CHAPTER 23

PROTECTION, SUPPORT, AND MOVEMENT

Outline

Concepts

1. The integumentary system of animals consists of an outer protective body covering called the integument. The integument of most multicellular invertebrates consists of a single layer of cells. The vertebrate integument is multilayered and is called skin. Skin contains nerves and blood vessels, as well as derivatives, such as glands, hair, and nails.
2. Skeletal systems move primarily by the actions of antagonistic muscles. Animals have three types of skeletons: fluid hydrostatic skeletons, rigid exoskeletons, and rigid endoskeletons. Many invertebrates have hydrostatic skeletons consisting of a core of liquid wrapped in a tension-resistant sheath containing muscles. Rigid exoskeletons completely surround an animal and are sites for muscle attachment and counterforces for muscle movements. They also offer protection and support. The vertebrate skeletal system is an endoskeleton. It consists mainly of supportive tissue composed of cartilage and bone.
3. Muscles provide the force for movement in animals from cnidarians to vertebrates. Vertebrates use their endoskeletons in conjunction with muscles to move. In vertebrates, striated skeletal muscles move the body, smooth muscles move material through tubular organs and change the size of tubular openings, and cardiac muscle produces the beating of the heart.

In animals, structure and function have evolved together. Several results of this evolution are protection, support, and movement. The integumentary, skeletal, and muscular systems are primarily responsible for these functions.

PROTECTION: INTEGUMENTARY SYSTEMS

The **integument** (L. *integumentum*, cover) is the external covering of an animal. It protects the animal from mechanical and chemical injury and invasion by microorganisms. Many other diverse functions of the integument have evolved in different animal groups. These functions include regulation of body temperature; excretion of waste materials; conversion of sunlight into vitamin D; reception of environmental stimuli, such as pain, temperature, and pressure; locomotion; and movement of nutrients and gases.

THE INTEGUMENTARY SYSTEM OF INVERTEBRATES

Some single-celled protozoa have only a **plasma membrane** for an external covering. This membrane is structurally and chemically identical to the plasma membrane of multicellular organisms (*see figure 2.4*). In protozoa, the plasma membrane has a large surface area

This chapter contains evolutionary concepts, which are set off in this font.

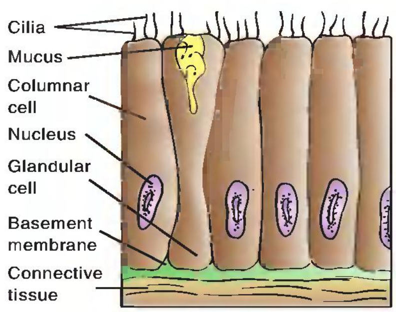


FIGURE 23.1

Integument of Invertebrates. The integument of many invertebrates consists of a simple layer of columnar epithelial cells (epidermis) resting on a basement membrane. A thin layer of connective tissue lies under the basement membrane. Cilia and glandular cells may or may not be present.

relative to body volume, so that gas exchange and the removal of soluble wastes occur by simple diffusion. This large surface area also facilitates the uptake of dissolved nutrients from surrounding fluids. Other protozoa, such as *Paramecium*, have a thick protein coat called a **pellicle** (L. *pellicula*, thin skin) outside the plasma membrane. This pellicle offers further environmental protection and is a semirigid structure that transmits the force of cilia or flagella to the entire body of the protozoan as it moves.

Most multicellular invertebrates have an integument consisting of a single layer of columnar epithelial cells (figure 23.1). This outer layer, the **epidermis** (Gr. *epi*, upon + *derm*, skin), rests on a basement membrane. Beneath the basement membrane is a thin layer of connective tissue fibers and cells. Epidermal cells exposed at the surface of the animal may possess cilia. The epidermis of some invertebrates also contains glandular cells, which secrete an overlying, noncellular material that encases part or most of the animal.

Some invertebrates possess **cuticles** (L. *cuticula*, *cutis*, skin) that are highly variable in structure (figure 23.2). For example, in some animals (rotifers), cuticles are thin and elastic, whereas in others (crustaceans, arachnids, insects), cuticles are thick and rigid and support the body. Such cuticles consist of chitin and proteins in rigid plates that a flexible membrane links together. A disadvantage of cuticles is that animals have difficulty growing within them. As a result, some of these invertebrates (e.g., arthropods) periodically shed the old, outgrown cuticle in a process called molting or ecdysis (*see figure 14.5*).

In cnidarians, such as *Hydra*, the epidermis is only a few cell layers thick. Other cnidarians (e.g., the corals) have mucous glands that secrete a calcium carbonate ($CaCO_3$) **shell.** The outer covering of parasitic flukes and tapeworms is a complex syncytium called a **tegument** (L. *tegumentum*, *tegere*, to cover). Its main functions are nutrient ingestion and protection against digestion by host enzymes. Nematodes and annelids have an epidermis that is one cell thick and secretes a multilayered cuticle. The integument of echinoderms consists of a thin, usually ciliated epidermis and an underlying connective-tissue dermis containing $CaCO_3$. Arthropods have the most complex of invertebrate integuments, in part because their integument is a specialized exoskeleton.

THE INTEGUMENTARY SYSTEM OF VERTEBRATES

Skin is the vertebrate integument. It is the largest organ (with respect to surface area) of the vertebrate body and grows with the animal. Skin has two main layers. As in invertebrates, the epidermis is the outermost layer of epithelial tissue and is one to several cells thick. The **dermis** (Gr. *derma*, hide, skin) is a thicker layer of connective tissue beneath the epidermis. A **hypodermis** ("below the skin"), consisting of loose connective tissue, adipose tissue, and nerve endings, separates the skin from deeper tissues.

The Skin of Jawless Fishes

Jawless fishes, such as lampreys and hagfishes, have relatively thick skin (figure 23.3). Of the several types of epidermal glandular cells that may be present, one secretes a protective cuticle. In hagfishes, multicellular slime glands produce large amounts of mucous slime that covers the body surface. This slime protects the animals from external parasites and has earned hagfishes the descriptive name "slime eels."

The Skin of Cartilaginous Fishes

The skin of cartilaginous fishes (e.g., sharks) is multilayered and contains mucous and sensory cells (figure 23.4). The dermis contains bone in the form of small placoid scales called **denticles** (L. *denticulus*, little teeth). Denticles contain blood vessels and nerves and are similar to vertebrate teeth. Because cartilaginous fishes grow throughout life, the skin area also increases. New denticles are produced to maintain enough of these protective structures at the skin surface. Like teeth, once denticles reach maturity, they do not grow; thus, they continually wear down and are lost. Since denticles project above the surface of the skin, they give cartilaginous fishes a sandpaper texture.

The Skin of Bony Fishes

The skin of bony fishes (teleosts) contains **scales** (Fr. *escale*, shell, husk) composed of dermal bone. A thin layer of dermal tissue overlaid by the superficial epidermis normally covers scales (figure 23.5). Because scales are not shed, they grow at the margins and over the lower surface. In many bony fishes, growth lines, which are useful in determining the age of a fish, can often be detected. The skin of bony fishes is permeable and functions in gas exchange, particularly in the smaller fishes that have a large skin surface area relative to body volume. The dermis is richly supplied with capillary beds to facilitate its use in respiration. The epidermis also contains many mucous glands. Mucus production helps prevent bacterial and fungal infections, and it reduces friction as the fish swims. Some species have granular glands that secrete an irritating—or to some species, poisonous—alkaloid. Many teleosts that live in deep aquatic habitats have photophores that facilitate species recognition or act like lures and warning signals.

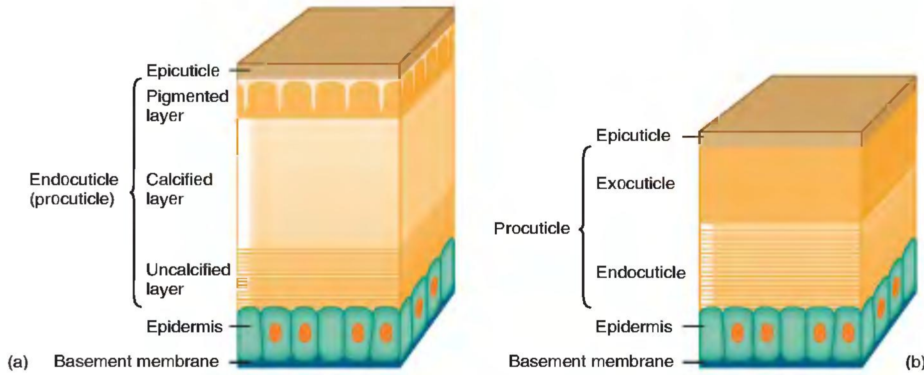


FIGURE 23.2

Cuticles. The cuticles of *(a)* a crustacean and *(b)* an insect. The underlying epidermis secretes the cuticles of both groups of animals. *From: "A LIFE OF INVERTEBRATES" © 1979 W. D. Russell-Hunter.*

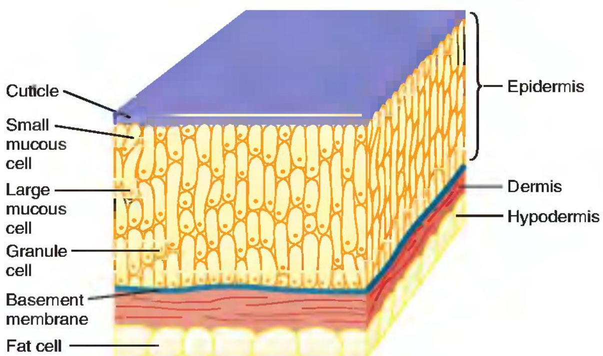


FIGURE 23.3

Skin of Jawless Fishes. The skin of an adult lamprey has a multilayered epidermis with glandular cells and fat storage cells in the hypodermis.

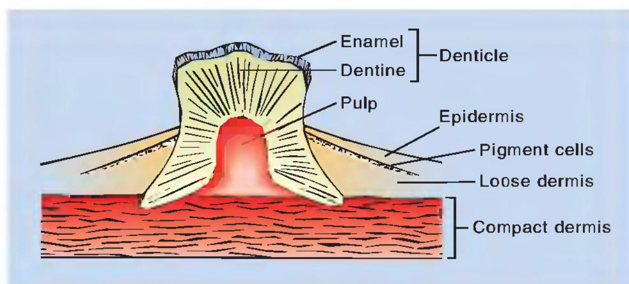


FIGURE 23.4

Skin of Cartilaginous Fishes. Shark skin contains toothlike denticles that become exposed through loss of the epidermal covering. The skin is otherwise fishlike in structure.

The Skin of Amphibians

Amphibian skin consists of a stratified epidermis and a dermis containing mucous and serous glands plus pigmentation cells (figure 23.6). ***Phylogenetically, amphibians are transitional between aquatic and terrestrial vertebrates. The earliest amphibians were covered by dermal bone scales like their fish ancestors.*** Three problems associated with terrestrial environments are desiccation, the damaging effects of ultraviolet light, and physical abrasion. During amphibian evolution, keratin production increased in the outer layer of skin cells. (Keratin is a tough, impermeable protein that protects the skin in the physically abrasive, rigorous terrestrial environment.) The increased keratin in the skin also protects the cells, especially their nuclear material, from ultraviolet light. The mucus that mucous glands produce helps prevent desiccation, facilitates gas exchange when the skin is used as a respiratory organ, and makes the body slimy, which facilitates escape from predators.

Within the dermis of some amphibians are poison glands that produce an unpleasant-tasting or toxic fluid that acts as a predator deterrent. Sensory nerves penetrate the epidermis as free nerve endings. Interestingly, the "warts" of toads seem to be specialized sensory structures, since they contain many sensory cells.

The Skin of Reptiles

The skin of reptiles reflects their greater commitment to a terrestrial existence. The outer layer of the epidermis (stratum corneum) is thick (figure 23.7), lacks glands, and is modified into keratinized scales, scutes (thick scales) in snakes and turtles, beaks in turtles, rattles on snakes, and claws, plaques, and spiny crests on most other reptiles. This thick, keratinized layer resists abrasion, inhibits dehydration, and protects like a suit of armor. During shedding or molting of the skin of many reptiles (e.g., snakes and lizards), the old outer layer separates from newly formed epidermis. Diffusion of fluid between the layers aids this separation.

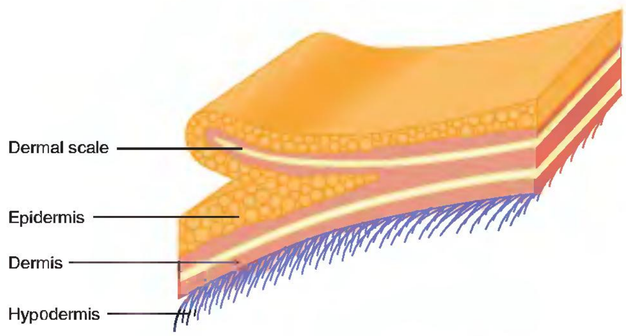


FIGURE 23.5

Skin of Bony Fishes. The skin of a typical bony fish has overlapping scales (two are shown here). The scales are layers of collagenous fibers covered by a thin, flexible layer of bone.

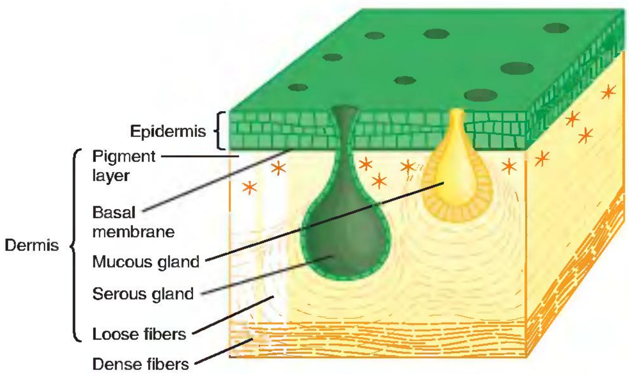


FIGURE 23.6

Skin of Amphibians. Frog skin has a stratified epidermis and several types of glands in the dermis. Notice the pigment layer in the upper part of the dermis.

The Skin of Birds

The skin of birds shows many typically reptilian features with no epidermal glands (the only epidermal gland of birds is the uropygial or preen gland). Over most of the bird's body, the epidermis is usually thin and only two or three cell layers thick (figure 23.8). Indeed, the term "thin skinned," sometimes applied figuratively to humans, is literal when applied to birds. The outer keratinized layer is often quite soft. The most prominent parts of the epidermis are the feathers. ***Feathers are derived from the scales of reptilian ancestors and are the most complex of all the deriviates of the vertebrate stratum corneum*** (see figure 21.4).

The dermis of birds is similar in structure to that of reptiles and contains blood and lymphatic vessels, nerves, and epidermally derived sensory bodies. Air spaces that are part of the avian respiratory system extend into the dermis. These air spaces are involved in thermal regulation. Associated with the feathers and their normal functioning is an incredibly complicated array of dermal smooth-muscle fibers that control the position of the feathers.

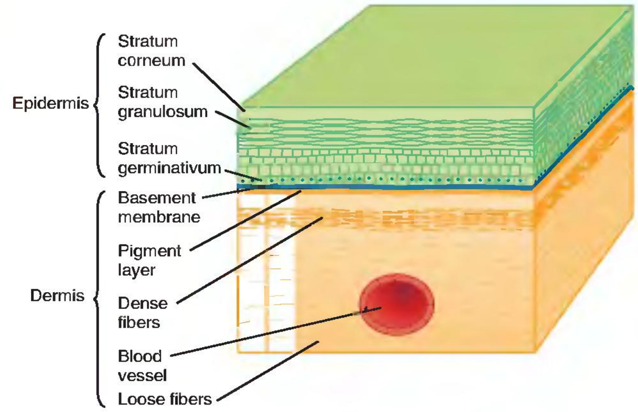


FIGURE 23.7

Skin of Reptiles. Lizard skin has the heavily keratinized outer epidermis (scales) characteristic of reptiles. Notice the absence of integumentary glands, making reptilian skin exceptionally dry.

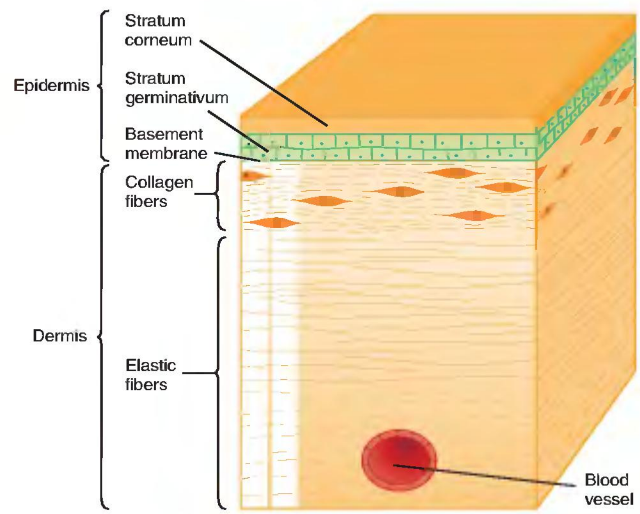


FIGURE 23.8

Skin of Birds. Bird skin has a relatively soft and thin epidermis with no epidermal glands.

Feather position is important in thermal regulation, flying, and behavior. Aquatic birds may also have fat deposits in the hypodermal layer that store energy and help insulate the body.

The Skin of Mammals

The notable features of mammalian skin are: (1) hair; (2) a greater variety of epidermal glands than in any other vertebrate class; (3) a highly stratified, cornified epidermis; and (4) a dermis many times thicker than the epidermis.

The epidermis of mammalian skin is composed of stratified squamous epithelium and consists of several layers of a variety of

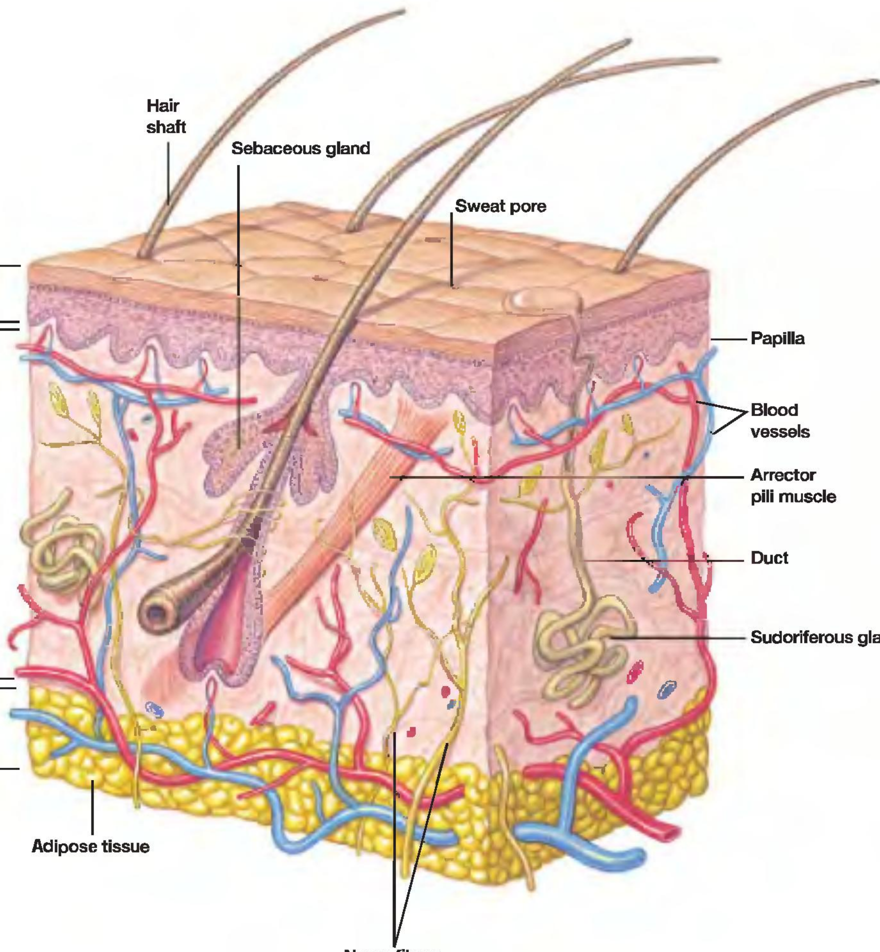


FIGURE 23.9
Skin of Mammals. Notice the various structures in the dermis of human skin.

cells. Rapid cell divisions in the deepest layer of the epidermis push cells toward the surface of the skin. As cells progress toward the surface, they die and become keratinized (contain the protein keratin). Keratinized cells make up the outer skin layer, called the stratum corneum. Because keratin is virtually insoluble in water, the stratum corneum prevents dehydration and is a first line of defense against many toxic substances and microorganisms. ***The prevention of dehydration is one of the evolutionary reasons mammals and other animals have been able to colonize terrestrial environments.***

The thickest portion of mammalian skin is composed of dermis, which contains blood vessels, lymphatic vessels, nerve endings, hair follicles, small muscles, and glands (figure 23.9). A special tanning process makes leather from the dermal layer of mammalian skin.

The hypodermis underneath the dermis is different from that of other vertebrate classes in that it consists of loose connective tissue, adipose tissue, and skeletal muscles. Adipose tissue stores energy in the form of fat and provides insulation in cold environments. Skeletal muscle allows the skin above it to move somewhat independently of underlying tissues. Blood vessels thread from the hypodermis to the dermis and are absent from the epidermis.

In humans and a few other animals (e.g., horses), the skin regulates body temperature by opening and closing sweat pores and perspiring or sweating. The skin screens out excessive harmful ultraviolet rays from the sun, but it also lets in some necessary rays that convert a chemical in the skin into vitamin D. The skin is also an important sense organ, containing sensory receptors for heat, cold, touch, pressure, and pain. Its many nerve endings keep the animal responsive to potentially harmful factors in the environment.

The skin of humans and other mammals contains several types of glands. **Sudoriferous glands** (L. *sudor*, sweat), also called sweat glands, are distributed over most of the human body surface (figure 23.9). These glands secrete sweat by a process called **perspiration** (L. *per*, through + *spirare*, to breathe). Perspiration helps to regulate body temperature and maintain homeostasis, largely by the cooling effect of evaporation. In some mammals, certain sweat glands also produce pheromones. (A pheromone is a chemical that an animal secretes and that communicates with other members of the same species to elicit certain behavioral responses.) **Sebaceous (oil) glands** (L. *sebum*, tallow or fat) are simple glands connected to hair follicles in the dermis (figure 23.9). They lubricate and protect by secreting **sebum.** Sebum is a permeability barrier, an emollient (skin-softening agent), and a protective agent against microorganisms. Sebum can also act as a pheromone.

Mammalian skin color is due either to pigments or to anatomical structures that absorb or reflect light. Pigments (e.g., melanin in human skin) are within the cells of the epidermal layer, in hair, or in specialized cells called chromatophores. Some skin color is due to the color of blood in superficial blood vessels reflected through the epidermis. Bright skin colors in venomous, toxic, or bad-tasting animals may deter potential predators. Other skin colors may camouflage the animal. In addition, colors serve in social communication, helping members of the same species to identify each other, their sex, reproductive status, or social rank.

Hair is composed of keratin-filled cells that develop from the epidermis. The portion of hair that protrudes from the skin is the hair shaft, and the portion embedded beneath the skin is the root (figure 23.9). An arrector pili muscle (smooth muscle; involuntary muscle) attaches to the connective-tissue sheath of a hair follicle surrounding the bulb of the hair root. When this muscle contracts, it pulls the follicle and its hair to an erect position. In humans, this is referred to as a "goose bump." In other mammals, this action helps warm the animal by producing an insulating layer of warm air between the erect hair and skin. If hair is erect because the animal is frightened instead of cold, the erect hair also makes the animal look larger and less vulnerable to attack.

Nails, like hair, are modifications of the epidermis. Nails are flat, horny plates on the dorsal surface of the distal segments of the digits (e.g., fingers and toes of primates). Other mammals have **claws** and hooves *(see figure 22.7)*. Other keratinized derivatives of mammalian skin are **horns** (not to be confused with bony antlers) and the **baleen plates** of the toothless whales.

MOVEMENT AND SUPPORT: SKELETAL SYSTEMS

As organisms evolved from the ancestral protists to the multicellular animals, body size increased dramatically. Systems involved in movement and support evolved simultaneously with the increase in body size.

Four cell types contribute to movement: (1) amoeboid cells, (2) flagellated cells, (3) ciliated cells, and (4) muscle cells. With respect to support, organisms have three kinds of skeletons: (1) fluid hydrostatic skeletons, (2) rigid exoskeletons, and (3) rigid endoskeletons. These skeletal systems also function in animal movement that requires muscles working in opposition (antagonism) to each other.

THE SKELETAL SYSTEM OF INVERTEBRATES

Many invertebrates use their body fluids for internal support. For example, sea anemones (figure 23.10*a*) and earthworms have a form of internal support called the hydrostatic skeleton.

Hydrostatic Skeletons

The **hydrostatic** (Gr. *hydro*, water + *statikos*, to stand) **skeleton** is a core of liquid (water or a body fluid such as blood) surrounded by a tension-resistant sheath of longitudinal and/or circular muscles. It is similar to a water-filled balloon because the force exerted against the incompressible fluid in one region can be transmitted to other regions. Contracting muscles push against a hydrostatic skeleton, and the transmitted force generates body movements, as the movement of a sea anemone illustrates (figure 23.10*b,c*). Another example is the earthworm, *Lumbricus terrestris*. It contracts its longitudinal and circular muscles alternately, creating a rhythm that moves the earthworm through the soil. In both of these examples, the hydrostatic skeleton keeps the body from collapsing when its muscles contract.

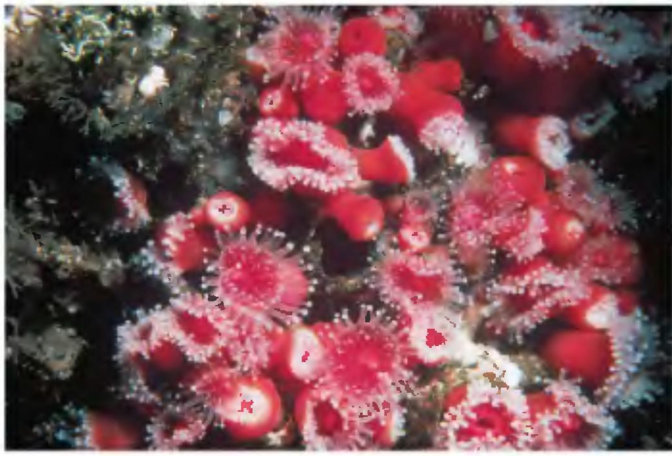
The invertebrate hydrostatic skeleton can take many forms and shapes, such as the gastrovascular cavity of acoelomates, a rhynchocoel in nemertines, a pseudocoelom in aschelminths, a coelom in annelids, or a hemocoel in molluscs. *Overall, the hydrostatic skeleton of invertebrates is an excellent example of adaptation of major body functions to this simple but efficient principle of hydrodynamics—use of the internal pressure of body fluids.*

Exoskeletons

Rigid **exoskeletons** (Gr. *exo*, outside + skeleton) also have locomotor functions because they provide sites for muscle attachment and counterforces for muscle movements. Exoskeletons also support and protect the body, but these are secondary functions.

In arthropods, the epidermis of the body wall secretes a thick, hard cuticle that waterproofs the body *(see figure 14.3)*. The cuticle also protects and supports the animal's soft internal organs. In crustaceans (e.g., crabs, lobsters, shrimp), the exoskeleton contains calcium carbonate crystals that make it hard and inflexible—except at the joints. Besides providing shieldlike protection from enemies and resistance to general wear and tear, the exoskeleton also prevents internal tissues from drying out. *This important evolutionary adaptation contributed to arthropods' successful colonization of land. Exoskeletons, however, limit an animal's growth.* Some animals shed the exoskeleton periodically, as arthropods do when they molt (figure 23.11*a*).

Certain regions of the arthropod body have thin, flexible cuticle, and joints (articulations) are usually in these areas (figure 23.11*b*). It is in these areas that pairs of antagonistic muscles



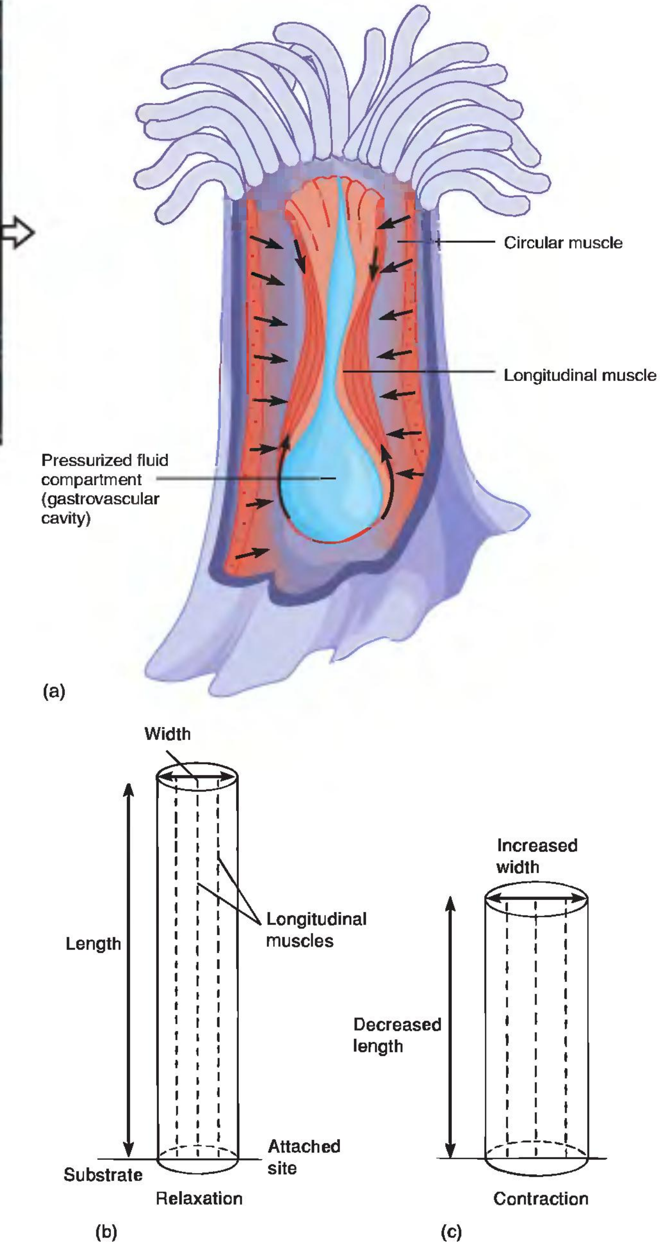


FIGURE 23.10

Hydrostatic Skeletons. *(a)* The hydrostatic skeleton of sea anemones *(Corynactis californic)* allows them to shorten or close when longitudinal muscles contract, or to lengthen or open when circular muscles contract. *(b,c)* How a hydrostatic skeleton changes an invertebrate's shape with only longitudinal muscles. Because the fluid volume is constant, a change (increase) in width must accompany a change (decrease) in length.

function through a system of levers to produce coordinated movement. Interestingly, some arthropod joints (e.g., the wing joints of flying beetles and the joints of fleas involved in jumping) possess a highly elastic protein called "animal rubber," or resilin. Resilin stores energy on compression and then releases the energy to produce movement (*see figure 23.23*). ***From an evolutionary perspective, the development of a jointed, flexible exoskeleton that permitted flight is one of the reasons for the success of arthropods.***

Endoskeletons

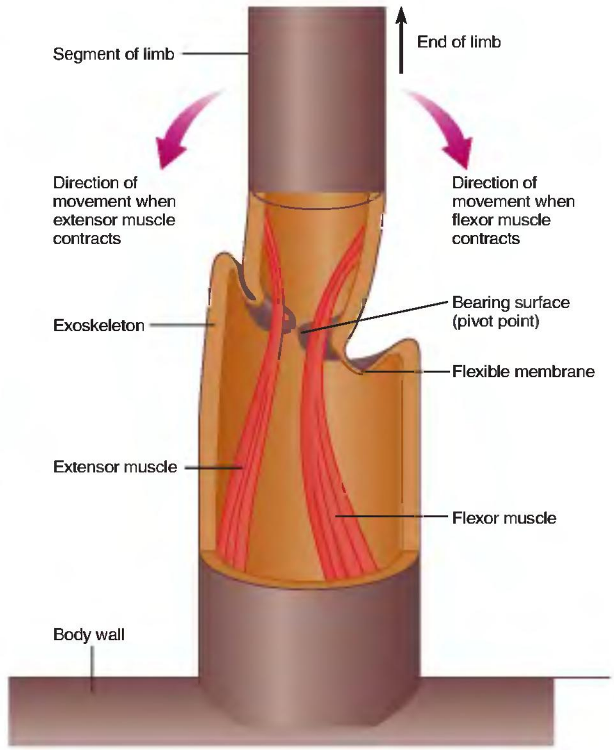
Like the term implies, other body tissues enclose **endoskeletons** (Gr. *endo,* within + skeleton). For example, the endoskeletons of sponges consist of mineral spicules and fibers of spongin that keep the body from collapsing *(see figure 9.5)*. Since adult sponges attach to the substrate, they have no need for muscles attached to the endoskeleton. Similarly, the endoskeletons of echinoderms (sea stars, sea urchins) consist of small, calcareous plates called ossicles. The most familiar endoskeletons, however, are in vertebrates and are discussed under "The Skeletal System of Vertebrates."

Mineralized Tissues and the Invertebrates

Hard, mineralized tissues are not unique to the vertebrates. In fact, over two-thirds of the living species of animals that contain mineralized tissues are invertebrates. Most invertebrates have inorganic calcium carbonate crystals embedded in a collagen matrix. (Vertebrates have calcium phosphate crystals.) Bone, dentin, cartilage, and enamel were all present in Ordovician ostracoderms *(see figure 18.3)*.

Cartilage is the supportive tissue that makes up the major skeletal component of some gastropods, invertebrate chordates (amphioxus), jawless fishes such as hagfishes and lampreys, and sharks and rays. Since cartilage is lighter than bone, it gives these predatory fishes the speed and agility to catch prey. It also provides buoyancy without the need for a swim bladder.

(a)



(b)

FIGURE 23.11

Exoskeletons. *(a)* A cicada nymph *(Platypedia)* leaves its old exoskeleton as it molts. This exoskeleton provides external support for the body and attachment sites for muscles. *(b)* In an arthropod, muscles attach to the interior of the exoskeleton. In this articulation of an arthropod limb, the cuticle is hardened everywhere except at the joint, where the membrane is flexible. Notice that the extensor muscle is antagonistic to (works in an opposite direction than) the flexor muscle. *(b) Source: After Russell-Hunter.*

THE SKELETAL SYSTEM OF VERTEBRATES

The vertebrate skeletal system is an endoskeleton enclosed by other body tissues. This endoskeleton consists of two main types of supportive tissue: cartilage and bone.

Cartilage

Cartilage is a specialized type of connective tissue that provides a site for muscle attachment, aids in movement at joints, and provides support *(see figure 2.24 h–j)*. Like other connective tissues, it consists of cells (chondrocytes), fibers, and a cellular matrix.

Bone or Osseous Tissue

Bone (osseous) tissue is a specialized connective tissue that provides a point of attachment for muscles and transmits the force of muscular contraction from one part of the body to another during movement (figure 23.12*a*). In addition, bones of the skeleton support the internal organs of many animals, store reserve calcium and phosphate, and manufacture red blood cells and some white blood cells.

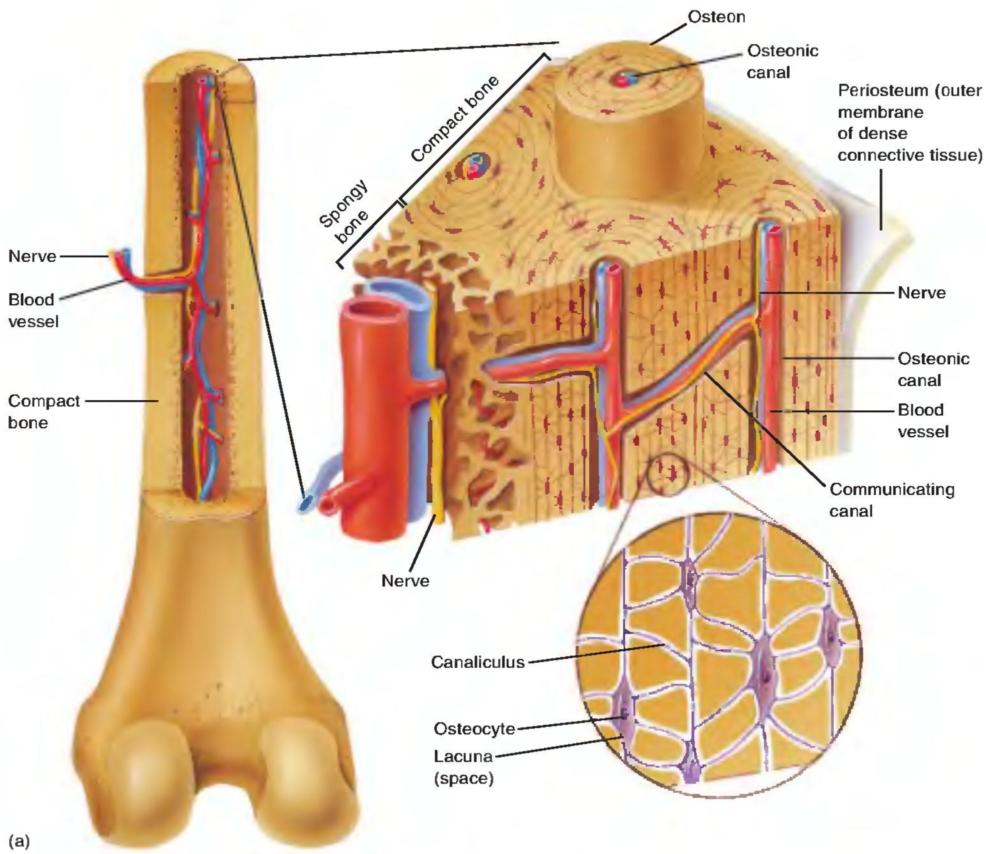
Bone tissue is more rigid than other connective tissues because its homogeneous, organic ground substance also contains inorganic salts—mainly calcium phosphate and calcium carbonate. When an animal needs the calcium or phosphate stored within bones, metabolic reactions (under endocrine control) release the required amounts.

Bone cells (osteocytes) are in minute chambers called lacunae (sing., lacuna), which are arranged in concentric rings around osteonic canals (formerly called Haversian systems) (figure 23.12*b*). These cells communicate with nearby cells by means of cellular processes passing through small channels called canaliculi (sing., canaliculus).

The Skeleton of Fishes

Both cartilaginous and bony endoskeletons first appeared in the vertebrates. Since water has a buoyant effect on the fish body, the requirement for skeletal support is not as demanding in these vertebrates as it is in terrestrial vertebrates. Although most vertebrates have a well-defined vertebral column (the reason they are called "vertebrates"), the jawless vertebrates do not. For example, lampreys only have isolated cartilaginous blocks along the notochord, and hagfishes do not even have these.

Most jawed fishes have an axial skeleton (so named because it forms the longitudinal axis of the body) that includes a notochord, ribs, and cartilaginous or bony vertebrae (figure 23.13). Muscles used in locomotion attach to the axial skeleton.




(b)

FIGURE 23.12

Bone. *(a)* Structural organization of a long bone (femur) of mammals. Compact bone is composed of osteons connected together. Spongy bone is latticelike rather than dense. *(b)* Single osteon in compact bone (SEM ×450). *(b) Copyright by Richard G. Kessel and Randy H. Kardon,* Tissues and Organs: A Text-Atlas of Scanning Electron Microscopy, *1979, W.H. Freeman and Company. All rights reserved.*

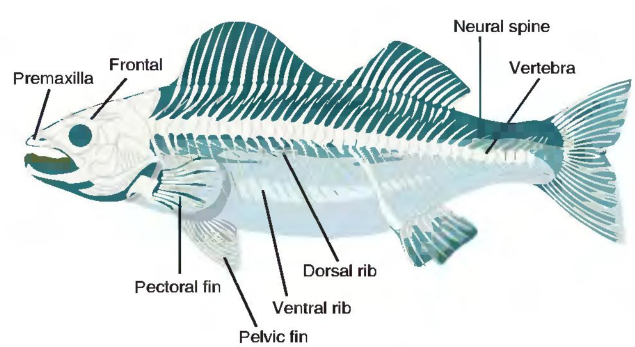


FIGURE 23.13

Fish Endoskeleton. Lateral view of the perch skeleton.

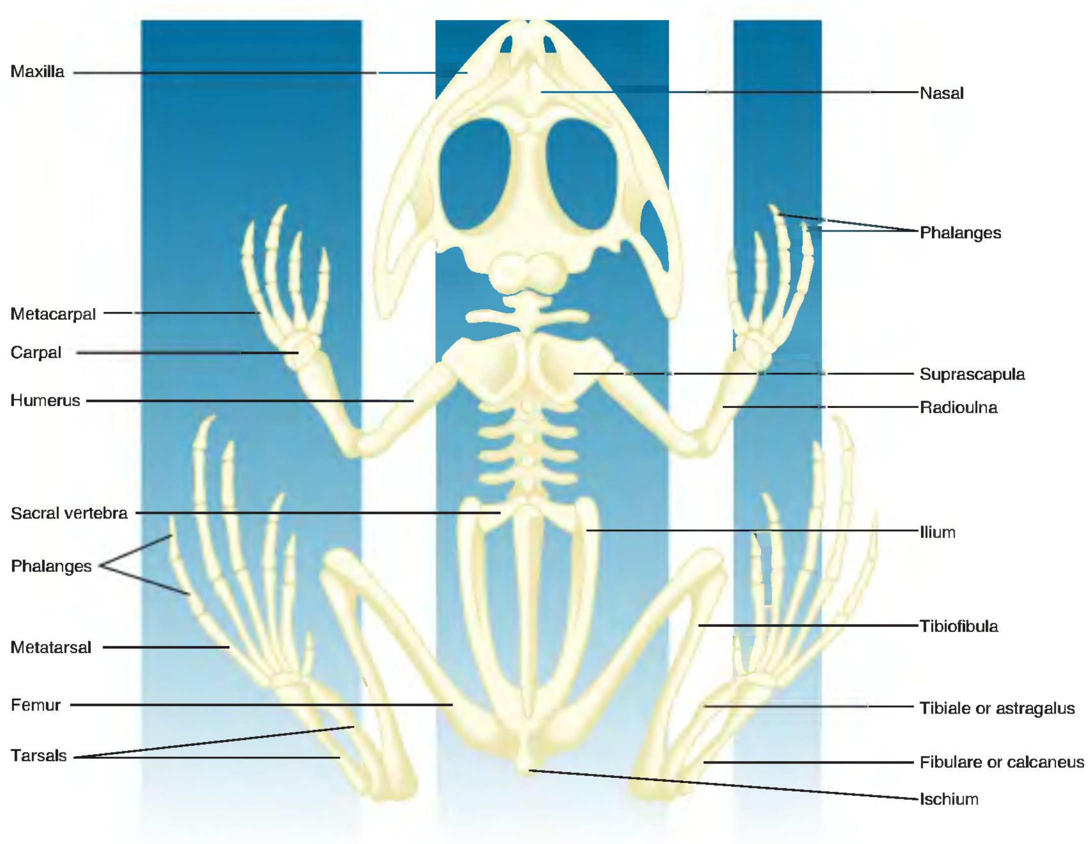


FIGURE 23.14

Tetrapod Endoskeleton. Dorsal view of the frog skeleton.

The Skeleton of Tetrapods

Tetrapods must lift themselves to walk on land. The first amphibians needed support to replace the buoyancy of water. *For the earliest terrestrial animals, support and locomotion were difficult and complicated processes. Adaptations for support and movement on land occurred over a period of approximately 200 million years.* During this evolution, the tetrapod endoskeleton became modified for support on land (figure 23.14). This added support resulted from the specializations of the intervertebral disks that articulate with adjoining vertebrae. The intervertebral disks help hold the vertebral column together, and they also absorb shock and provide joint mobility. Bone replaced cartilage in the ribs, which became more rigid. The various types of connective tissue that connect to the axial skeleton helped keep elevated portions from sagging. Appendages became elongated for support on a hard surface, and changes in the shoulder enabled the neck to move more freely.

The Human Endoskeleton

The human endoskeleton has two major parts: the axial skeleton and the appendicular skeleton. The **axial skeleton** is made up of the skull, vertebral column, sternum, and ribs. The **appendicular skeleton** is composed of the appendages, the pectoral girdle, and the pelvic girdles. These girdles attach the upper and lower appendages to the axial skeleton.

MOVEMENT: NONMUSCULAR MOVEMENT AND MUSCULAR SYSTEMS

Movement is a characteristic of certain cells, protists, and animals. For example, certain white blood cells, coelomic cells, and protists such as *Amoeba* utilize nonmuscular amoeboid movement. Amoeboid movement also occurs in embryonic tissue movements, in wound healing, and in many cell types growing in tissue

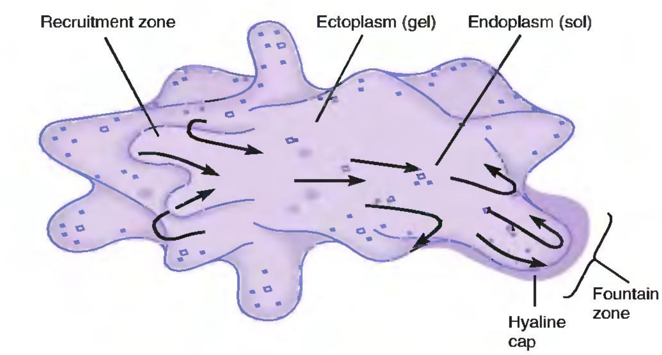


FIGURE 23.15

Mechanism of Amoeboid Movement. Endoplasm (sol) flows into an advancing pseudopodium. At the tip (fountain zone) of the pseudopodium, endoplasm changes into ectoplasm (gel). At the opposite end (recruitment zone) of the amoeba, ectoplasm changes into endoplasm and begins flowing in the direction of movement.

culture. Other protists and some invertebrates utilize cilia or flagella for movement. Muscles and muscle systems are found in various invertebrate groups from the primitive cnidarians to the arthropods (e.g., insect flight muscles). In more complex animals, the muscles attach to exo- and endoskeletal systems to form a motor system, which allows complex movements.

NONMUSCULAR MOVEMENT

Nearly all cells have some capacity to move and change shape due to their cytoskeleton (*see figure 2.19*). *It is from this basic framework of the cell that specialized contractile mechanisms emerged.* For example, protozoan protists move by means of specific nonmuscular structures (pseudopodia, flagella, or cilia) that involve the contractile proteins, actin and myosin. *Interactions between these proteins are also responsible for muscle contraction in animals, and the presence of actin and myosin in protozoa and animals is evidence of evolutionary ties between the two groups.*

Amoeboid Movement

As the name suggests, **amoeboid movement** was first observed in *Amoeba*. The plasma membrane of an amoeba has adhesive properties since new **pseudopodia** (sing., pseudopodium) (Gr. *pseudes*, false + *podion*, little foot) attach to the substrate as they form. The plasma membrane also seems to slide over the underlying layer of cytoplasm when an amoeba moves. The plasma membrane may be "rolling" in a way that is (roughly) analogous to a bulldozer track rolling over its wheels. A thin fluid layer between the plasma membrane and the ectoplasm may facilitate this rolling.

As an amoeba moves, the fluid endoplasm flows forward into the fountain zone of an advancing pseudopodium. As it reaches the tip of a pseudopodium, endoplasm changes into ectoplasm. At the same time, ectoplasm near the opposite end in the recruitment zone changes into endoplasm and begins flowing forward (figure 23.15).

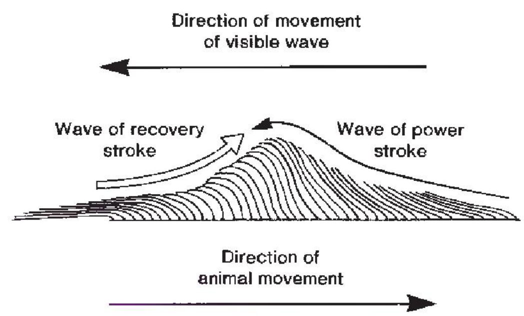


FIGURE 23.16

Ciliary Movement. A metachronal (coordinated) wave passing along a row of cilia.

Ciliary and Flagellar Movement

With the exception of the arthropods, locomotor cilia and flagella occur in every animal phylum. Structurally, **cilia** (sing., cilium) (L. "eyelashes") and **flagella** (sing., flagellum) (L. "small whips") are similar, but cilia are shorter and more numerous, whereas flagella are long and generally occur singly or in pairs.

Ciliary movements are coordinated. For example, in some ciliated protozoa, pairs of cilia occur in rows. Rows of cilia beat slightly out of phase with one another so that ciliary waves periodically pass over the surface of the protozoan (figure 23.16). In fact, many ciliates can rapidly reverse the direction of ciliary beating, which changes the direction of the ciliary waves and the direction of movement.

The epidermis of free-living flatworms (e.g., turbellarians) and nemertines is abundantly ciliated. The smallest specimens (about 1 mm long) lie at the upper end of the size range for efficient locomotion using cilia. Larger flatworms (e.g., triclads and polyclads) have retained **ciliary creeping** as the principal means of locomotion, and the largest animals to move by ciliary creeping are the nemertines. The muscular activities of the flatworms and nemertines are varied and involve pedal locomotion, peristalsis, or looping movements with anterior and posterior adhesion. *Since ciliary and muscular means of movement (locomotion) coexist in some free-living flatworms and nemertines, the transition from ciliary to muscular locomotion is likely to have taken place among the flatworm-like ancestors.*

AN INTRODUCTION TO ANIMAL MUSCLES

Muscular tissue is the driving force, the power behind movement in most invertebrates and vertebrates. The basic physiological property of muscle tissue is contractility, the ability to contract or shorten. In addition, muscle tissue has three other important properties: (1) excitability (or irritability), the capacity to receive and respond to a stimulus; (2) extensibility, the ability to be stretched; and (3) elasticity, the ability to return to its original shape after being stretched or contracted.

Animals may have one or more of the following types of muscle tissue: smooth, cardiac, and skeletal. The contractile cells of these tissues are called **muscle fibers.**

Smooth muscle is also called involuntary muscle because higher brain centers do not control its contractions. Smooth-muscle fibers have a single nucleus, are spindle shaped, and are arranged in a parallel pattern to form sheets *(see figure 2.24p)*. Smooth muscle maintains good tone (a normal degree of vigor and tension) even without nervous stimulation. It contracts slowly, but it can sustain prolonged contractions and does not fatigue (tire) easily.

Smooth muscle is the predominant muscle type in many invertebrates. For example, it forms part of the adductor ("catch") muscles that close the valves of clams and other bivalve molluscs. These smooth muscles give bivalves the ability to "clam up" against predators for days with little or no energy expenditure.

Striated muscle fibers (cells) with single nuclei are common in invertebrates, but they occur in adult vertebrates only in the heart, where they are called cardiac muscle. **Cardiac muscle** fibers are involuntary, have a single nucleus, are striated (have dark and light bands), and are branched *(see figure 2.24q)*. This branching allows the fibers to interlock for greater strength during contraction. Hearts do not fatigue because cardiac fibers relax completely between contractions.

Skeletal muscle, also a striated muscle, is a voluntary muscle because the nervous system consciously controls its contractions. Skeletal muscle fibers are multinucleated and striated *(see figure 2.24o)*. Skeletal muscles attach to skeletons (both endo- and exoskeletons). When skeletal muscles contract, they shorten. Thus, muscles can only pull; they cannot push. Therefore, skeletal muscles work in antagonistic pairs. For example, one muscle of a pair bends (flexes) a joint and brings a limb close to the body. The other member of the pair straightens (extends) the joint and extends the limb away from the body *(see figure 23.11b)*.

THE MUSCULAR SYSTEM OF INVERTEBRATES

A few functional differences among invertebrate muscles indicate some of the differences from the vertebrate skeletal muscles (discussed next). In arthropods, at least two motor nerves innervate a typical muscle fiber. One motor nerve fiber causes a fast contraction and the other a slow contraction. Another variation occurs in certain insect (bees, wasps, flies, beetles) flight muscles. These muscles are called asynchronous muscles, since the upward wing movement (rather than a nerve impulse) activates the muscles that produce the downstroke. In the midge (a dipteran related to the fly/mosquito), for example, this can happen a thousand times a second.

An understanding of the structure and function of invertebrate locomotion (movement) is crucial to an understanding of the evolutionary origins of the various invertebrate groups. Discussion of several types of invertebrate locomotion that involve muscular systems follows.

The Locomotion of Soft-Bodied Invertebrates

Many soft-bodied invertebrates can move over a firm substratum. For example, flatworms, some cnidarians, and the gastropod molluscs move by means of waves of activity in the muscular system that are applied to the substrate. This type of movement is called **pedal locomotion.** Pedal locomotion can be easily seen by examining the undersurface of a planarian or a snail while it crawls along a glass plate. In the land snail *Helix*, several waves cross the length of the foot simultaneously, each moving in the same direction as the locomotion of the snail, but at a greater rate.

Many large flatworms and most nemertine worms exhibit a muscular component to their locomotion. In this type of movement, alternating waves of contraction of circular and longitudinal muscles generate peristaltic waves, which enhance the locomotion that the surface cilia also provide. This system is most highly developed in the septate coelomate worms, especially earthworms (figure 23.17).

Leeches and some insect larvae exhibit **looping movements.** Leeches have anterior and posterior suckers that provide alternating temporary points of attachment (figure 23.18*a*). Lepidopteran caterpillars exhibit similar locomotion, in which arching movements are equivalent to the contraction of longitudinal muscles (figure 23.18*b*).

Polychaete worms move by the alternate movement of multiple limbs (parapodia), the tips of which move backward relative to the body; however, since the tips attach to the ground, the body of the worm moves forward (figure 23.19).

The **water-vascular system** of echinoderms provides a unique means of locomotion. For example, sea stars typically have five arms, with a water-vascular canal in each. Along each canal are reservoir ampullae and tube feet (figure 23.20*a,b*). Contraction of the muscles comprising the ampullae drives water into the tube feet, whereas contraction of the tube feet moves water into the ampullae. Thus, the tube feet extend by hydraulic pressure and can perform simple steplike motions (figure 23.20*c*).

Terrestrial Locomotion in Invertebrates: Walking

Invertebrates (terrestrial arthropods) living in/on terrestrial environments are much denser than the air in which they live. As a result, they require structural support, and those that move quickly make use of rigid skeletal elements that interact with the ground. These elements include flexible joints, tendons, and muscles that attach to a rigid cuticle and form limbs. The walking limbs of the most highly evolved arthropods (Crustacea, Chelicerata, and Uniramia) are remarkably uniform in structure. The limbs are composed of a series of jointed elements that become progressively less massive toward the tip (figure 23.21*a*). Each joint is articulated to allow movement in only one plane. These limb joints allow extension (a motion that increases the angle of a joint) and flexion (a motion that decreases the angle of a joint) of the limb. The limb plane at the basal joint with the body can also rotate, and this rotation is responsible for forward movement. The body is typically carried slung between the laterally projected

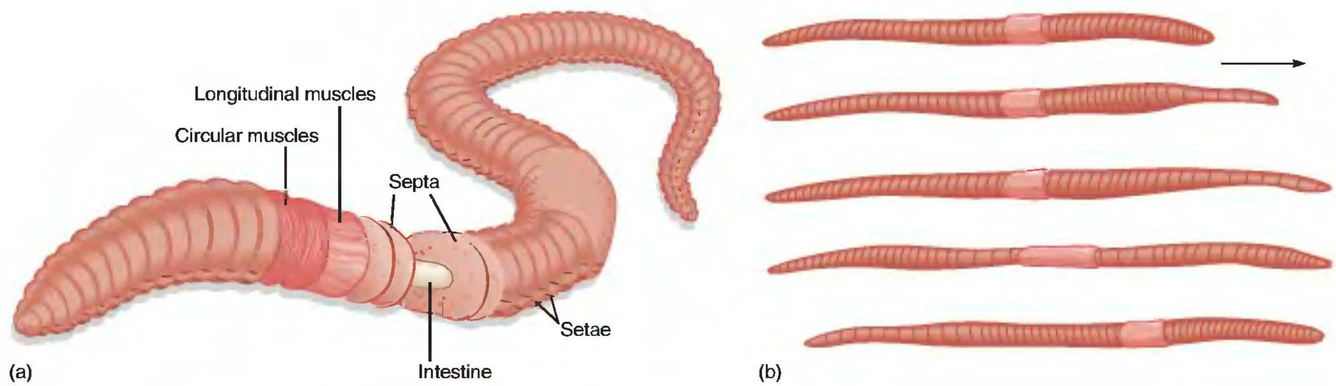


FIGURE 23.17

Successive Stages in Earthworm Movement. *(a)* When the longitudinal muscles contract and the circular muscles relax, the segments of the earthworm bulge and are stationary with respect to the ground. *(b)* In front of each region of longitudinal muscle contraction, circular muscles contract, causing the segments to elongate and push forward. Contraction of longitudinal muscles in segments behind a bulging region cause those segments to be pulled forward. For reasons of simplification, setae movements are not shown.

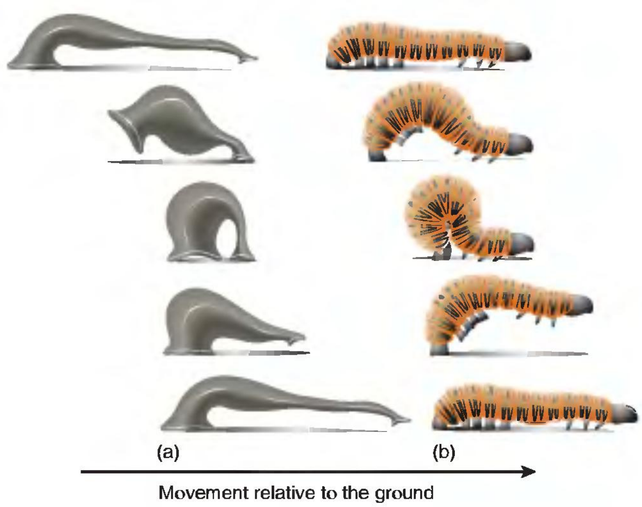


FIGURE 23.18

Looping Movements. *(a)* Leeches have anterior and posterior suckers, which they altenately attach to the substrate in looping movements to move forward. *(b)* Some insect larvae, such as lepidopteran caterpillars, exhibit similar movements. The caterpillar uses arching movements to move forward.

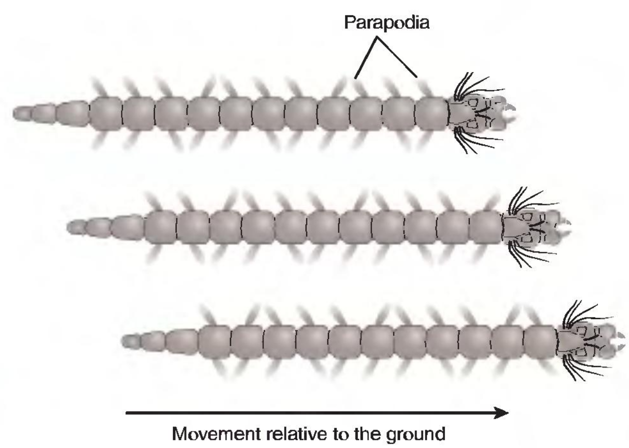


FIGURE 23.19

Locomotion in a Polychaete. When a polychaete (e.g., *Nereis*) crawls slowly, the tips of the multiple limbs (parapodia) move backward relative to the body. Since the tips of the parapodia touch the ground, this moves the body forward. In addition, a coordinated wave of activity in the parapodia passes forward from the tail to the head, with the left and right parapodia being exactly one-half wavelength out of phase. This ensures that each parapodium executes its power stroke without interfering with the parapodium immediately posterior. For simplification, setae movements are not shown.

limbs (figure 23.21*b*), and walking movements do not involve raising or lowering the body. Depending on the arthropod, the trajectory of each limb is different and nonoverlapping (figure 23.22). Most arthropods walk forward, rotating the basal joint of the limb relative to the body, but crabs walk in a sideways fashion.

Terrestrial Locomotion in Invertebrates: Flight

The physical properties (e.g., strengthening so that the exoskeleton does not deform under muscle contraction) of an arthropod cuticle are such that true flight evolved for the pterygote insects some 200 million years ago. Since then, the basic mechanism of flight has been modified. Consequently, present-day insects exhibit a wide range of structural adaptations and mechanisms for flight *(see figure 15.5)*.

Terrestrial Locomotion in Invertebrates: Jumping

Some insects (fleas, grasshoppers, leafhoppers) can jump. Most often, this is an escape reaction. To jump, an insect must exert a force against the ground sufficient to impart a takeoff velocity

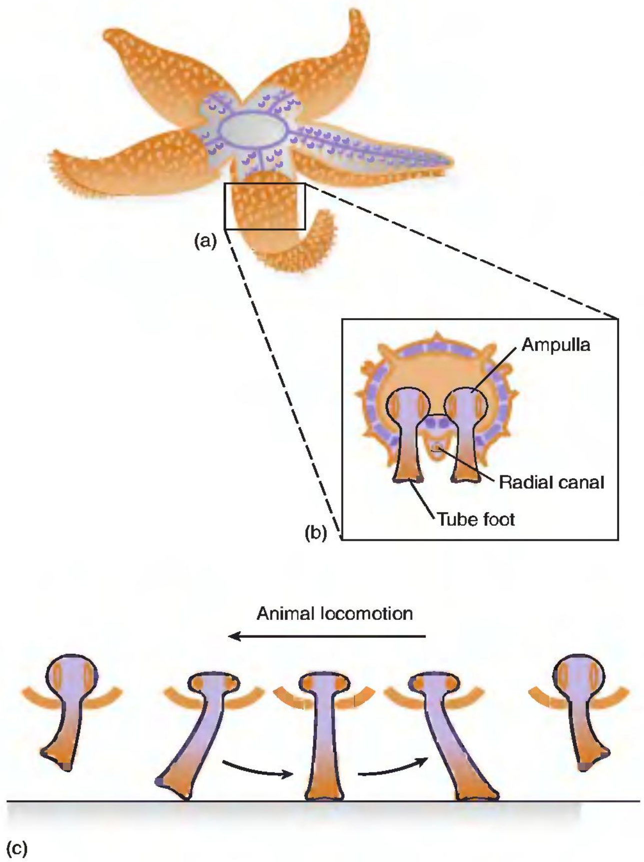


FIGURE 23.20

Water-Vascular System of Echinoderms. *(a)* General arrangement of the water-vascular system. *(b)* Cross section of an arm, showing the radial canal, ampullae, and tube feet of the water-vascular system. *(c)* Stepping cycle of a single tube foot. For simplification, the retractor muscles in the tube foot are not shown.

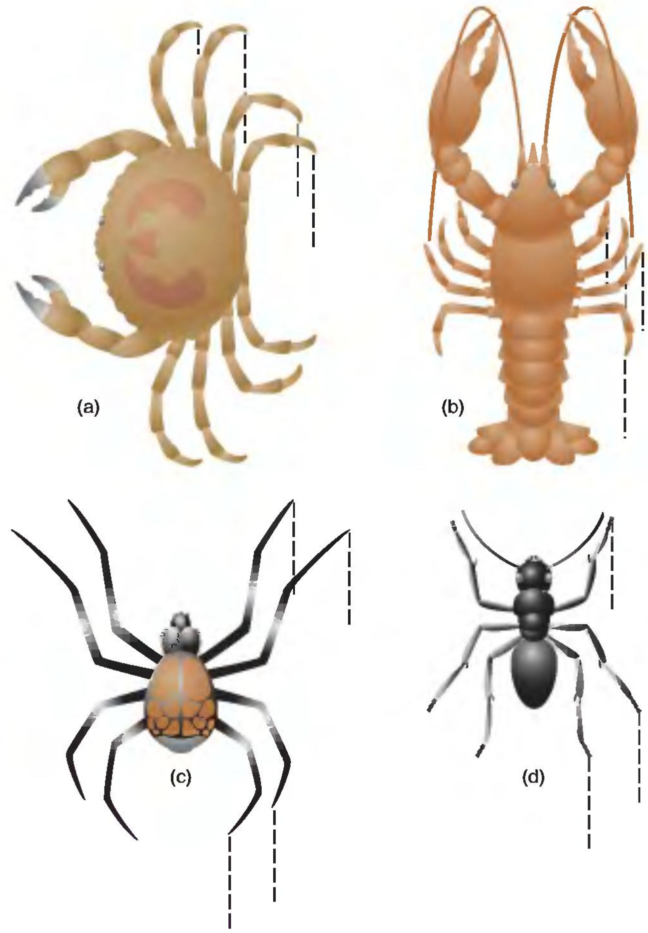


FIGURE 23.22

Walking: Limb Trajectories of Several Arthropods. *(a)* Crabs walk in a sideways fashion, a movement achieved by extension and retraction of the lower limb joints. Other arthropods, such as *(b)* the lobster, *(c)* the spider, and *(d)* an insect, have nonoverlapping limb trajectories and move forward by rotating the basal joint of the limb relative to their body.

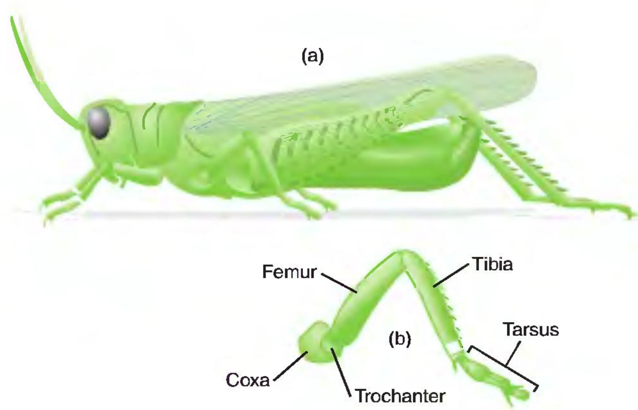


FIGURE 23.21

Typical Arthropod Limb. *(a)* Notice that most of the muscles are in the basal section. *(b)* Characteristic projection of the arthropod limb.

greater than its weight (figure 23.23). Long legs increase the mechanical advantage of the leg extensor muscles. This is why insects that jump have relatively long legs. The mechanical strength of the insect cuticle acting as the lever in this system probably determines the limit to this line of evolution.

THE MUSCULAR SYSTEM OF VERTEBRATES

The vertebrate endoskeleton provides sites for skeletal muscles to attach. **Tendons,** which are tough, fibrous bands or cords, attach skeletal muscles to the skeleton.

Most of the musculature of fishes consists of segmental **myomeres** (Gr. *myo*, muscle + *meros*, part) (figure 23.24*a*). Myomere segments cause the lateral undulations of the trunk and tail that produce fish locomotion (figure 23.24*b*).

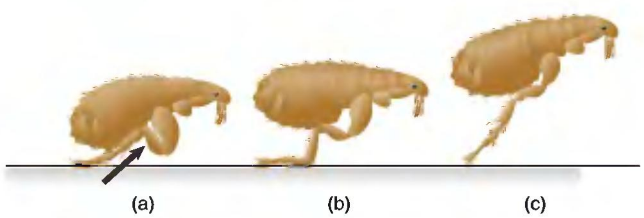


FIGURE 23.23

Jump of Flea. A flea has a jointed exoskeleton. *(a)* When a flea is resting, the femur (black arrow) of the leg (for simplicity, only one leg is shown) is raised, the joints are locked, and energy is stored in the deformed elastic protein ("animal rubber" or resilin) of the cuticle. *(b)* As a flea begins to jump, the relaxation of muscles unlocks the joints. *(c)* The force exerted against the ground by the tibia gives the flea a specific velocity that determines the height of the jump. The jump is the result of the explosive release of the energy stored in the resilin of the cuticle.

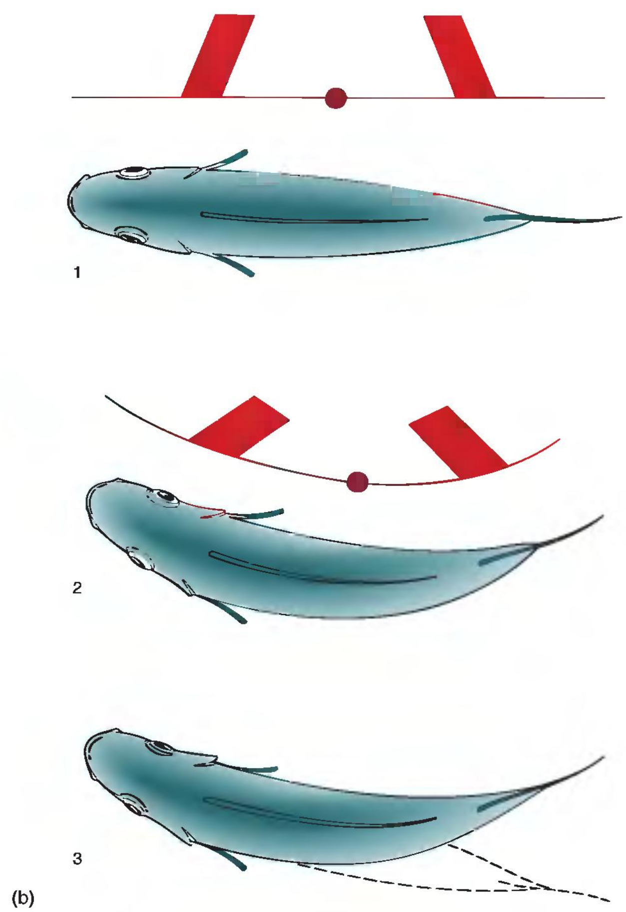


FIGURE 23.24

Fish Musculature. *(a)* Skeletal muscles of a bony fish (perch), showing mainly the large muscles of the trunk and tail. These muscles occur in blocks called myomeres separated by connective tissue sheaths. Notice that the myomeres are flexed so that they resemble the letter *W* tipped at a 90° angle. The different colors (red, orange, blue) represent different myomeres. *(b)* Fish movements based on myomere contractions. *(1)* Muscular forces cause the myomere segments to rotate rather than constrict. *(2)* The rotation of cranial and caudal myomere segments bends the fish's body about a point midway between the two segments. *(3)* Alternate bends of the caudal end of the body propel the fish forward.

The transition from water to land entailed changes in the body musculature. As previously noted, the appendages became increasingly important in locomotion, and movements of the trunk became less important. The segmental nature of the myomeres in the trunk muscles was lost. Back muscles became more numerous and powerful. These evolutionary adaptations are well illustrated by comparing what is eaten in a fish dinner to a plate of frog legs.

Skeletal Muscle Contraction

When observed with the lighr microscope, each skeletal muscle fiber (cell) has a pattern of alternate dark and light bands (*see figure 2.24o*). This striation of whole fibers arises from the alternating dark and light bands of the many smaller, threadlike **myofibrils** in each muscle fiber (figure 23.25*a–c*). Electron microscopy and biochemical analysis show that these bands are

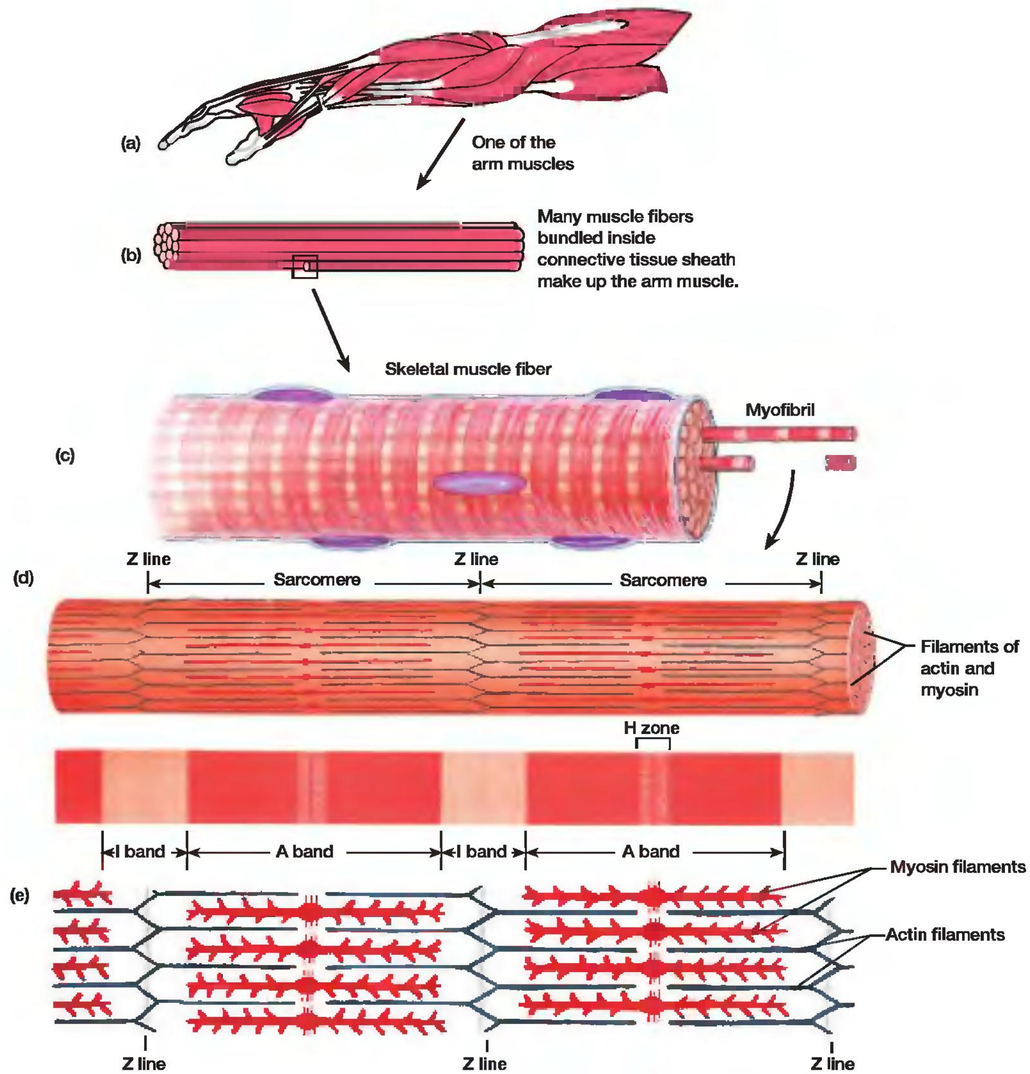


FIGURE 23.25

Structure of Skeletal Muscle Tissue. *(a)* A skeletal muscle in the forearm consists of many muscle fibers (cells) *(b)* bundled inside a connective tissue sheath. *(c)* A skeletal muscle fiber contains many myofibrils, each consisting of *(d)* functional units called sarcomeres. *(e)* The characteristic striations of a sarcomere are due to the arrangement of actin and myosin filaments.

due to the placement of the muscle proteins **actin** and **myosin** within the myofibrils. Myosin occurs as thick filaments and actin as thin filaments. As figure 23.25*c–e* illustrates, the lightest region of a myofibril (the I band) contains only actin, whereas the darkest region (the A band) contains both actin and myosin.

The functional (contractile) unit of a myofibril is the **sarcomere,** each of which extends from one Z line to another Z line. Notice that the actin filaments attach to the Z lines, whereas myosin filaments do not (figure 23.25*e*). When a sarcomere contracts, the actin filaments slide past the myosin filaments as they approach one another. This process shortens the sarcomere. The combined decreases in length of the individual sarcomeres account for contraction of the whole muscle fiber, and in turn, the whole muscle. This movement of actin in relation to myosin is called the sliding-filament model of muscle contraction.

A ratchet mechanism between the two filament types produces the actual contraction. Myosin contains globular projections that attach to actin at specific active binding sites, forming attachments called cross-bridges (figure 23.26). Once cross-bridges form, they exert a force on the thin actin filament and cause it to move.

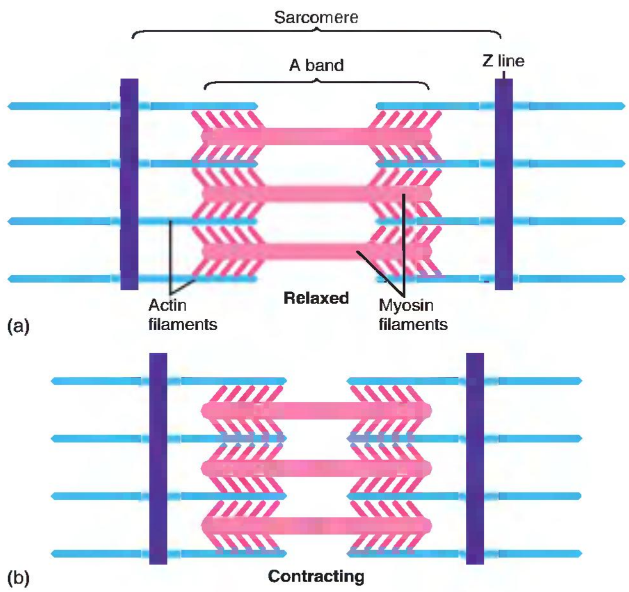


FIGURE 23.26

Sliding-Filament Model of Muscle Contraction. *(a)* A sarcomere in a relaxed position. *(b)* As the sarcomere contracts, the myosin filaments form attachments called cross-bridges to the actin filaments and pull the actin filaments so that they slide past the myosin filaments. Compare the length of the sarcomere in *(a)* to that in *(b)*.

Control of Muscle Contraction

When a motor nerve conducts nerve impulses to skeletal muscle fibers, the fibers are stimulated to contract via a motor unit. A **motor unit** consists of one motor nerve fiber and all the muscle fibers with which it communicates. A space separates the specialized end of the motor nerve fiber from the membrane **(sarcolemma)** of the muscle fiber. The motor end plate is the specialized portion of the sarcolemma of a muscle fiber surrounding the terminal end of the nerve. This arrangement of structures is called a **neuromuscular junction** or cleft (figure 23.27).

When nerve impulses reach the ends of the nerve fiber branches, synaptic vesicles in the nerve ending release a chemical called acetylcholine. Acetylcholine diffuses across the neuromuscular cleft between the nerve ending and the muscle-fiber sarcolemma and binds with acetylcholine receptors on the sarcolemma. The sarcolemma is normally polarized; the outside is positive, and the inside is negative. When acetylcholine binds to the receptors, ions are redistributed on both sides of the membrane, and the polarity is altered. This altered polarity flows in a wavelike progression into the muscle fiber by conducting paths called transverse tubules. Associated with the transverse tubules is the endoplasmic reticulum *(see figure 2.15)* of muscle cells, called sarcoplasmic reticulum. The altered polarity of the transverse tubules causes the sarcoplasmic reticulum to release calcium ions (Ca^{2+}), which diffuse into the cytoplasm. The calcium

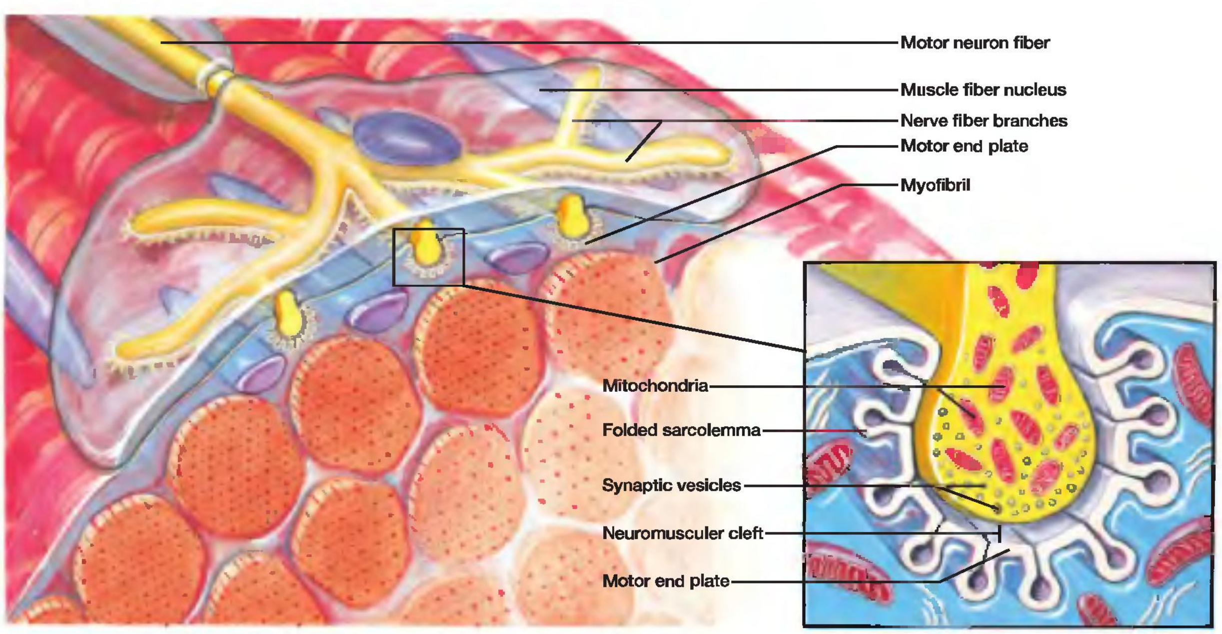


FIGURE 23.27

Nerve-Muscle Motor Unit. A motor unit consists of one motor nerve and all the muscle fibers that it innervates. A neuromuscular junction, or cleft, is where the nerve fiber and muscle fiber meet.

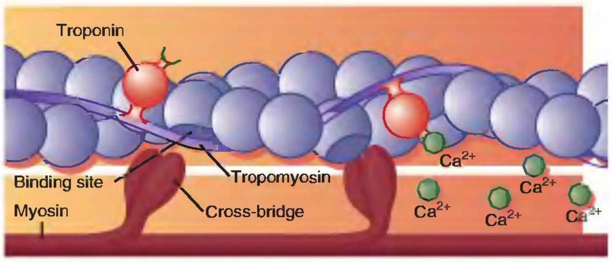


FIGURE 23.28

Model of the Calcium-Induced Changes in Troponin that Allow Cross-Bridges to Form between Actin and Myosin. The attachment of $Ca2^{+}$ to troponin moves the troponin-tropomyosin complex, which exposes a binding site on the actin. The myosin cross-bridge can then attach to actin and undergo a power stroke.

then binds with a regulatory protein called troponin that is on another protein called tropomyosin. This binding exposes the myosin binding sites on the actin molecule that tropomyosin had blocked (figure 23.28). Once the binding sites are open, the myosin filament can form cross-bridges with actin, and power strokes of cross-bridges result in filament sliding and muscular contraction.

Relaxation follows contraction. During relaxation, an active transport system pumps calcium back into the sarcoplasmic reticulum for storage. By controlling the nerve impulses that reach the sarcoplasmic reticulum, the nervous system controls Ca^{2+} levels in skeletal muscle tissue, thereby exerting control over contraction.

SUMMARY

1. The integumentary system is the external covering of an animal. It primarily protects against mechanical injury and invasion by microorganisms.
2. Some single-celled protozoa have only a plasma membrane for an external covering. Other protozoa have a thick protein coat, called a pellicle, outside the plasma membrane. Most invertebrates have an integument consisting of a single layer of columnar epithelial cells called an epidermis. Specializations outside of this epithelial layer may be in the form of cuticles, shells, or teguments.
3. Skin is the vertebrate integument. It has two main layers: the epidermis and the dermis. Skin structure varies considerably among vertebrates. Some of these variable structures include scales, hairs, feathers, claws, nails, and baleen plates.
4. The skin of jawless fishes (lampreys and hagfishes) is thick. The skin of cartilaginous fishes (sharks) is multilayered and contains bone in the form of denticles. The skin of bony fishes (teleosts) contains scales. The skin of amphibians is stratified and contains mucous and serous glands plus pigmentation. The skin of reptiles is thick and modified into keratinized scales. The skin of birds is thin and soft and contains feathers. Mammalian skin consists of several layers of a variety of cells.
5. Animals have three types of skeletons: hydrostatic skeletons, exoskeletons, and endoskeletons. These skeletons function in animal movement that requires muscles working in opposition (antagonism) to each other.
6. The hydrostatic skeleton is a core of liquid (water or a body fluid such as blood) surrounded by a tension-resistant sheath of longitudinal and/or circular muscles. Hydrostatic skeletons are found in invertebrates and can take many forms and shapes, such as the gastrovascular cavity of acoelomates, the rhynchocoel in nemertines, a pseudocoelom in aschelminths, a coelom in annelids, or a hemocoel in molluscs.
7. Rigid exoskeletons also have locomotor functions because they provide sites for muscle attachment and counterforces for muscle movements. Exoskeletons also support and protect the body, but these are secondary functions. In arthropods, the epidermis of the body wall secretes a thick, hard cuticle. In crustaceans (crabs, lobsters, shrimp), the exoskeleton contains calcium carbonate crystals that make it hard and inflexible, except at the joints.
8. Rigid endoskeletons are enclosed by other body tissues. For example, the endoskeletons of sponges consist of mineral spicules, and the endoskeletons of echinoderms (sea stars, sea urchins) are made of calcareous plates called ossicles.
9. The most familiar endoskeletons, both cartilaginous and bony, first appeared in the vertebrates. Endoskeletons consist of two main types of supportive connective tissue: cartilage and bone. Cartilage provides a site for muscle attachment, aids in movement at joints, and provides support. Bone provides a point of attachment for muscles and transmits the force of muscular contraction from one part of the body to another.
10. Movement (locomotion) is characteristic of certain cells, protists, and animals. Amoeboid movement and movement by cilia and flagella are examples of locomotion that does not involve muscles.
11. The power behind muscular movement in both invertebrates and vertebrates is muscular tissue. The three types of muscular tissue are smooth, cardiac, and skeletal. Muscle tissue exhibits contractility, excitability, extensibility, and elasticity.
12. The functional (contractile) unit of a muscle myofibril is the sarcomere. Nerves control skeletal muscle contraction.

SELECTED KEY TERMS

amoeboid movement (p. 360)
ciliary creeping (p. 360)
denticle (p. 351)
dermis (p. 351)
endoskeleton (p. 356)
epidermis (p. 351)
exoskeleton (p. 355)
hydrostatic skeleton (p. 355)
integument (p. 350)
neuromuscular junction (p. 366)
skin (p. 351)