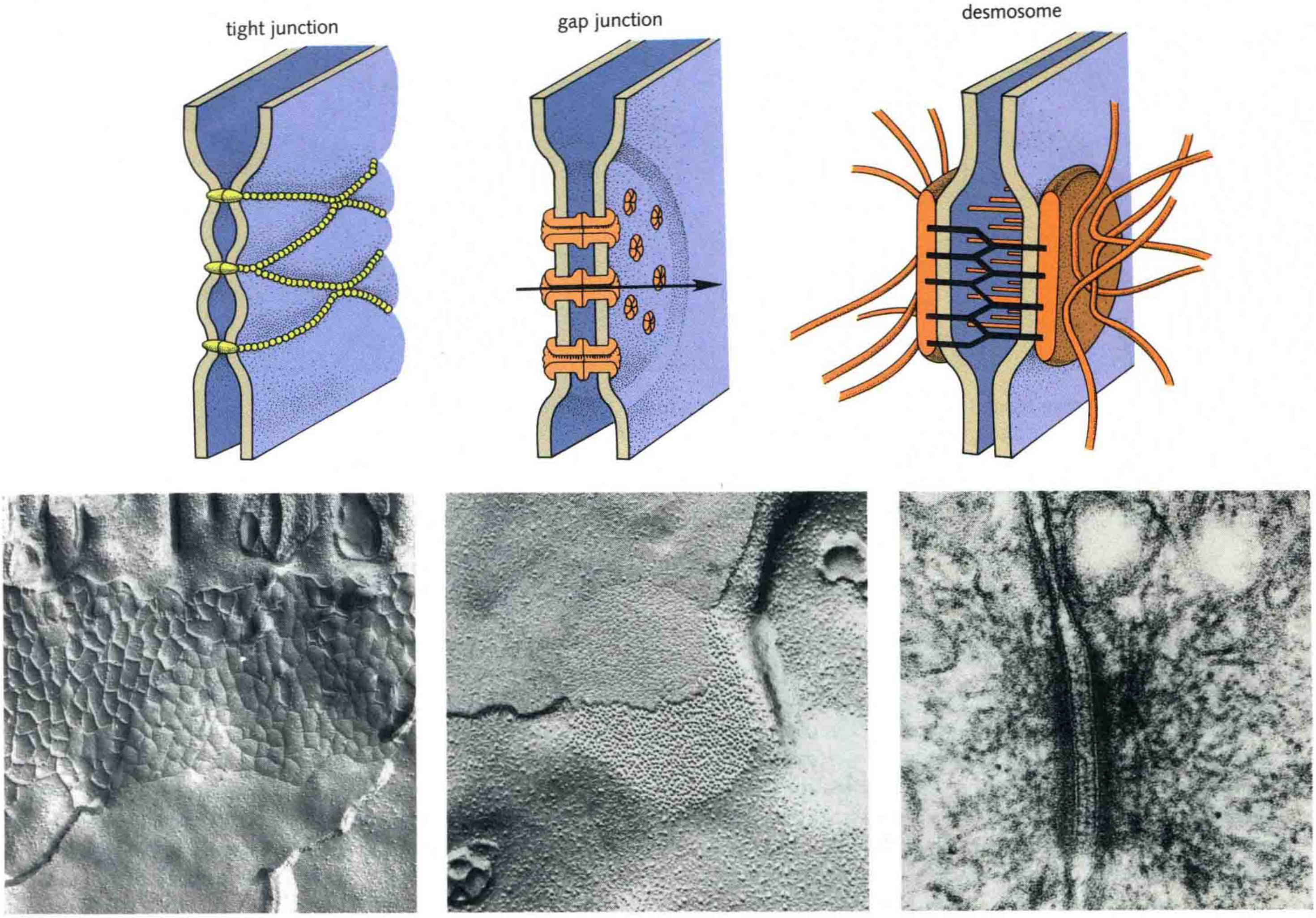


Figure 1.3 Diagrammatic representations of three major types of cell junctions in a simple epithelium. Tight junctions block the passage of materials in the extracellular space between cells, gap junctions form tiny, regulated channels through which small molecules may pass from cell to cell, and desmosomes provide for strong mechanical attachment between adjacent cells. The three major types of cell junctions are shown in the electron micrographs. Tight junctions (left) consist of a web-like series of sealing elements between the membranes of two adjacent cells. Several hundred gap junctions (center) are seen as a cluster of small particles in the center of this micrograph. Each particle is an individual connecting unit which allows material to pass from one cell to the next. A single desmosome (right) consists of extracellular attachments and thickened cell membrane regions anchored to filaments in the cytoskeleton.

junctions, specific attachments between adjacent cells, perform these tasks. Junctions are found in many non-epithelial tissues as well, and they can be grouped into three general types (Figure 1.3).

Tight junctions seal off the external space between two cells, preventing material from leaking between them. Tight junctions are particularly important in epithelia that line fluid-filled cavities, because they prevent the movement of fluid between cells. Tight junctions between cells of the intestine keep its contents from leaking across the intestinal wall into body cavities.

Gap junctions provide a means of intercellular communication. Gap junctions are small, pore-like protein channels that connect the cytoplasm of one cell to that of its neighbor. Compounds such as salts, sugars, and ions have been shown to pass from one cell to the next through gap junctions. They also allow electrical signals and metabolites to pass between cells, enabling groups of cells to function as a coordinated unit such as heart muscle.

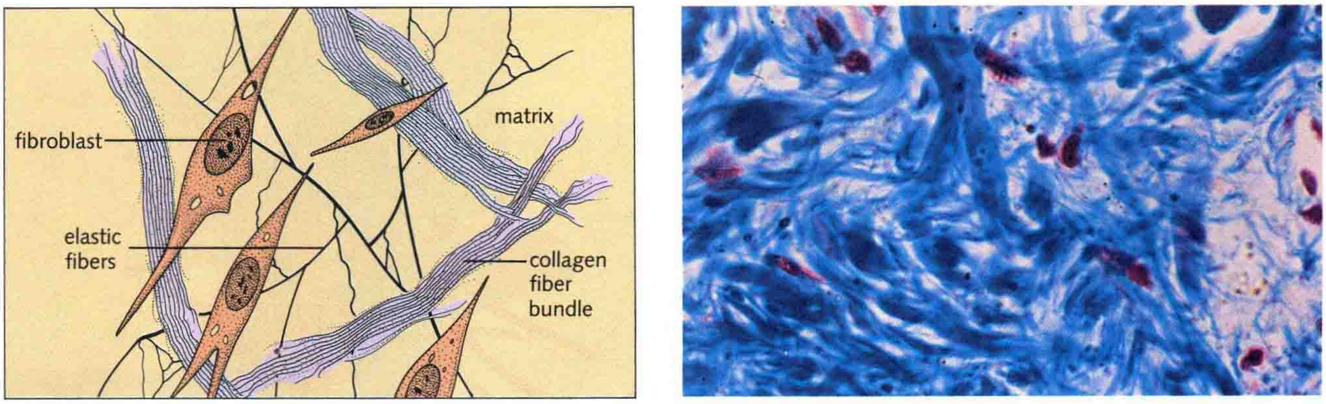


Figure 1.4 Loose connective tissue (left) consists of fibroblasts in a matrix of elastic fibers and tough bundles of collagen. Fibroblasts help to produce this matrix, and are embedded in it. Photomicrograph of fibroblasts (right) in the collagen-rich connective tissue just beneath the human scalp.

Recent studies have shown that gap junctions are quite sophisticated: they may open or close in response to certain cellular signals, including calcium ion and hydrogen ion (pH) concentration. Gap junctions between the contractile cells of the heart are the principal reason why the heart muscle is capable of contracting as a single unit.

Adhering junctions, which are also known as **desmosomes,** are strong mechanical attachments between adjacent cells. These junctions do not block the movement of material between cells. Desmosomes are attached to the *cytoskeleton* of each cell involved in the junction, and this enables the junction to act almost as a "spot weld"—a point at which two cells are cemented together. Desmosomes are particularly common in tissues that are subject to mechanical stress, such as skin, where they prevent the tissues from breaking apart.

Connective Tissue

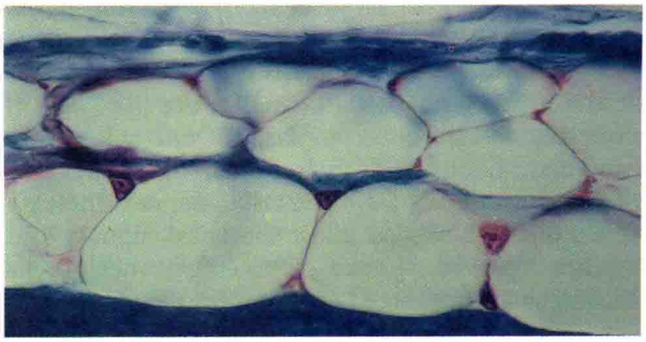
Connective tissue gets its name from the fact that it makes up the basic support structures of the body; it connects the body's other tissues in a manageable framework. If you place your hand around your upper arm as you flex your elbow, you will feel many of the basic types of connective tissues: bones, ligaments, and tendons.

One of the distinguishing characteristics of this tissue is the fact that cells of connective tissues generally produce an **extracellular matrix,** a layer of material that surrounds the cells. The extracellular matrix may be liquid or solid, loose or dense, flexible or rigid. The unique characteristics of the different types of extracellular matrices are often responsible for the different properties that we associate with various types of connective tissues.

Supporting tissue One fundamental role of connective tissue is providing mechanical support. **Loose connective tissue** surrounds major organs, blood vessels, and epithelial tissues. The support provided by its loose matrix of fibrous proteins is indispensable in forming the structure of an organism. In loose connective tissue the most common cell type is the **fibroblast** (Figure 1.4). The fibroblast produces fiber-like proteins that are woven into a complex extracellular bundle. The most important of these proteins, **collagen,** forms large, tough fibers that are found throughout the body. It is the single most abundant protein in the vertebrate body. In some tissues, the layers of collagen are denser and form the basis for connections between muscles and bones and other points subjected to mechanical stress.

Adipose tissue, or **fat,** is another type of connective tissue widely distributed throughout the body. Each fat cell contains a single large droplet of fat stored for possible future use (Figure 1.5).

Figure 1.5 Adipose tissue is a form of connective tissue.



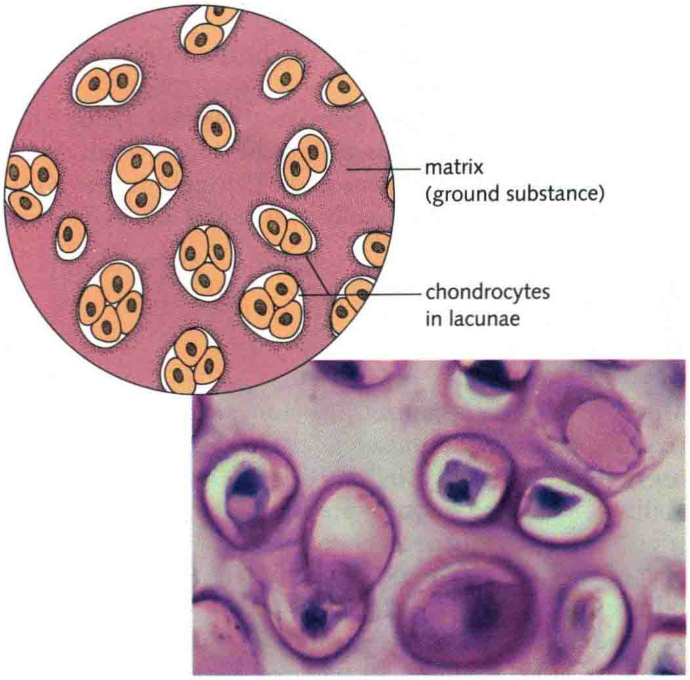


Figure 1.6 Cartilage is produced by chondrocytes, which secrete a tough, flexible extracellular matrix around spaces called lacunae ("holes") in which the chondrocytes remain. The photomicrograph of cartilage shows clusters of chondrocytes confined to isolated lacunae within the tissue matrix.

Cartilage is a form of connective tissue in which an extremely dense matrix containing collagen fibers is laid down in precise orientation (Figure 1.6). Later in development, elastic fibers are laid down with the collagen, and the result is a tough, resilient, springy tissue that can support great weight and still remain flexible. In some vertebrates, notably sharks and rays, the entire skeleton is made of cartilage. In adult humans, cartilage is found at the endpoints of many bones, in the knee, and in flexible structures such as the ear and the tip of the nose.

Bones are strong and rigid, and they provide support and protection for the vertebrate body and its organs. Bone is produced by cells that first lay down a matrix of cartilage and then gradually *mineralize* that matrix by filling it with crystals of calcium phosphate and calcium carbonate. Bone is not a solid matrix, however; it is penetrated by thousands of tiny microscopic canals through which blood vessels flow. The cells that produce the matrix remain alive and active within it, constantly dissolving old matrix and laying down new matrix. This activity enables broken bones to heal rapidly (Figure 1.7).

The inner portion of most large bones, the **bone marrow,** is the principal blood-forming tissue of the body. Most of the cellular components of the circulatory system are produced in bone marrow.

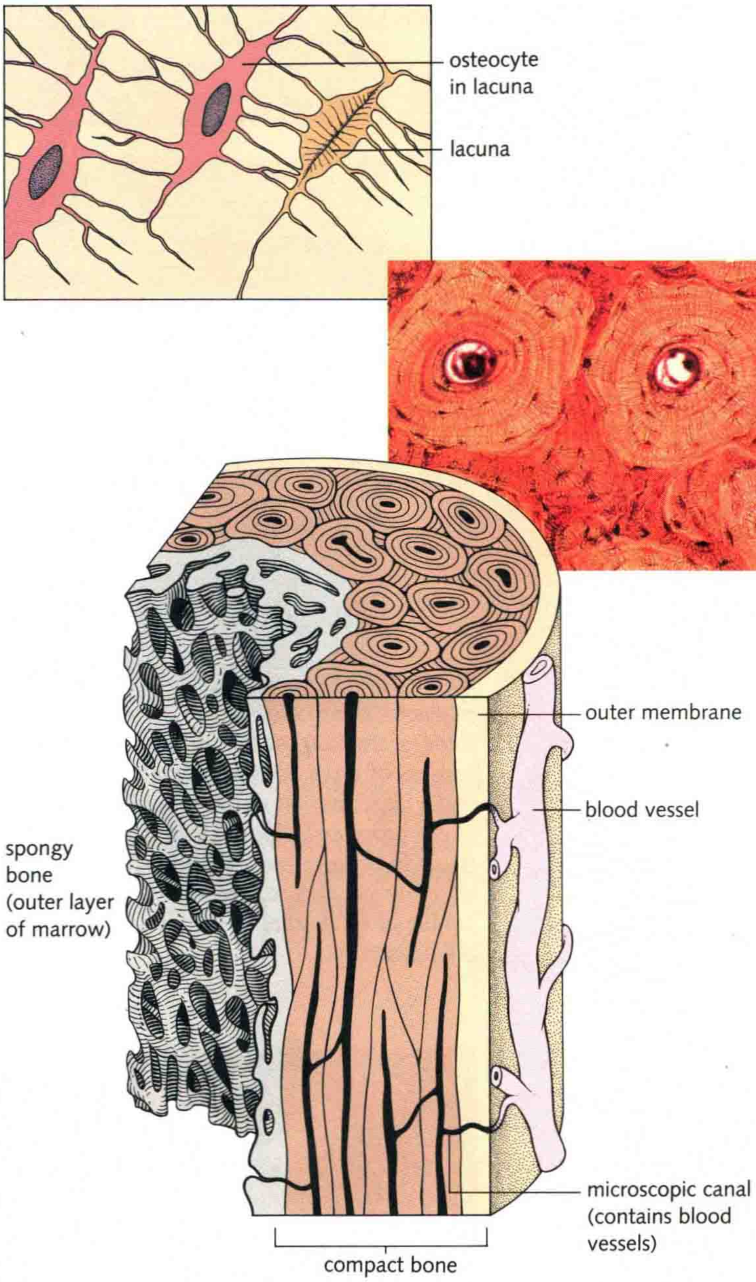


Figure 1.7 Bone is produced by bone cells called osteocytes, which surround their lacunae with a dense, calcium-rich matrix. In spongy bone, the organization of the matrix is loose and open. In compact bone, the tight matrix is penetrated by a series of microscopic canals through which blood vessels and nerves are able to reach the osteocytes. The photomicrograph of human compact bone clearly shows the system of microscopic canals which bring nutrients to osteocytes. It is important to remember that bone is a living tissue, filled with cells that carry on an active metabolism.